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APLICACIÓN DE LOS MODELOS DE DISTRIBUCIÓN DE ESPECIES HACIA EL PASADO

Análisis de la distribución y extinción las poblaciones europeas de hiena manchada (*Crocuta crocuta* (Erxleben, 1777)) durante el Pleistoceno

Sara Varela González
Madrid, 2011

Ilustración de la portada: Juvenil de *Crocuta crocuta*, Marga del Dedo

Aplicación de los modelos de distribución de especies hacia el pasado. Análisis de la distribución y extinción de las poblaciones europeas de hiena manchada (*Crocuta crocuta* (Erxleben, 1777)) durante el Pleistoceno

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Antecedentes generales

Hasta la fecha, el extenso registro fósil de los mamíferos que habitaron Europa durante el Pleistoceno ha sido analizado casi siempre desde un punto de vista sistemático y evolutivo. Es decir, se ha estudiado en profundidad la evolución de los caracteres anatómicos de las especies para derivar hipótesis sobre las relaciones filogenéticas existentes entre ellas y comprender el origen y la genealogía de las especies que habitan el planeta hoy en día (Turner *et al.*, 2008; Codron *et al.*, 2008). Sin embargo, la información relativa a las faunas que habitaron en el pasado apenas se ha analizado desde un enfoque macroecológico o biogeográfico, ni se han empleado las técnicas estadísticas que se usan en el estudio ecológico de los taxones actuales. Tradicionalmente, los trabajos que han abordado cuestiones sobre la distribución espacial de los seres vivos en el pasado lo han hecho en un estilo descriptivo, proponiéndose hipótesis narrativas para explicar los intercambios faunísticos y florísticos, relacionando los eventos cercanos en el tiempo y en el espacio con el registro fósil de las especies (Scott, 2010). Por ejemplo, los cambios que se observan en las faunas de mamíferos a finales del Mioceno o las extinciones ocurridas durante el Pleistoceno se han relacionado con los cambios climáticos globales que experimentó el planeta en esos períodos (Rodriguez-Sanchez *et al.*, 2008; Whitney-Smith, 2008). Las relaciones propuestas suelen ser muy generales y las explicaciones que se ofrecen son hipótesis *ad hoc* para cada evento. En este sentido, en el momento de inicio de esta tesis existían pocos trabajos que analizasen, de manera específica, el impacto que los cambios climáticos del pasado podrían haber ejercido sobre una única especie. Se asumía que la fuerte bajada de temperaturas registrada durante el último periodo glaciar, en combinación con la expansión del *Homo sapiens*, habría afectado drásticamente y de manera homogénea al conjunto de la fauna de mamíferos que habitaba el planeta a finales del Pleistoceno (Gibbons, 2004).

El punto de partida del trabajo que aquí se presenta buscó cuantificar, de manera más detallada, las relaciones que podrían haberse dado entre los cambios climáticos y la distribución espacial de las especies. Por este motivo nos planteamos analizar la historia biogeográfica de una especie ya extinta en Europa, la hiena manchada, utilizando metodologías novedosas dentro del campo de la paleontología. Queríamos comprobar hasta que punto los cambios climáticos ocurridos durante el Pleistoceno eran capaces de explicar la extinción de un gran carnívoro en la región Holártica. Elegimos la hiena manchada porque su abundante registro fósil y su amplia distribución actual nos permitirían obtener datos suficientes tanto para elaborar y calibrar los modelos, como para evaluar sus resultados. Entender, a nivel específico, las razones de la desaparición de las poblaciones de hiena manchada que habitaban Europa hasta hace solo 10.000 años, puede proporcionar información relevante para comprender los procesos desencadenantes de las extinciones y de esta manera, predecir estos eventos. Las causas que han originado las extinciones registradas a finales del Pleistoceno han sido objeto de múltiples estudios (Fiedel, 2009; Stuart *et al.*, 2007). El clima extremo, unido a la expansión de *Homo sapiens* son dos de las causas más plausibles de este efecto global (Nogues-Bravo *et al.*, 2008; Pushkina *et al.*, 2008). Sin embargo también se han explorado otras hipótesis, como una pandemia de escala mundial, o un evento catastrófico, como la caída de un meteorito (Rothschild *et al.*, 2006; Scott, 2010). En el caso de la hiena manchada no existía ningún estudio que analizase su distribución y su extinción en Eurasia, y antes de empezar esta investigación se asumía que *Crocuta crocuta* se había extinguido de Eurasia como consecuencia directa de las condiciones climáticas extremas del máximo glaciar. Por este motivo, nuestra primera hipótesis de trabajo fue comprobar qué influencia habrían ejercido los cambios climáticos del Pleistoceno sobre las poblaciones Euroasiáticas de hiena manchada. Para este cometido empleamos una metodología que se utiliza comúnmente en biogeografía, los modelos de distribución de especies (SDM). Los SDM reúnen una serie de herramientas estadísticas clásicas y novedosas que se utilizan en ecología y biogeografía para predecir la distribución espacial de una especie en función de sus requerimientos ecológicos (Guisan *et al.*, 2000), o para, del mismo modo, inferir que factores tienen mayor capacidad para explicar la distribución espacial de los organismos. La disponibilidad de modelos de circulación general, que simulan las condiciones climáticas de diferentes escenarios del Pleistoceno (http://pmip2.lsce.ipsl.fr/), nos permitió crear y proyectar estos modelos de distribución hacia el pasado, y así predecir las áreas del continente Europeo en las que podría habitar *Crocuta crocuta* a lo largo del tiempo. Además de este enfoque abiótico, también comprobamos el efecto que las interacciones bióticas podrían haber causado en la especie, poniendo especial atención a los cambios temporales en la diversidad de presas del Pleistoceno Superior. De modo que, tras describir las características básicas de la especie objeto de estudio en esta tesis (Capítulo 1), en los siguientes capítulos se desarrollarán y discutirán ampliamente las implicaciones teóricas de los resultados de los modelos de distribución de especies (Capítulos 2 y 3) y de la relación entre la biomasa de presas disponible y la extinción de la hiena manchada europea (Capítulo 4). Para finalizar, hemos ahondado en la parte teórica de los modelos de distribución de especies. En el Capítulo 5 hemos analizado la extrapolación temporal de los modelos, y en el Capítulo 6 hemos hecho una revisión sobre el uso de los modelos de distribución de especies para predecir los rasgos de los organismos en el pasado. Estos resultados, tanto teóricos como prácticos, forman parte del desarrollo de un campo novedoso en los estudios paleontológicos, la aplicación de metodologías cuantitativas y de modelos ecológicos al estudio de la distribución espacial de los seres vivos a lo largo de la historia.

Objetivos y esquema de la Tesis Doctoral

Los objetivos de esta tesis doctoral son, por una parte, analizar los factores que pudieron desencadenar la extinción de las poblaciones europeas de hiena manchada a finales del Pleistoceno y por otra, analizar las asunciones metodológicas de los modelos de distribución de especies y proponer un protocolo para su uso en paleontología.

La tesis doctoral está dividida en dos apartados; en el primero se analiza la extinción de las poblaciones europeas de hiena manchada y en el segundo se estudian algunas cuestiones metodológicas para la aplicación de los modelos de distribución de especies hacia el pasado. La tesis cuenta con cuatro trabajos publicados en revistas científicas, tanto españolas como internacionales y un artículo enviado para su publicación en una revista internacional. Además, como el manuscrito se presenta para obtener la mención de tesis europea, los capítulos 1, 2, 4 y 7 están escritos en castellano, pero cuentan todos ellos con resúmenes en inglés, y los capítulos 3, 5 y 6 están escritos completamente en inglés. El orden de los capítulos y su contenido resumido es el siguiente:

Apartado I:
Análisis de la extinción de las poblaciones europeas de hiena manchada

Capítulo 1: Introducción general

Descripción de *Crocuta crocuta* desde un punto de vista evolutivo y biogeográfico.

Capítulo 2: Influencia de los cambios climáticos en la extinción de la hiena manchada (*Crocuta crocuta* (Erxleben, 1777)) en la Península Ibérica.

Publicación: **Varela, S.**, J. M. Lobo, & J. Rodríguez. (2010). Influencia de los cambios climáticos en la extinción de la hiena manchada (*Crocuta crocuta* Erxleben, 1777) en la Península Ibérica. *Zona Arqueológica*, 13, 68-75.

Los datos fósiles más recientes de toda Europa que evidencian la presencia de *Crocuta crocuta* se encuentran en el sur de España. En este trabajo comprobamos hasta qué punto los cambios climáticos del Pleistoceno son suficientes para explicar la desaparición a nivel regional de estas últimas poblaciones ibéricas de hiena manchada.

Capítulo 3: Were the Late Pleistocene climatic changes responsible for the disappearance of the European spotted hyena populations? Hindcasting a species geographic distribution across time

Publicación: **Varela, S.**, J. M. Lobo, J. Rodríguez, & P. Batra (2010). Were the Late Pleistocene climatic changes responsible for the disappearance of the European spotted hyena populations? Hindcasting a species geographic distribution across time. *Quaternary Science Reviews* 29 (17-18), 2027-2035.

Análisis del impacto que los cambios climáticos del pasado tuvieron en las poblaciones de *Crocuta crocuta* en Europa. Para ello se realizó un modelo de distribución de especies en el que se utilizaron datos de 5 escenarios temporales diferentes: 4 del pleistoceno superior más el del presente. Este modelo lo proyectamos a los distintos escenarios climáticos del Pleistoceno, para así poder identificar las áreas favorables para la presencia de hiena manchada a lo largo del tiempo.

Capítulo 4: ¿Las extinciones de herbívoros a finales del Pleistoceno están relacionadas con la desaparición de las hienas manchadas?

Publicación: **Varela, S.**, M. L. Jorge, J. Rodríguez, & J. v. d. Made (2010) ¿Las extinciones de herbívoros a finales del Pleistoceno están relacionadas con la desaparición de las hienas manchadas? *Zona Arqueológica*, 13, 76-91.

El objetivo de este trabajo es describir los cambios que se produjeron en las comunidades de mamíferos herbívoros a lo largo del Pleistoceno para dilucidar si estas variaciones pudieron haber afectado a la supervivencia de las poblaciones de hiena manchada que habitaban la Península Ibérica. Para comprobar esta hipótesis nos servimos de datos actuales, comparando el comportamiento trófico que presenta *Crocuta crocuta* en el presente con las presas potenciales que habitaban la Península Ibérica antes y después de su extinción.

Apartado II:
Modelos de distribución de especies y su uso para predecir el pasado

En el segundo apartado analizamos los modelos de distribución de especies y su uso para predecir la distribución de los organismos en escenarios pasados.

Capítulo 5: Is current climatic equilibrium a guarantee for the transferability of distribution model predictions? A case study of the spotted hyena

Publicación: **Varela, S.**, J. Rodriguez, & J. M. Lobo (2009). Is current climatic equilibrium a guarantee for the transferability of distribution model predictions? A case study of the spotted hyena. *Journal of Biogeography* 36(9), 1645-1655.

Los modelos de distribución de especies se utilizan para predecir los rangos geográficos ocupados por los seres vivos y se extrapolan para estimar la distribución de una especie en un escenario del pasado o del futuro. Por ello, los resultados de los modelos dependen de la exactitud de los datos que hemos utilizado para construirlos. En este trabajo comprobamos si los datos de un solo escenario climático son capaces de producir resultados fiables cuando se extrapolan hacia el pasado.

Capítulo 6: Pleistocene Biogeography

(Enviado a Quaternary Science Reviews)

Los modelos de distribución de especies se basan en tres pilares fundamentales, los datos, las variables y las funciones que relacionan unos con otros. En este trabajo hemos analizado cada uno de estos pasos y hemos realizado una labor de revisión de las metodologías utilizadas hasta el momento para la construcción de modelos de distribución de especies para predecir el pasado.

Capítulo 7: Discusión general, conclusiones y futuras líneas de investigación

General background

Fossil record morphological characteristics have been widely used to study the evolution and phylogeny of species (Turner et al., 2008; Codron et al., 2008). However, few studies have analyzed the fossil record from a quantitative macroecological or a biogeographical perspective. Traditionally, species turnover has been related to both catastrophic events and/or global climatic changes (Scott, 2010). For instance, climate change is the main hypothesis for explaining the faunal temporal turnover at the end of the Miocene or the mammal extinction events of the Pleistocene (Rodriguez-Sanchez et al., 2008; Whitney-Smith, 2008). However, the proposed relationships are simplistic and *ad hoc* hypothesis, assuming that there are warm and cold adapted species which migrate or go extinct over time.

In the spotted hyena case, before this work, it was assumed that the European subpopulation disappeared as a consequence of the extreme last glacial maximum climatic conditions. For that reason, we first test the strength of the relationship between the spotted hyena distribution vs. climatic conditions. Understanding the role of the climatic changes at the species level is important to comprehend the European Late Pleistocene extinction events.

In this thesis we aim to analyze in detail the relationship between climatic changes and species distributions, using species distribution models as our methodological tool. By doing so, we incorporate a new method in the investigation of Pleistocene biogeography. Species distribution models are used to estimate the potential geographic ranges of species in the current scenario, and are increasingly used to hindcast past species distribution shifts.

We selected *Crocuta crocuta* as our target species because of the high number of fossil records available in Europe and the fact that there are current spotted hyena populations in Africa. Therefore, we had enough data to construct the models, calibrate them and validate their predictions.

Our second approach was to test the relationship between the prey species diversity across time and the extinction of the last populations of *Crocuta crocuta*. As *Crocuta crocuta* is a large carnivore, we expected that prey diversity fluctuations across time could have influenced the survival of the last European populations of this species, and chapter 4 analyzes this predator-prey hypothesis.

To conclude the thesis, we study the species distribution models' prediction accuracy when transferred across time, and we review the most recent papers that use species distribution models to predict the past geographic ranges of species.

Objectives and outline:

The two principal objectives of this thesis are to 1) analyze the European spotted hyena extinction event, and to 2) discuss the use of species distribution models to predict the past geographic ranges of species. The document is divided in two Sections and 7 Chapters. Each chapter (except the introduction and conclusion) have been published in Spanish or international journals. Chapters 3, 5 and 6 are written in English and Chapters 1, 2, 4 and 7 are written in Spanish and summarized in English.

Section I: European spotted hyena's extinction event

Chapter 1: General introduction

Evolution and biogeography of *Crocuta crocuta*.

Chapter 2: Influencia de los cambios climáticos en la extinción de la hiena manchada (*Crocuta crocuta* (Erxleben, 1777)) en la Península Ibérica

In: Varela, S., J. M. Lobo, & J. Rodríguez. (2010). Influencia de los cambios climáticos en la extinción de la hiena manchada (Crocuta crocuta (Erxleben, 1777)) en la Península Ibérica. Zona Arqueológica, 13, 68-75.

The youngest European *Crocuta crocuta* fossil records are located in Southern Spain. Here we tested whether the climatic changes of the Late Pleistocene in the Iberian Peninsula are related to the spotted hyena extinction event.

Chapter 3: Were the Late Pleistocene climatic changes responsible for the disappearance of the European spotted hyena populations? Hindcasting a species geographic distribution across time

In: Varela, S., J. M. Lobo, J. Rodríguez, & P. Batra (2010). Were the Late Pleistocene climatic changes responsible for the disappearance of the European spotted hyena populations? Hindcasting a species geographic distribution across time. Quaternary Science Reviews 29 (17-18), 2027-2035.

We tested whether the whole continental Late Pleistocene European climatic changes were related to the disappearance of *Crocuta crocuta*. We constructed a model using both fossil and current species data and we projected this model into the different Late Pleistocene climatic scenarios.

Chapter 4: ¿Las extinciones de herbívoros a finales del Pleistoceno están relacionadas con la desaparición de las hienas manchadas?

In: Varela, S., M. L. Jorge, J. Rodríguez, & J. v. d. Made (2010) ¿Las extinciones de herbívoros a finales del Pleistoceno están relacionadas con la desaparición de las hienas manchadas? Zona Arqueológica, 13, 76-91.

We tested whether the changes in the prey species diversity that occurred at the end of the Pleistocene could be related to the extinction of hyenas. For doing so we analyzed the Late Pleistocene Iberian Peninsula mammal diversity across time.

Section II: The use of species distribution models to predict past species' ranges

Chapter 5: Is current climatic equilibrium a guarantee for the transferability of distribution model predictions? A case study of the spotted hyena

In: Varela, S., J. Rodriguez, & J. M. Lobo (2009). Is current climatic equilibrium a guarantee for the transferability of distribution model predictions? A case study of the spotted hyena. Journal of Biogeography 36(9), 1645-1655.

Species distribution models are trained using data from the actual current distribution of species. However, this data could underestimate the potential climatic requirements of species. In this paper we use current spotted hyena distribution to train a model and we transferee the so-obtained model into the European Last Interglacial climatic scenario.

Chapter 6: Pleistocene Biogeography

(Submitted to Quaternary Science Reviews)

We discuss the three main steps for constructing a species distribution model (SDM); data, predictors and models itself, and we alo review the latest papers that use SDM to predict the past distribution of species.

Chapter 7: Conclusions and future research lines

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Capítulo 1: Introducción

Evolución y Biogeografía de *Crocuta crocuta*

1.- La Familia Hyaenidae

Crocuta crocuta forma, junto a *Hyaena hyaena*, *Hyaena brunnea* y *Proteles cristata*, la Familia Hyaenidae, incluida dentro del Orden Carnivora (Fig. 1a, 1b, 1c y 1d). *Crocuta crocuta*, *Hyaena hyaena* y *Hyaena brunnea* son carnívoros de tamaño medio-grande (>35 kg), mientras que *Proteles cristata* es un mamífero insectívoro de tamaño pequeño (9 kg). Sin embargo, a pesar de que hoy en día existen únicamente cuatro especies de hiena, el registro fósil ha permitido identificar más de 60 especies diferentes (Werdelin *et al*., 1991), lo cual significa que en la actualidad podemos observar una pequeña parte de la gran diversidad de ecotipos y morfotipos que ha presentado esta familia a lo largo de su historia evolutiva.

Como los restos fósiles permiten conocer las características esqueléticas de las especies extintas, la clasificación de la Familia Hyaenidae y su historia evolutiva se han determinado a partir de la anatomía ósea de las especies descritas (Werdelin *et al*., 1991). La Familia Hyaenidae presenta unos caracteres esqueléticos conservados, con un esqueleto postcraneal similar al que tendrían los mamíferos más primitivos (4/5 falanges, 4/5 metápodos, huesos tarsales y carpales sin fusionar, radio/ulna sin fusionar, tibia/fíbula sin fusionar, Figuras 2, 3 y 4). Werdelin y Solounias (1991) establecen que, entre las características claves que identifican esta familia, se incluye una dentición primitiva: 3 incisivos, 1 canino, 4 premolares, 3 molares (dentición que se ha ido modificando y en algunas especies se pierden premolares o molares). La fórmula dental

Figura 1. a) *Proteles cristata.* Fotografía: Phil Richardson, b) *Hyaena hyaena.* Fotografía: Keith Wilson, c) *Hyaena brunnea.* Fotografía: Ingrid Wiesel, d) *Crocuta crocuta.* Fotografía: Stig Nygaard

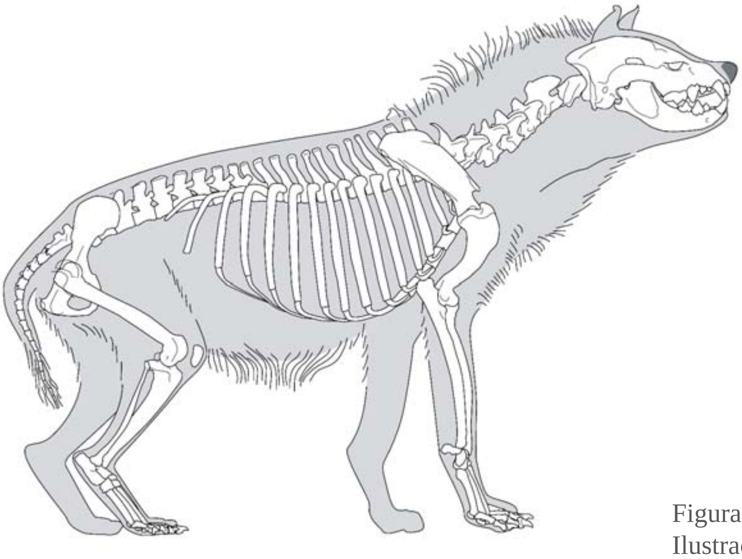


Figura 2: Esqueleto de *Crocuta crocuta.*
Ilustración: C. Beauval y M. Coutureau, 2004

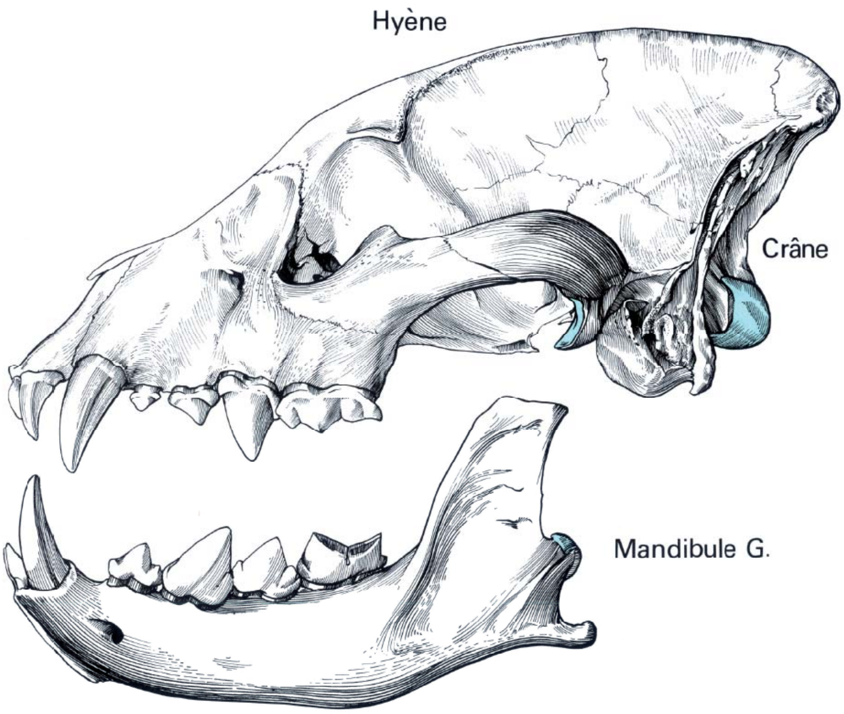


Figura 3. Cráneo y mandíbula de *Crocuta crocuta* (Pales *et al.*, 1971).

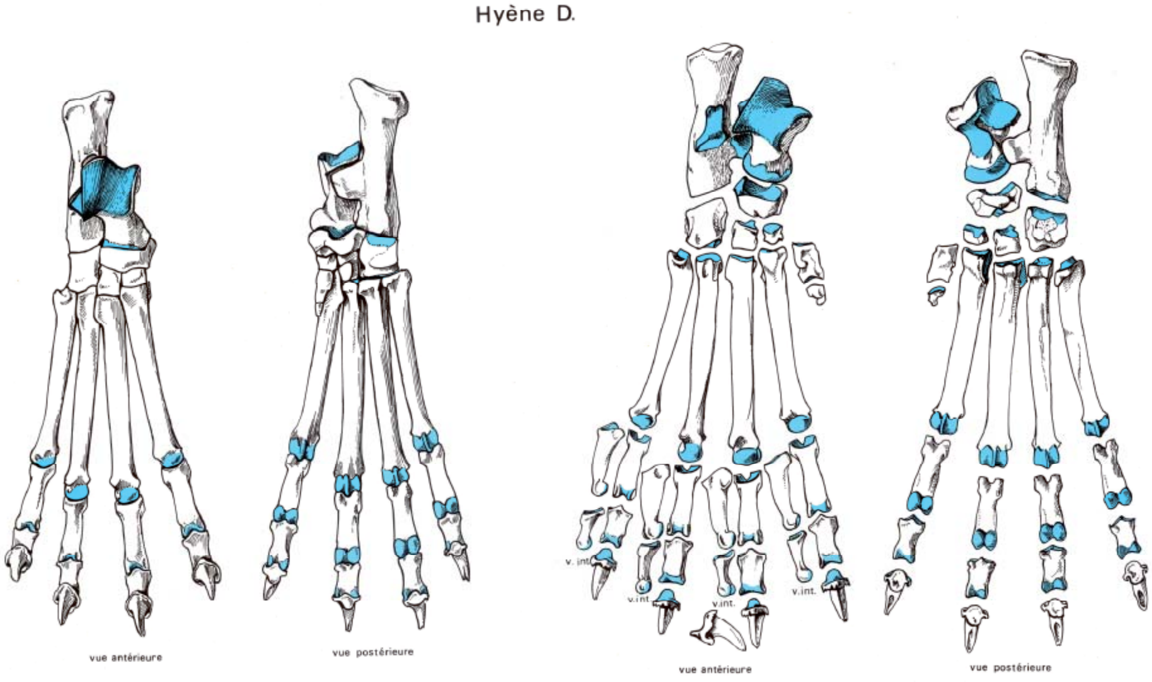


Figura 4. Carpo, tarso y falanges anteriores y posteriores de *Crocuta crocuta* (Pales *et al.*, 1971)

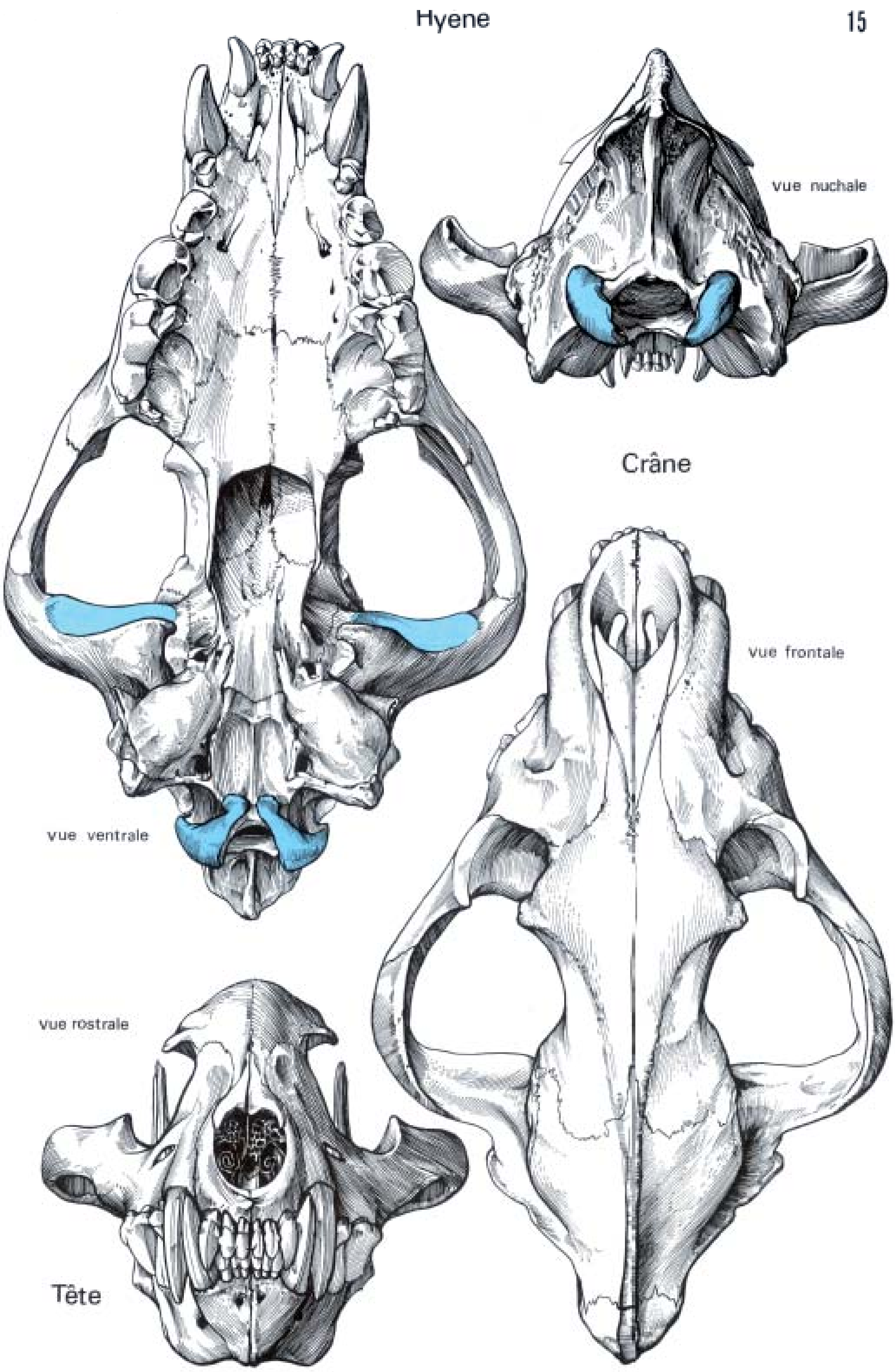


Figura 5. Cráneo de *Crocuta crocuta* (Pales *et al.*, 1971)

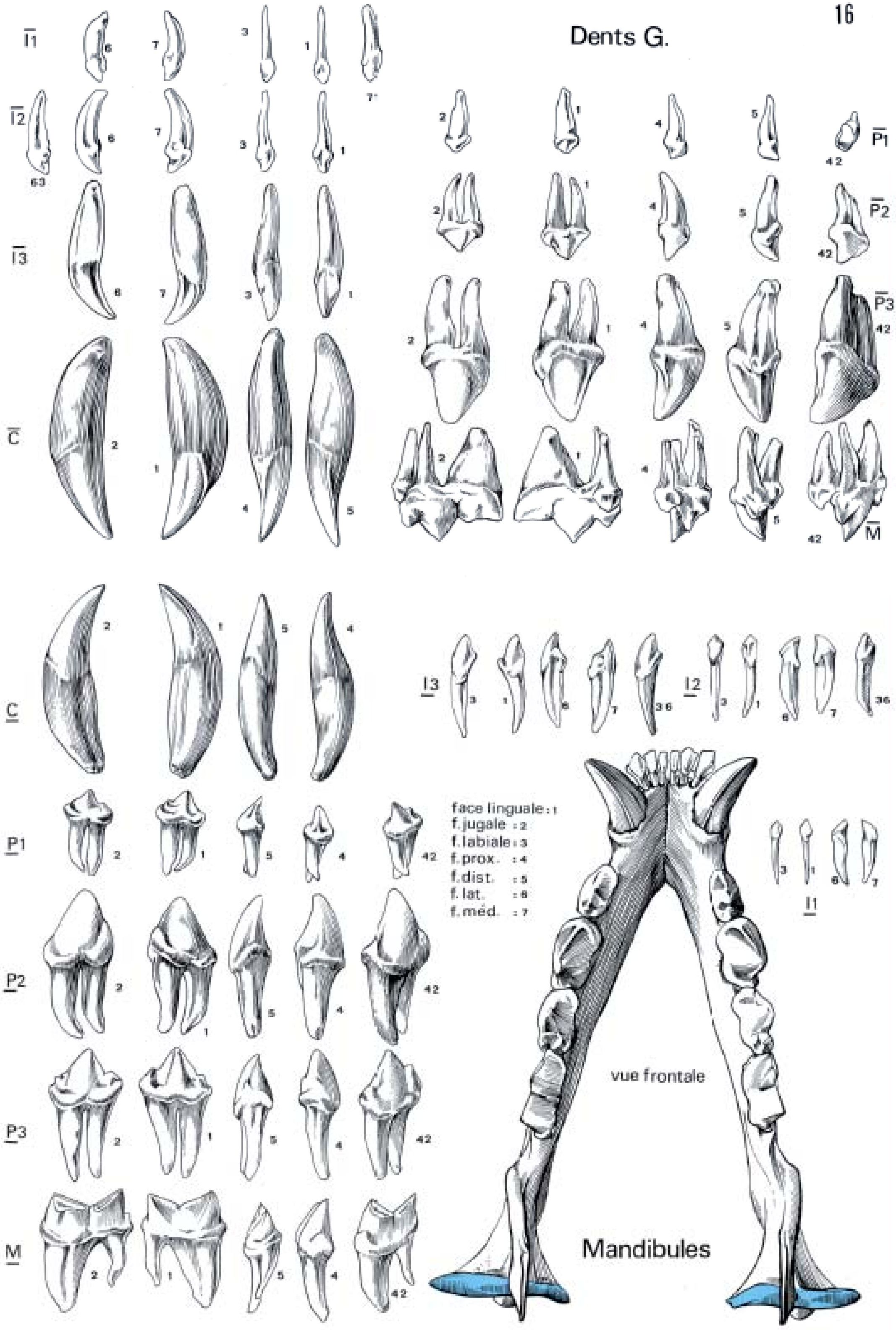


Figura 6. Dentición superior e inferior de *Crocuta crocuta* (Pales *et al.*, 1971)

actual de las hienas es i 3/3, c 1/1, p 4/3, m 1/1 (Figura 3, 5 y 6). Es decir, cada hemimandíbula tiene 3 incisivos, 1 canino, 4 premolares y 1 molar, mientras que cada maxila tiene 3 incisivos, 1 canino, 3 premolares y 1 molar. Esta fórmula varía en el caso de *Proteles*, una especie en la cual los premolares y molares son similares, pudiendo tener entre 3 y 4 dientes molariformes inferiores, y entre 2 y 4 superiores. Poseen una cresta sagital desarrollada, que permite el anclaje de una potente musculatura temporal y les proporciona una gran fuerza de mordida (Fig. 3). Además, la principal característica morfológica que diferencia a este grupo es la presencia de un septo timpánico (Fig. 7), ausente en otros carnívoros (Hunt, 1974). Sin embargo, este resulta no ser un carácter excluyente, ya que también está presente en *Uncia uncia*, el leopardo de las nieves y en algunas especies de la Familia Viverridae. Además, este septo no aparece en las primeras hienas del Mioceno (Werdelin, 1991). Otras características anatómicas de esta familia incluyen la ausencia actual de garras retráctiles (Pocock, 1916) (excluyendo a *Ictitherium*, que sí las presenta (Werdelin *et al*., 1991)), y a diferencia del resto de carnívoros, en lugar de 13/14 vértebras torácicas tienen 15/16 (Ewer, 1973; Rieger, 1981) y no tienen baculum (hueso peneano) (Brehm, 1915; Ewer, 1973).

Se trata entonces de una familia que presenta características óseas primitivas, similares a la que tendrían los primeros mamíferos. La ausencia de caracteres osteológicos únicos e identificativos de esta familia ha complicado el establecimiento del origen y la evolución de las hienas. Esta particularidad, unida a la gran plasticidad morfológica de las especies que integran esta familia, ha dificultado la tarea de crear una clasificación que funcione correctamente en función de su anatomía, tanto entre ellas como en relación al resto de integrantes del Orden Carnivora. En 1991 Werdelin y Solounias proponen 47 caracteres diagnósticos para clasificar a las hienas, tanto fósiles como actuales, basados en su morfología esquelética. A partir de los estados que presentan estos caracteres crean una serie de matrices sobre las cuales generan diferentes cladogramas. El resultado de esta clasificación establece que *Crocuta crocuta* y *Hyena brunnea* serían especies hermanas. Sin embargo, en 2006 Koepfli *et al.* elaboran una filogenia basada en ADN nuclear y ADN del citocromo b, que contradice la hipótesis morfológica e indica que son *Hyaena brunnea* y *Hyaena hyaena* las especies hermanas, con un 100% de apoyo en un análisis bootstrap, y que *Crocuta crocuta* es una especie basal respecto a las dos anteriores. De este modo, sería necesaria una revisión de los caracteres morfológicos anteriormente utilizados para realizar la filogenia de la familia Hyaenidae (Werdelin *et al*., 1991). A un nivel taxonómico más elevado también ha habido complicaciones en las clasificaciones basadas en caracteres anatómicos; la familia Hyaenidae se incluyó dentro del Suborden Caniformia porque sus características anatómicas eran similares a los cánidos (Erxleben, 1777), para más adelante incluirse definitivamente dentro del Suborden Feliformia (Kretzoi, 1945). Por otra parte, el estudio del material fósil tampoco ha ayudado a esclarecer los vínculos filogenéticos existentes entre las especies. Así, los géneros del Mioceno *Tungurictis*, *Plioviverrops, Ictitherium* y *Thalassictis* fueron incluidos dentro de la Familia Viverridae, mayoritariamente debido a sus semejanzas morfológicas con este grupo (Werdelin *et al*., 1991). De este modo, los resultados de los estudios de anatomía comparada han proporcionado resultados controvertidos, y las clasificaciones han variado a medida que se incluían nuevos caracteres o nuevas especies a los análisis. Una cita histórica ilustra como la comunidad científica ha sido consciente de la polémica que ha generado la clasificación de esta familia: "*There are few animals, whose history has passed under the consideration of naturalists, that have give occasion to so much confusion and equivocation as the Hyaena has done. It began very early among the ancients, and the moderns have fully contributed their share*" (Bruce, 1790, citado por Kruuk en 1972 y por Koepfli en 2008).

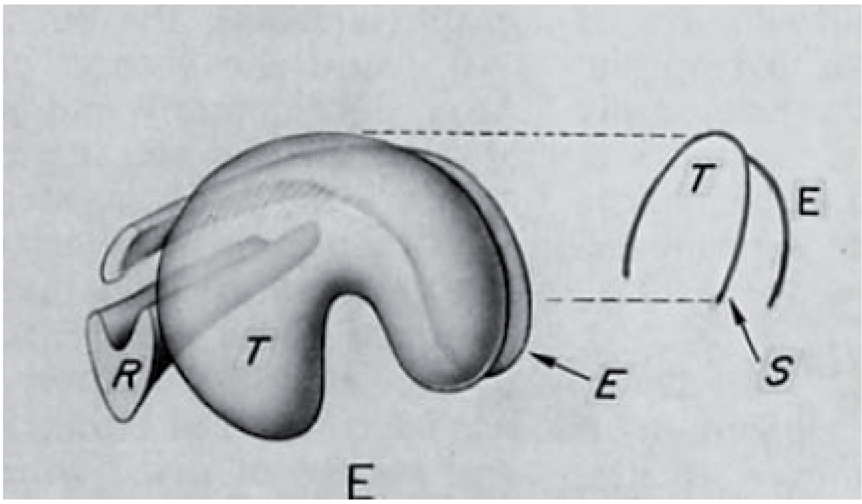
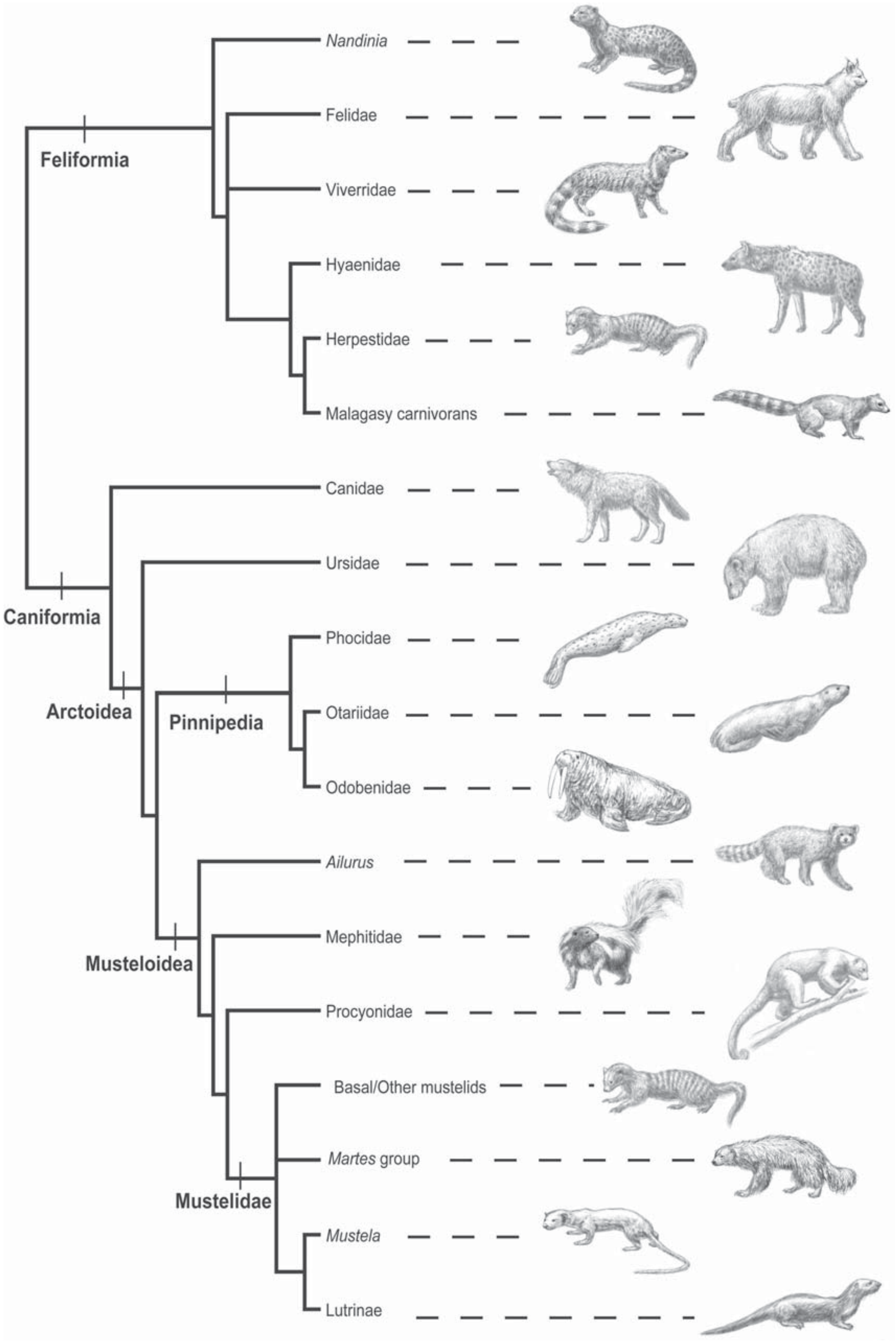


Figura 7. Septo timpánico presente en la Familia Hyaenidae (Hunt, 1974).


Nandinia
Felidae
Feliformia
Viverridae
Hyaenidae
Herpestidae
Malagasy carnivorans
Canidae
Ursidae
Caniformia
Phocidae
Arctoidea
Pinnipedia
Otariidae
Odobenidae
Ailurus
Mephitidae
Musteloidea
Procyonidae
Basal/Other mustelids
Martes group
Mustelidae
Mustela
Lutrinae

Las clasificaciones propuestas en la actualidad, basadas en el análisis de los caracteres morfológicos de las especies fósiles y las especies actuales, y en el estudio de su ADN, establecen que la Familia Hyaenidae pertenece a la Clase Mammalia, Orden Carnivora, Suborden Feliformia. El resultado del análisis de su genotipo indica que los Herpéstidos son su grupo más cercano evolutivamente (Fig. 8) (Flynn *et al.*, 2005). Además, el estudio de 7 segmentos de genes nucleares, además del citocromo b completo, indican que la divergencia entre estos grupos se produjo hace 29,2 m.a., durante el Oligoceno Medio (Koepfli *et al.*, 2006). Este dato coincide con los resultados obtenidos a partir del análisis de los caracteres morfológicos de los restos fósiles y de las especies actuales. En 1991 Werdelin y Solounias propusieron que el origen de la Familia Hyaenidae habría ocurrido hace 25 millones de años, después de analizar 44 caracteres diagnósticos del cráneo y la mandíbula. A pesar de que tanto el ADN como los estudios paleontológicos apuntan a que el origen de la Familia Hyaenidae se produjo durante el Oligoceno, los primeros restos fósiles aparecen en Eurasia y África durante el Mioceno Inferior/Medio (Turner *et al*., 2004). Es decir, casi 10 millones de años más tarde de su supuesta radiación.

Hace 20 millones de años la disposición de las masas terrestres era ligeramente diferente de su situación actual (Fig. 9) (Steppuhn *et al.*, 2006). Europa estaba conectada al continente Asiático por un corredor septentrional, mientras que en el Sur existía una intrincada orografía de archipiélagos y penínsulas, el denominado mar Paratethys, formado durante el Oligoceno tras la aparición de los Alpes, los Cárpatos, la cordillera del Tauro y los montes Elburz, al norte del océano Tethys, que en ese momento se cierra en su parte más oriental. El clima del planeta estaba cambiando de un clima cálido y húmedo a uno más seco y estacional. Los datos provenientes del registro fósil de la flora del Norte de Alemania han proporcionado estimas de la temperatura y la humedad a lo largo del Cenozoico que permiten corroborar como a comienzos del Mioceno Medio (*c.* 15 m.a.) la temperatura media aumenta varios grados mientras que la precipitación desciende en casi 500 mm anuales (Utescher *et al.*, 2009) (Fig. 10). Debido al cambio climático global que experimentó el planeta, los bosques se fragmentan,

Figura 8 (izquierda). Cladograma del Orden Carnivora propuesto por Flynn et. al, 2005. Para su construcción se utilizaron seis genes (3 nucleares, 2 mitocondriales y 1 ribosómico). Las especies ilustradas, de arriba abajo, son *Nandinia binotata*; Felidae (*Lynx rufus*); Viverridae (*Viverra zibetha*); Hyaenidae (*Crocuta crocuta*); Herpestidae (*Mungos mungo*); Carnívoros Malgaches (*Eupleres goudotii*); Canidae (*Canis lupus*); Ursidae (*Ursus americanus*); Phocidae (*Phoca vitulina*); Otariidae (*Zalophus californianus*); Odobenidae (*Odobenus rosmarus*); *Ailurus fulgens*; Mephitidae (*Mephitis mephitis*); Procyonidae (*Potos flavus*); Mustelidae, otros mustélidos (dibujo representativo de un mustélido africano del grupo de *Ictonyx striatus*); Mustelidae, *Martes*-group (*Gulo gulo*); Mustelidae, *Mustela* (*Mustela frenata*); Mustelidae, Lutrinae (*Lontra canadensis*). Las hienas aparecen dentro del suborden Feliformia, emparentadas con los herpéstidos y con los carnívoros de Madagascar.

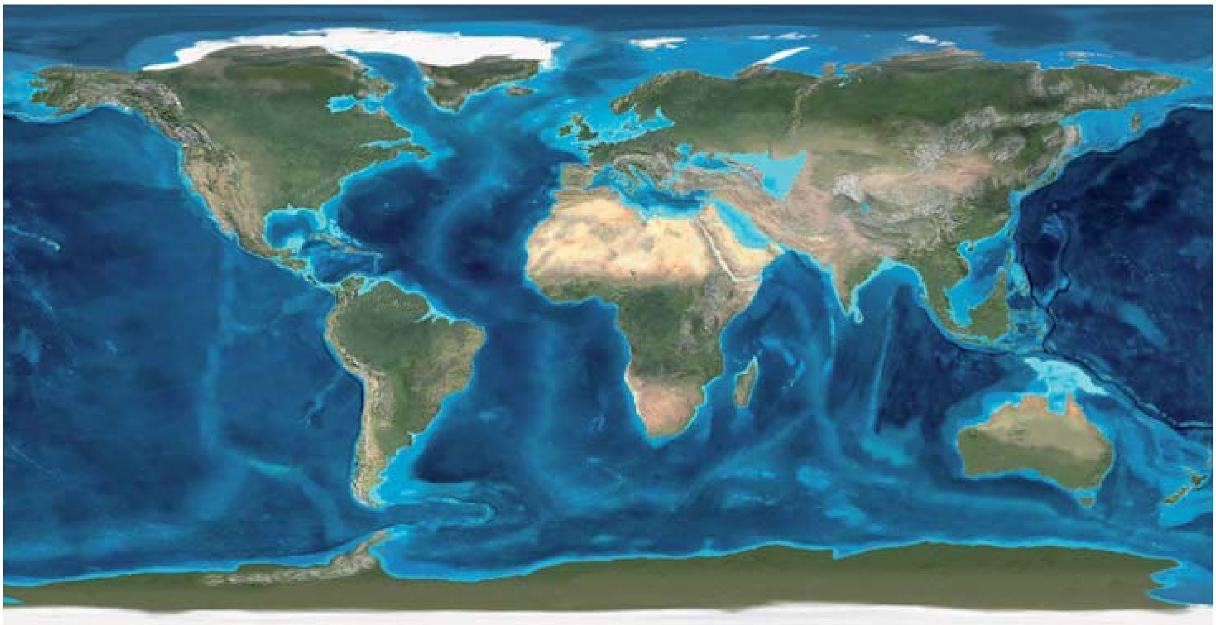


Figura 9. Paleogeografía durante el Mioceno, hace 20 millones de años. Reconstrucción: Ron Blakey

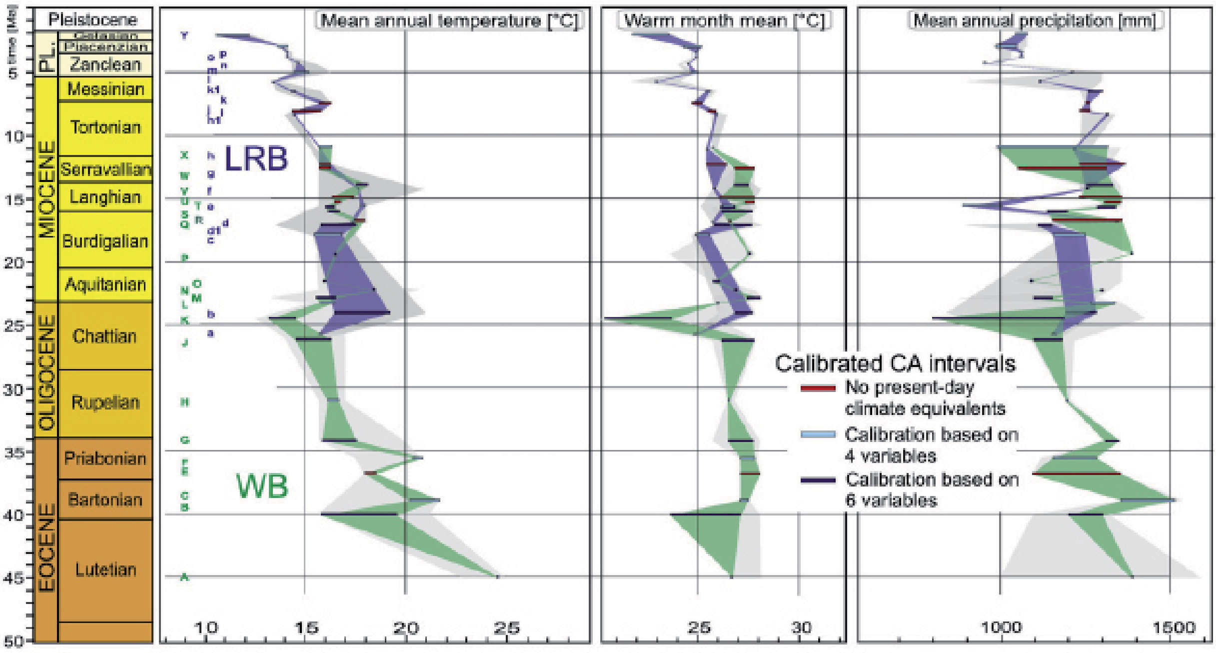


Figura 10. Estimaciones de la variación en la temperatura y precipitación a lo largo del Cenozoico en el Norte de Alemania (Utescher *et al*., 2009).

aparecen las primeras praderas dominadas por herbáceas y como consecuencia los paisajes se hacen más abiertos (Bobe, 2006). Las faunas africanas y europeas de ungulados consistían en especies de rinocerontes, súidos, bóvidos, jirafas, etc. diferentes de las que existen hoy en día (Turner, 2004). Además, en África aparecen por primera vez los équidos, los elefantes y los hipopótamos (Turner, 2004), y en Europa los calicotéridos (familia extinta de perisodáctilos). En este contexto, donde los carnívoros dominantes eran los creodontos (Familia Creodonta) (Morales *et al.*, 2007), aparecen los restos fósiles más antiguos de la Familia Hyaenidae.

Las primeras hienas eran mamíferos de pequeño tamaño y de alimentación insectívora u omnívora. Los restos excavados más antiguos se incluyen dentro de los géneros *Plioviverrops* Kretzoi, 1938 y *Protictitherium* Kretzoi, 1938. *Plioviverrops* es similar a una mangosta, mientras que *Protictitherium* es un animal de hábitos arborícolas parecido a las actuales ginetas. El origen biogeográfico de la Familia Hyeanidae continúa siendo ambiguo, ya que aunque existen restos fósiles datados tanto en África como en Europa, por el momento el error asociado a estas dataciones es lo suficientemente grande como para impedir esclarecer esta cuestión (Turner *et al.*, 2008). De modo que, a partir de las poblaciones de pequeñas hienas insectívoras/omnívoras que existían en Europa y en África, la familia habría radiado ampliamente originando más de 60 especies diferentes (Werdelin y Solounias, 1991). Para ordenar la gran variedad de ecomorfotipos o ecotipos que presentan las especies del Mioceno, Plioceno y Pleistoceno de la Familia Hyaenidae, Werdelin y Solounias proponen en 1991 una clasificación en seis grupos. Las descripciones de estos ecotipos están basadas principalmente en las características de la dentición porque es el elemento esquelético que mejor se conserva en el registro fósil (Fig. 11).

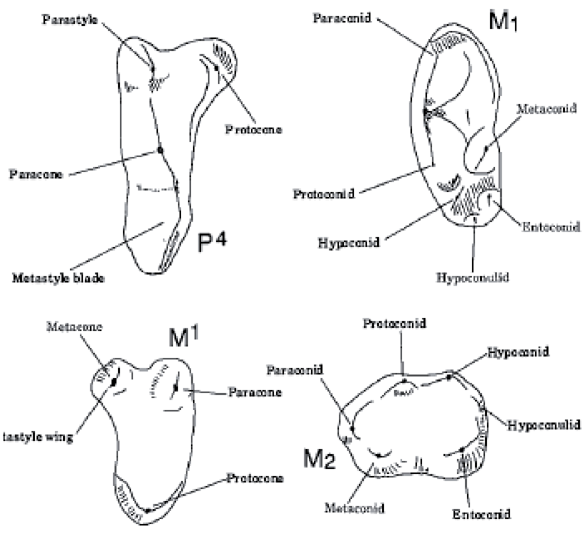


Figura 11. Cúspides del premolar 4 y el molar 1 superiores (izquierda) y del molar 1 y 2 inferiores (derecha). Estas piezas dentarias son fundamentales para la identificación y clasificación de las hienas en el registro fósil (Werdelin et al., 1991)

La clasificación propuesta por Werdelin y Solounias es la siguiente:

1) “Civet-like insectivore/omnivore morph”, el que presentan las hienas más antiguas, del género *Protictitherium.* Dentición “primitiva” tipo “gineta”. Tienen todos los premolares y molares. El M1 inferior tiene un paracónido bajo, protocónido alto y metacónido grande y un talónido tricúspido grande. Presentan garras retráctiles, lo cual supone una adaptación para trepar, e indica que estos animales vivían en bosques.

2) “Mongoose-like insectivore/omnivore type” *Plioviverrops.* La dentición se hace menos secodonta, menos especializada en cortar. Aumenta el número de cúspides en los premolares y en los molares. El Paracónido, protocónido y metacónido son de altura similar. Se produce una reducción del protocono y un alargamiento del metacono.

3) “Jackal and wolf-like meat and bone eaters” *lctitheium, Thalassictis, Hyaenotherium*, y *Hyaenictitherium.* Dentición “primitiva”, no especializada, similar a la de los cánidos. Carniceras con el metacónido reducido. El esqueleto postcraneal presenta adaptaciones para la vida terrestre, sin adaptaciones cursoriales significativas (es decir, son hiénidos terrestres pero no especializados para la carrera).

4) “Cursorial meat and bone eaters” *Lycyaena*, *Lycyaenops*, *Hyaenictis*, y C*hasmaporthetes*, M1 inferior y M1-2, P1 superiores reducidos o incluso ausentes. El esqueleto poscraneal presenta adaptaciones cursoriales, lo cual indica una adaptación a la carrera y en consecuencia, a los ambientes abiertos.

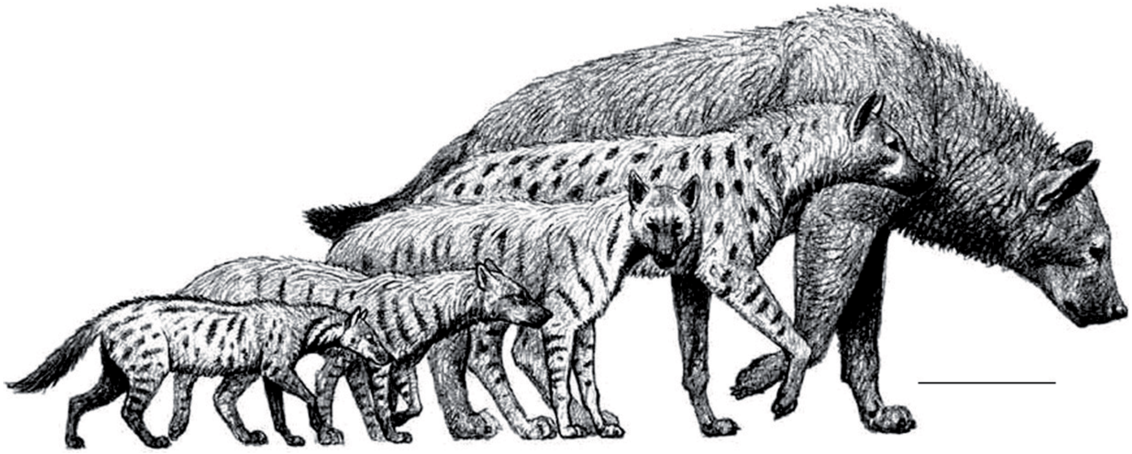


Figura 12. Hienas del Mioceno de Europa, de derecha a izquierda; *Adcrocuta eximia, Hyaenotherium wongii, Ictitherium viverrinum, Protictitherium crassum* and *Plioviverrops orbignyi*. La escala representa 25 centímetros. Ilustración: Mauricio Antón (Turner *et al.*, 2008)

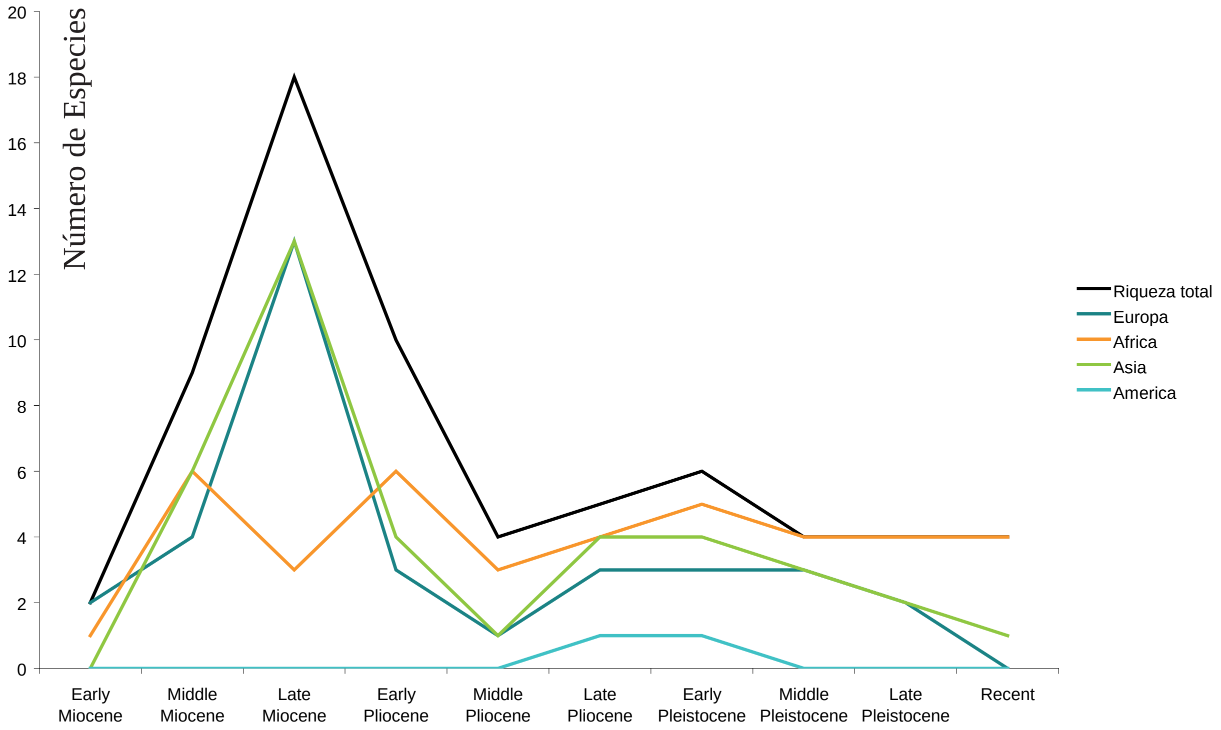


Figura 13. Número de especies de hiena descritas. McKenna & Bell, 1997.

5) "Transitional bone-crackers" *Metahyaena*, *Palinhyaena*, *Ikelohyaena*, *Belbus*, y *Leecyaena*. Premolares grandes y robustos, con cúspides asimétricas. Adaptaciones todas ellas para romper huesos.

6) "Bone-crackers" *Hyaena*, *Allohyaena*, *Pliocrocuta*, *Pachycrocuta*, *Adcrocuta*, *Crocuta*. Premolares grandes adaptados para la rotura de huesos. Algunos géneros, como *Crocuta*, tienen adaptaciones cursoriales, otros, como *Adcrocuta*, no las presentan.

Estudiando los restos esqueléticos fosiles se ha constatado una tendencia evolutiva en la Familia Hyaenidae hacia formas cada vez más grandes y más carnívoras, ya que los restos óseos de las especies se hacen más masivos y robustos conforme pasa el tiempo (Fig. 12). De manera que las hienas más antiguas son mamíferos insectívoros de tamaño pequeño, y según va pasando el tiempo aparecen ecotipos más carnívoros y cursoriales (adaptados para la carrera), y finalmente los "bone-crackers", el ecotipo al que pertenecen las actuales *Hyaena hyaena* o *Crocuta crocuta* (Werdelin & Solounias, 1991). Durante el Mioceno Superior la familia llega a tener 15 especies en Europa y 6 en África (Turner & Werdelin, 2008) (Fig. 13 y 14). Sin embargo, el cambio climático del Plioceno (comienzan las glaciaciones), unido a la aparición de

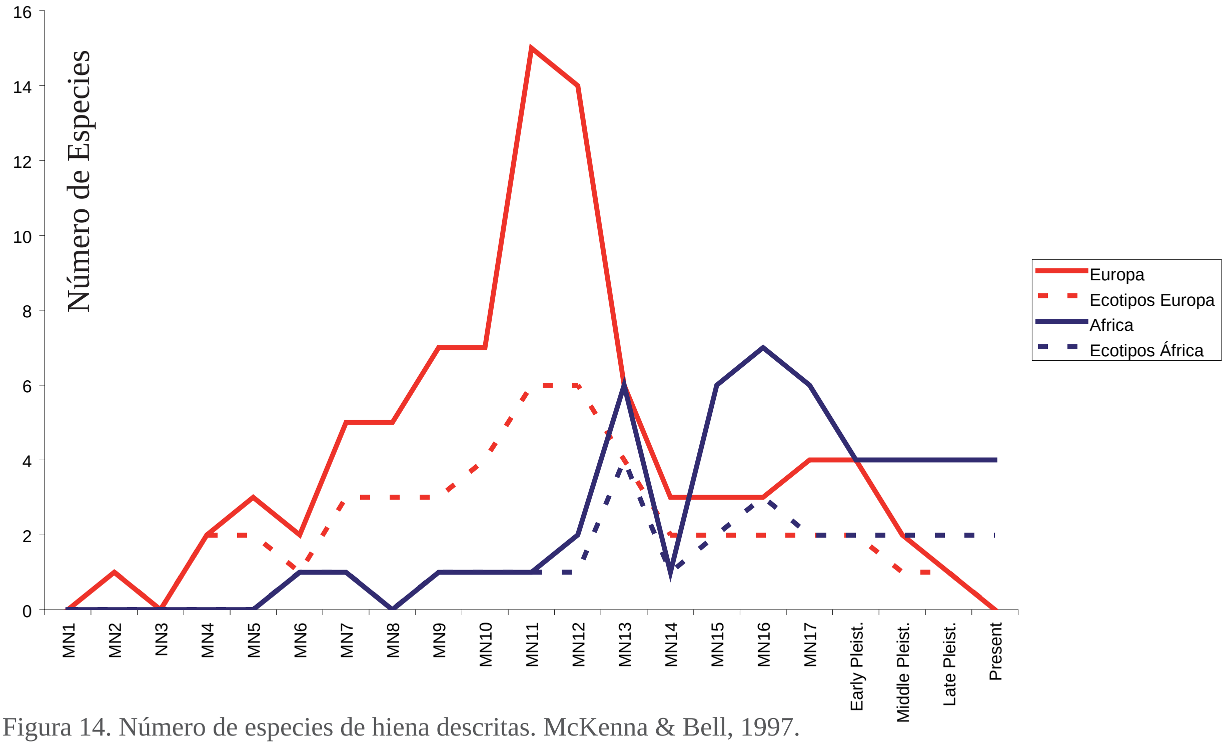


Figura 14. Número de especies de hiena descritas. McKenna & Bell, 1997.

los primeros cánidos (el denominado "Wolf event" (Sardella & Palombo, 2007)) y los félidos, son dos eventos que afectan de manera drástica a las poblaciones de hiénidos. A partir de la crisis del Mioceno-Plioceno (MN12) la evolución de la Familia Hyaenidae se ve comprometida por la desaparición de los ecotipos más pequeños, los insectívoros, omnívoros y los pequeños

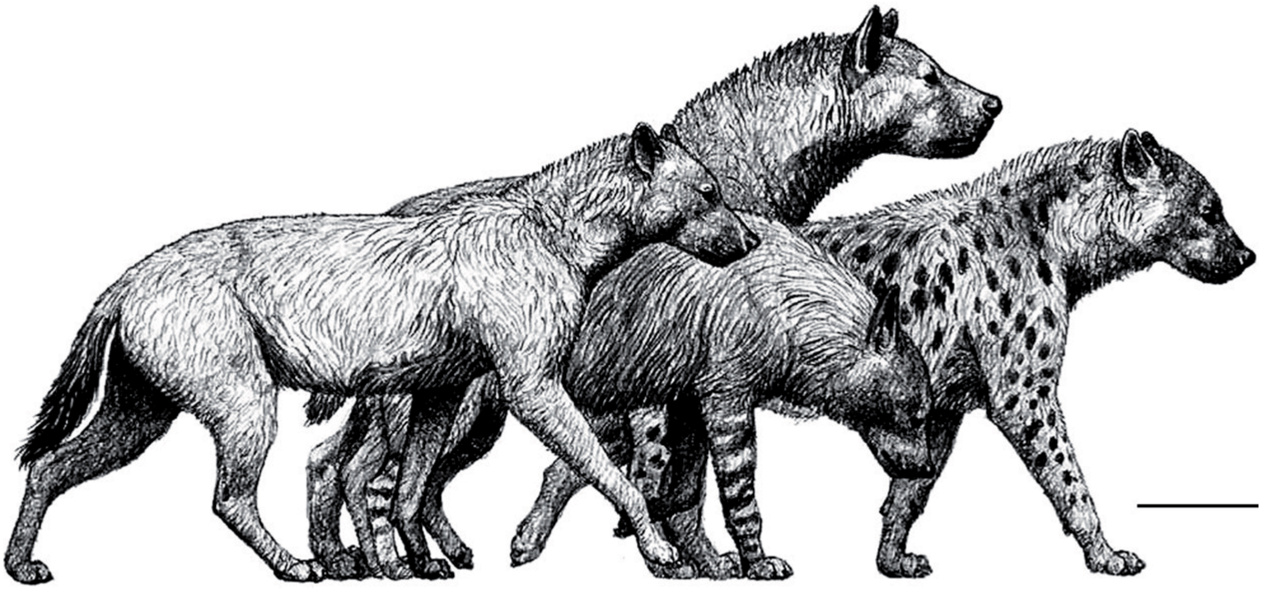


Figura 13. Hienas del Plioceno y del Pleistoceno de Europa, de izquierda a derecha, *Crocuta crocuta*, *Pliocrocuta perrieri* (delante), *Pachycrocuta brevirostris* (detrás) y *Chasmaporthetes lunensis*. La escala representa 25 centímetros. Ilustración: Mauricio Antón (Turner *et al.*, 2008).

carnívoros (Fig. 15). Durante el Plioceno hay una radiación inicial y aparecen nuevas especies grandes y carnívoras que pertenecen a los ecotipos denominados "transitional bone crackers", géneros *Ikelohyaena*, *Belbus*, *Chasmaporthetes*, *Leecyaena*, *Palinhyaena* y a los morfotipos llamados "bone crackers", generos *Pliocrocuta*, *Hyaena*, *Pachicrocuta*, *Adcrocuta* y *Crocuta*. Es en este momento cuando llega a América la única especie de la Familia Hyaenidae que, probablemente, atravesó Beringia: *Chasmaporthetes lunensis*. De forma que en el Pleistoceno, los ecotipos "bone crackers" dominan los ecosistemas Africanos y Europeos. *Pachicrocuta* y sobre todo, *Crocuta*, son los dos carnívoros muy abundantes en el registro fósil. Sin embargo, a pesar de su aparente abundancia, la diversidad de esta familia siguió decreciendo a lo largo del Pleistoceno, y su rango geográfico se fue haciendo cada vez más restringido. De manera que,

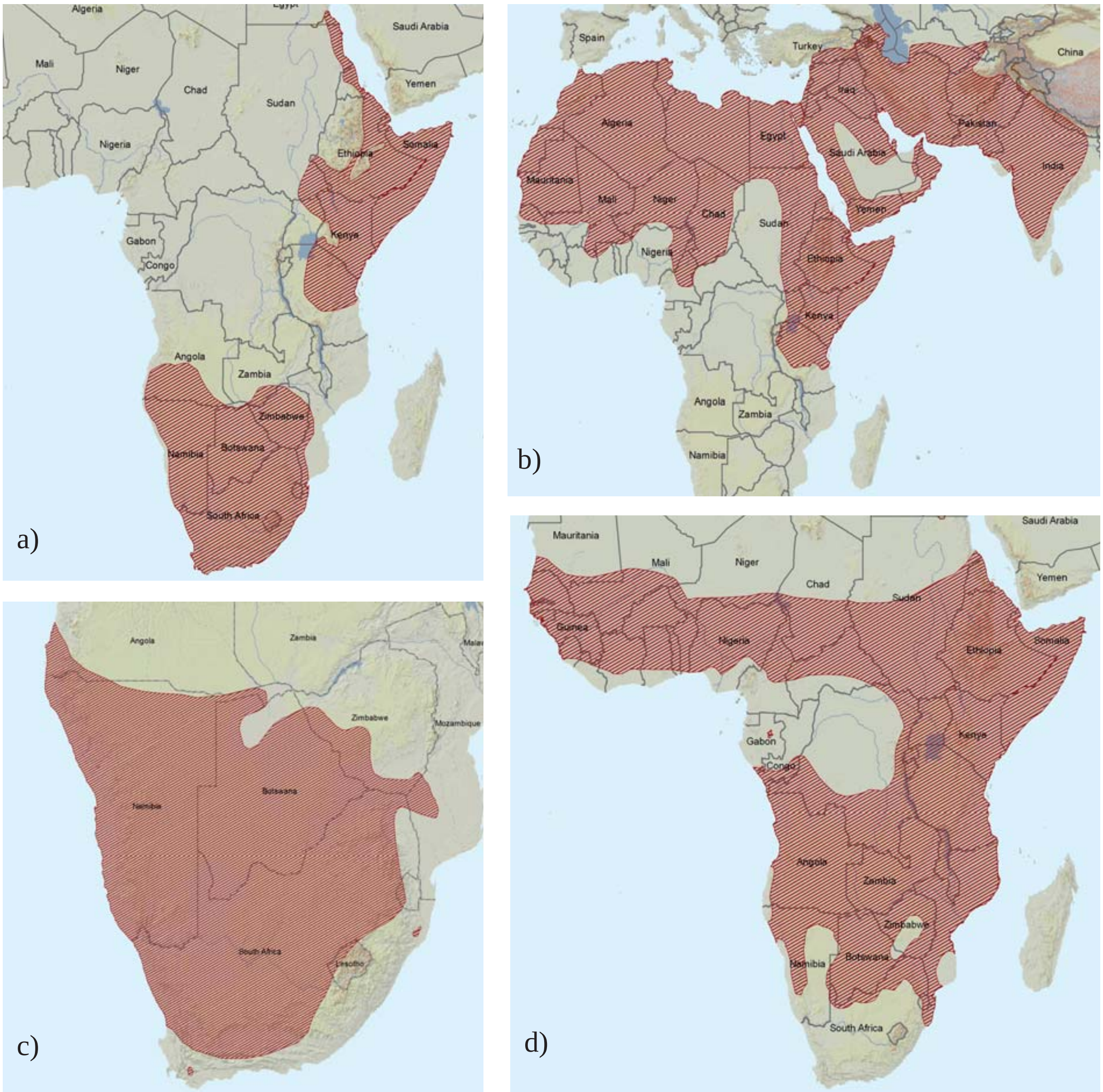


Figura 16 . Distribución geográfica de a) *Proteles cristata*, b) *Hyaena hyaena*, c) *Hyaena brunnea*, d) *Crocuta crocuta*. www.iucn.org en la actualidad, solo han sobrevivido cuatro especies de hienas, *Hyaena hyaena* (Linnaeus, 1758), *Hyaena brunnea* Thunberg, 1820, *Proteles cristata* (Sparrman, 1783) y *Crocuta crocuta* (Erxleben, 1777), tres de ellas distribuidas en África y una, *Hyaena hyeaena*, cuyas poblaciones se encuentran actualmente en el Norte de África y en Asia (Fig. 16 a, b, c, d)

2.- *Crocuta crocuta*:

Como ya hemos adelantado, la similitud morfológica entre las hienas y los cánidos propició que, en un primer momento, se las relacionase con el Suborden Caniformia (en el cual se encuentran los úrsidos, mustélidos y cánidos). En el caso de *Crocuta crocuta*, Erxleben describió la especie en 1777 dentro de la Familia Canidae, como *Canis crocuta.* Sin embargo, en el año 1828 Kaup creó un nuevo género, *Crocuta*, que se ha mantenido vigente hasta nuestros días. *Crocuta crocuta* es el representante de la Familia Hyaenidae de mayor tamaño que habita en la actualidad, pudiendo llegar a pesar hasta 70 kg de media en las poblaciones de Sudáfrica (Mills *et al*., 1998; Reynolds, 2007). Sin embargo, la talla de esta especie es muy variable, tanto intra como interpoblacionalmente (Kruuk, 1966), pudiendo oscilar entre los 40-86 kg (Koepfli *et al.*, 2006; Mills, 1998). En el Pleistoceno se han documentado variaciones de la talla de los individuos que habitaban Europa y estas variaciones se han relacionado con las oscilaciones climáticas que sufría este continente de manera cíclica, de modo que en los periodos glaciares las hienas aumentaban su tamaño, mientras que durante los periodos interglaciares el tamaño medio volvía a disminuir nuevamente, siguiendo la regla de Bergmann (Klein & Scott, 1989).

A pesar de ser un animal robusto, sus extremidades tienen adaptaciones cursoriales, lo cual la capacita para la carrera (Spoor, 1985; Spoor & Badoux, 1989). Característica que le permite dar caza a sus presas mediante persecuciones largas a gran velocidad, siendo uno de los métodos de caza más empleados por las hienas manchadas el perseguir a sus presas hasta la extenuación (Cooper, 1990). Tiene una musculatura, un cráneo y una dentición muy desarrollados (Rensberger & Stefen, 2006), que le permiten triturar y consumir sus presas casi por completo (Tanner *et al.*, 2008) (Fig. 3, 5 y 6). Sin embargo, no posee caninos desarrollados y esto le dificulta la tarea de matar a sus presas después de abatirlas (como hacen los félidos). Las hienas son animales oportunistas, de modo que su alimentación se adapta a las circunstancias del medio en el que habitan (Tilson *et al.*, 1980). A la hora de conseguir alimento pueden carroñear o cazar, y su elección dependerá de sus necesidades y las oportunidades que se presenten (Gasaway *et al.*, 1991; Salnicki *et al.*, 2001; Honer *et al.*, 2002; Wambuguh, 2008; Trinkel *et al.*, 2006).

Crocuta crocuta. Fotografía: Sara Varela

Sus presas más habituales incluyen ungulados de talla media y grande (Hofer & East, 1993a; Owen-Smith & Mills, 2008). Las especies varían en función de su disponibilidad en el medio (Sillero Zubiri & Gottelli, 1992a; Skinner *et al.*, 1992; Cooper *et al.*, 1999; Di Silvestre *et al.*, 2000). De forma que, a modo de ejemplo, en Namibia, las presas preferentes son el *Oryx gazella* y *Equus zebra* (Henschel & Tilson, 1988), mientras que en Sudáfrica, las presas más comunes son otras especies de ungulados como *Aepyceros melampus* o *Tragelaphus strepsiceros* y un súido, *Phacochoerus aethiopicus* (Henschel & Skinner, 1990).

La competencia con otros grandes carnívoros ha sido comprobada en diversas estudios (Hayward, 2006; Hayward & Kerley, 2008). Entre las especies con las que compite de manera directa por los recursos están *Panthera leo*, *Hyaena brunnea*, (Mills, 1987), y *Hyaena hyaena*. Normalmente son dominantes, como se ha demostrado en diferentes trabajos de campo (Gorman *et al.*, 1998; Creel & Creel, 1996), pero en el caso particular de *Panthera pardus* y *P. leo*, el tamaño y el número de hienas determina el resultado final de la contienda (Bothma & Le Riche, 1984; Cooper, 1991).

Las hienas manchadas son animales sociales que viven en grupos de tamaño variable (Mills *et al.*, 2001; Smith *et al.*, 2008; Graf *et al.*, 2009). Se han documentado grupos de 3 a 5 individuos en zonas del desierto de Namibia (Tilson & Henschel, 1986), clanes de 42 individuos en zonas de montaña (Sillero Zubiri & Gottelli, 1992b) y grupos de más 70 individuos en las áreas abiertas con gran cantidad de presas (Mills, 2001). El tamaño del territorio de los clanes varía en función de los recursos del medio pudiendo llegar a ocupar más de 130 km^2 en zonas de savana (Henschel & Skinner, 1991) o solamente 32 km^2, en el ecosistema forestal del Parque Nacional Aberdare, en Kenia (Sillero Zubiri & Gottelli, 1992b). Además, las incursiones fuera del territorio del clan son frecuentes cuando la densidad de presas disminuye (Hofer & East, 1993b).

Los vínculos entre los individuos son complejos y la estructura jerárquica del grupo se basa en una red matrilineal, con una hembra dominante como cabeza de grupo (Frank, 1986) (Van Horn *et al.*, 2004). Este aspecto social ha sido abordado en numerosas ocasiones, ya que se trata de una estructura única dentro de los mamíferos, donde las hembras pasan a ser el género dominante después de modificar el nivel de sus hormonas (Dloniak *et al.*, 2006b; Szykman *et al.*, 2007). Las hembras de hiena manchada presentan una elevada tasa de andrógenos y como consecuencia, una masculinización de su genitalia femenina (Licht *et al.*, 1998), mientras que los niveles de andrógenos de los mahos son relativamente bajos (Dloniak *et al.*, 2006a). Forman complejas redes sociales en las cuales los rangos se heredan (Engh *et al.*, 2000; Holekamp & Smale, 1991) y los juveniles adoptan los roles adultos a partir de los 6/8 meses (Smale *et al.*, 1995; Holekamp & Smale, 1993; Drea *et al.*, 1996). Estudios sobre el comportamiento social de la hiena manchada formando grupos artificiales con individuos que no se conocían de antemano demuestran que las hienas interaccionan, cooperan y establecen vínculos afectivos y jerárquicos de manera inmediata (Drea & Carter, 2009). En 2005 Engh realizó un experimento en el cual pudo comprobar como las hienas manchadas recuerdan los conflictos que sufren con otros miembros del grupo y penalizan tanto a su oponente como a los familiares de este. Además, se ha comprobado como las glándulas anales proporcionan señales olfativas que permiten el reconocimiento individual (Burgener *et al.*, 2009). Es decir, existe un reconocimiento individual de los miembros del grupo y de las relaciones familiares que existen entre ellos. Las hienas manchadas también emiten vocalizaciones prolongadas, cuyo objeto sería el mantener la cohesión del grupo (Peters *et al.*, 2004: East & Hofer, 1991a; East & Hofer, 1991b). Se ha demostrado que estas vocalizaciones también son identificativas a nivel individual (Holekamp *et al.*, 1999a) y que sirven para enviar información a larga distancia sobre el sexo o la edad de los individuos que las emiten (Theis *et al.*, 2007).

La cría de los cachorros se realiza de manera comunal (White, 2007), en oquedades que funcionan como guarderías o cubiles (Cooper, 1993). Dentro del territorio de un clan puede haber varios cubiles y las hienas mueven a sus crías entre ellos, sin que se haya comprobado ninguna causa aparente que justifique los cambios observados (Boydston *et al.*, 2006; Pokines & Kerbis Peterhans, 2007). Las madres realizan visitas periódicas a los cubiles para alimentar a sus crías, que se hacen más o menos frecuentes en función de la abundancia de presas en el medio (Hofer & East, 1993c). El éxito reproductivo de las hembras puede estar relacionado con su rango social, de manera que las hembras no dominantes pueden ver mermada su capacidad de reproducción en función de las condiciones externas, mientras que las hembras dominantes tienen asegurada la supervivencia de sus crías debido a que su estatus dentro del grupo les permite acceder preferentemente a los recursos (Holekamp *et al.*, 1996; Holekamp *et al.*, 1999b). Sin embargo, también existen estudios que no han encontrado relación alguna entre el rango social y la supervivencia de las crías (White, 2005), e incluso se ha documentado un caso de lactancia compartida, comportamiento que incrementa las probabilidades de supervivencia de crías ajenas cuando las condiciones son extremas (Knight *et al.*, 1992). Al nacer, los cachorros tienen dientes y están bastante desarrollados. Además el crecimiento es rápido (Van Jaarsveld *et al.*, 1988; Glickman *et al.*, 1992). Las agresiones entre las crías de una misma camada son frecuentes (Golla *et al.*, 1999; Wahaj & Holekamp, 2006), llegando incluso a la muerte de uno de los dos cachorros (James & Hofer, 1999; Smale *et al.*, 1999).

La supervivencia de las poblaciones de hiena manchada se ha relacionado con la cantidad de presas de los ecosistemas o con la presión antrópica (Watts & Holekamp, 2009). La desaparición de la vegetación, unida al intenso pastoreo, afectan de manera negativa a la supervivencia de las hienas manchadas (Kolowski & Holekamp, 2009). Además, la interferencia humana puede ser indirecta. Las hienas modifican su comportamiento en las zonas con gran afluencia turística, disminuyendo su actividad debido a la actividad antrópica (Boydston *et al.*, 2003; Kolowski *et al.*, 2007), y se ha documentado como la presencia de basureros locales modifica el comportamiento de las hienas manchadas, siendo aprovechados como recurso alimentario por los individuos de menor rango (Kolowski & Holekamp, 2008). Los conflictos directos entre hienas y humanos se concentran cerca de las áreas cercanas a los parques naturales, cuando las hienas depredan sobre el ganado, preferentemente sobre especies de tamaño pequeño como cabras, ovejas o terneros (Gusset *et al.*, 2009; Kissui, 2008; Holmern *et al.*, 2007). La colocación de veneno es una estrategia común para evitar los ataques de las hienas al ganado domestico (Kissui, 2008). Sin embargo, existen otras soluciones menos lesivas basadas en la modificación de las prácticas de pastoreo (Woodroffe *et al.*, 2007). De todas formas, a pesar de la caza o el envenenamiento que sufre esta especie, la hiena manchada tiene estatus “least concern” en IUCN (http://www.iucnredlist.org/apps/redlist/details/5674/0), lo que significa que sus poblaciones africanas son viables y están fuera de peligro.

Concluyendo, las hienas manchadas son carnívoros sociales (Holekamp *et al.*, 2007a), que establecen grupos y cooperan entre ellas en la búsqueda de alimento y en la defensa del grupo (Holekamp *et al.*, 2007b). Tienen unas características anatómicas adecuadas para la carrera y persecución de sus presas, y su estructura craneo-facial masiva y robusta les permite aprovechar los cadáveres casi por completo. Además, entre las adaptaciones que han sido descritas se incluyen variaciones en el tamaño de los individuos, en relación con las oscilaciones climáticas, o cambios en el número de individuos de un clan en relación con la abundancia de presas del medio. Estas características describen a un carnívoro versátil, inteligente y adaptable, que habitó tanto en Eurasia como en África durante la mayor parte del Pleistoceno.

Crocuta crocuta. New York, Bronx Zoo. Source: Wikimedia Commons

3.- El registro fósil de *Crocuta crocuta* en Europa:

Como ocurre con otras especies de hienas, la escasez de restos fósiles y su estado de conservación impiden establecer de manera clara el origen biogeográfico de *Crocuta crocuta*. Los primeros restos fósiles que tienen una anatomía similar a las hienas manchadas actuales tienen una antigüedad de más de 3 millones de años y se han excavado en África (Tanzania) y en Asia (Pakistán) (Turner, 2008). Estos fósiles se identificaron en un principio como *Crocuta sivalensis*, yacimiento de Siwalik en Pakistán (Khan, 1972) (Figura 17), yacimiento de Pabbi Hills, Pakistán, 1.2-1.4 m.a. (Dennell *et al.*, 2006) y como *Crocuta dietrichi*, yacimiento de Laetoli en Tanzania, 3.46 m.a. (Petter & Howell, 1989; Turner, 1990). Sin embargo, más adelante las diferencias anatómicas observadas se reinterpretaron como consecuencia de la variación intraespecífica de esta especie (Turner, 1990; Werdelin *et al*, 1991). Esta última interpretación invalida como especies a *Crocuta sivalensis* y a *Crocuta dietrichi*, considerándolas sinónimos de *Crocuta crocuta*. De modo que el origen de las hienas manchadas, al igual que ocurre con el de la familia Hyaenidae, podría ser tanto euroasiático como africano. Werdelin y Turner se inclinan por un origen africano de la especie, atendiendo al registro fósil de especies anteriores dentro de la línea de *Crocuta*, como *Adcrocuta*, (Turner, 2008). Sin embargo, para comprobar cualquiera de estas hipótesis hace falta obtener más datos del registro fósil de *Crocuta crocuta*. Estudios de ADN indican que Eurasia podría haber sido poblada por tres oleadas consecutivas de hienas manchadas provenientes de África (Rohland *et al.*, 2005). La primera de ellas ocurriría durante el Plioceno, hace más de 3 millones de años (Fig. 18a). Esta primera expansión podría relacionarse con los restos fósiles hallados en Pakistán. Posteriormente, habría una segunda colonización de Eurasia, que dataría en torno a 1.3-1.5 millones de años, a comienzos del Pleistoceno Inferior (Fig. 18b). Como consecuencia de segunda oleada, las hienas manchadas llegarían a poblar Europa. En este sentido, los primeros fósiles de *Crocuta crocuta* en Europa se localizan en el estrato TD 6 de Atapuerca, Burgos, España y se han datado en más de 780.000

Figura17. Cráneo de *Crocuta* sp. encontrado en Siwalik, Pakistán (Khan, 1972).

años, constituyendo la prueba de esta migración temprana (Garcia & Arsuaga, 1999). A partir de ese momento, la densidad de fósiles no aumenta en los siguientes 500.000 años, a pesar de que se ha estimado que habría una última oleada migratoria desde África hace 360.000 años (Rohland *et al.*, 2005) (Fig. 18c). En Europa no es hasta finales del Pleistoceno, justo antes del último máximo glaciar, cuando esta especie se hace superabundante en el registro fósil, para luego extinguirse definitivamente (Turner, 2009).

El registro fósil de *Crocuta crocuta* en Europa es muy abundante, y las variaciones observadas de tamaño han llevado a algunos investigadoras a catalogar a la hiena manchada del Pleistoceno Europeo como una especie o subespecie diferenciada: *Crocuta spelaea*, o *C. crocuta spelaea* (Tsoukala, 1991; Dockner, 2006). Sin embargo, Turner opina que las diferencias anatómicas entre los individuos del Pleistoceno euroasiático y los africanos actuales no son suficientes para establecer dos especies diferenciadas (Fig. 19) (Turner *et al,* 2008). Además,

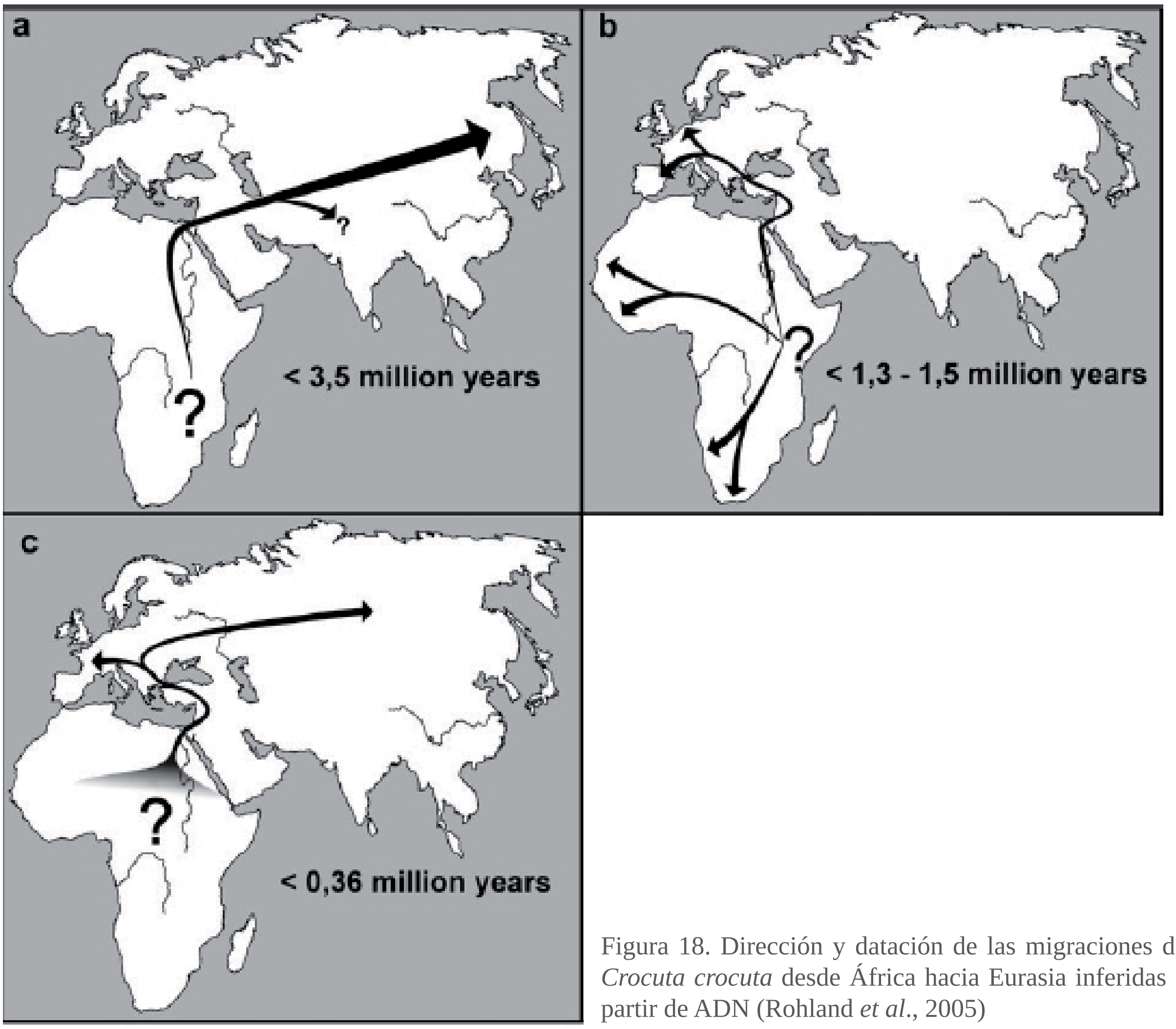


Figura 18. Dirección y datación de las migraciones de *Crocuta crocuta* desde África hacia Eurasia inferidas a partir de ADN (Rohland *et al*., 2005)

Figura 19 (arriba). Comparación entre el cráneo de *Crocuta crocuta spelaea*. Yacimiento de Löwentormuseum, Stuttgart. (en gris) y un cráneo de *Crocuta crocuta* actual (Dockner, 2006).

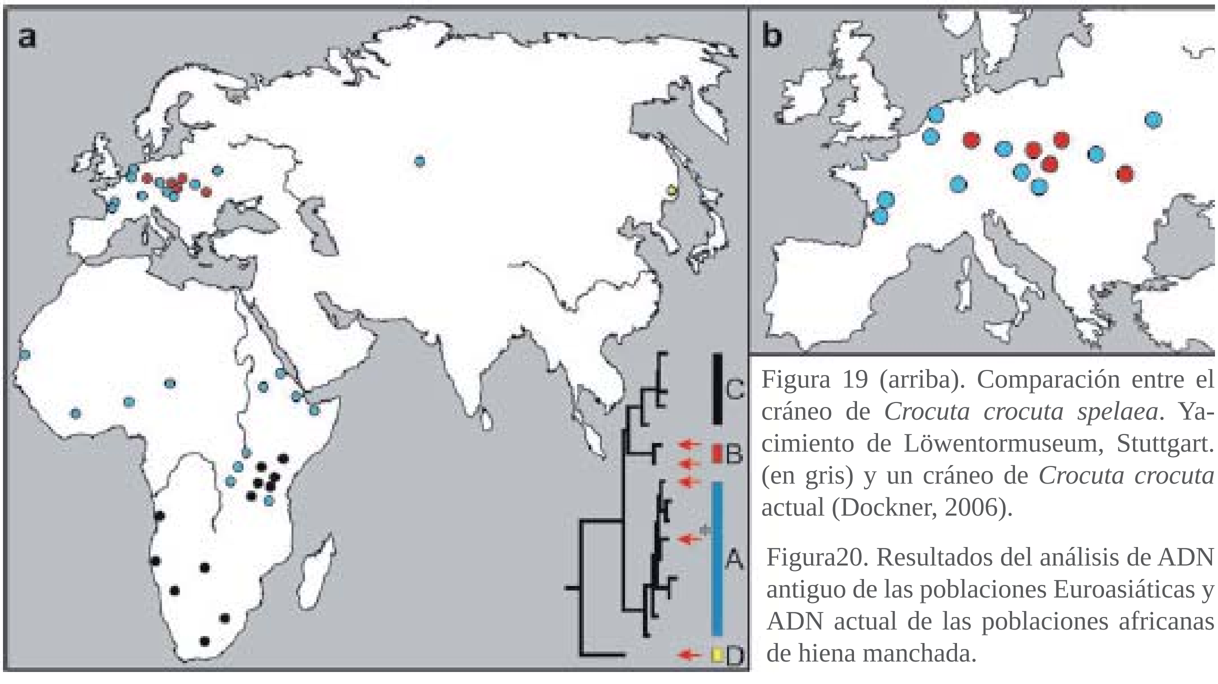


Figura20. Resultados del análisis de ADN antiguo de las poblaciones Euroasiáticas y ADN actual de las poblaciones africanas de hiena manchada.

los resultados del estudio del ADN antiguo de estos restos fósiles sugieren que las poblaciones de hiena manchada europeas serían un subconjunto de la población africana, y no una especie diferenciada (Rohland *et al.*, 2005) (Fig. 20).

Las figuras 21, 22, 23, 24, 25 y 26 muestran la situación geográfica de los yacimientos con registro fósil de *Crocuta crocuta* desde el Pleistoceno Inferior hasta el final del Pleistoceno. Todos los yacimientos incluidos forman parte de la base de datos que se ha generado a partir de referencias bibliográficas y que ha servido como base para realizar esta tesis doctoral, si bien es cierto que para hacer los análisis se han filtrado los registros dudosos o con dataciones imprecisas. En los mapas se puede comprobar como, aparentemente, la abundancia de restos fósiles de hiena manchada en Europa se incrementa a partir del estadio isotópico 4, en un momento en el que el clima de Eurasia está haciéndose cada vez más frío. Si se comprueba que esta tendencia es cierta y no está causada por algún sesgo de muestreo, indicaría que las hienas manchadas no solo pueden vivir en condiciones de clima estacional y frío, sino que éstas son condiciones óptimas para su supervivencia.

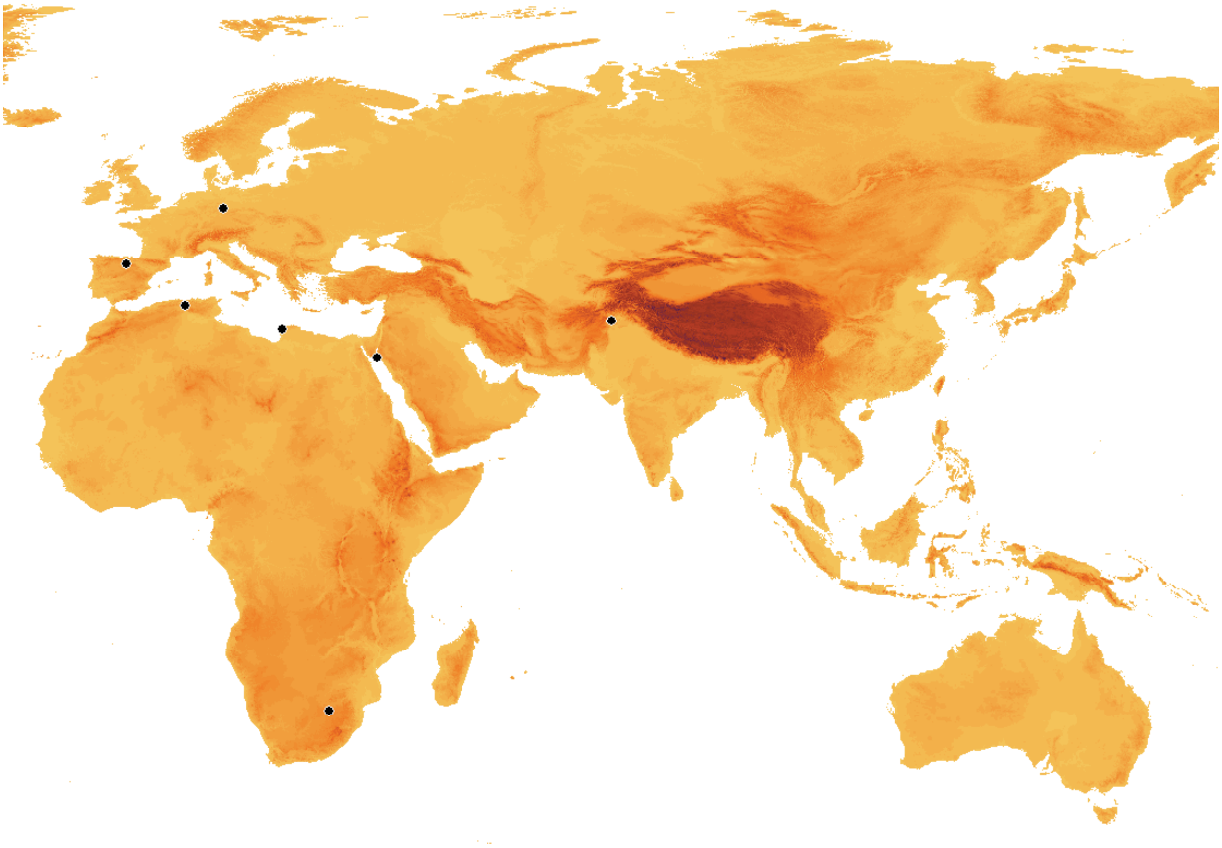


Figura 21. Yacimientos del Plioceno-Pleistoceno Inferior con presencia de hiena manchada (anteriores a 780.000 años)

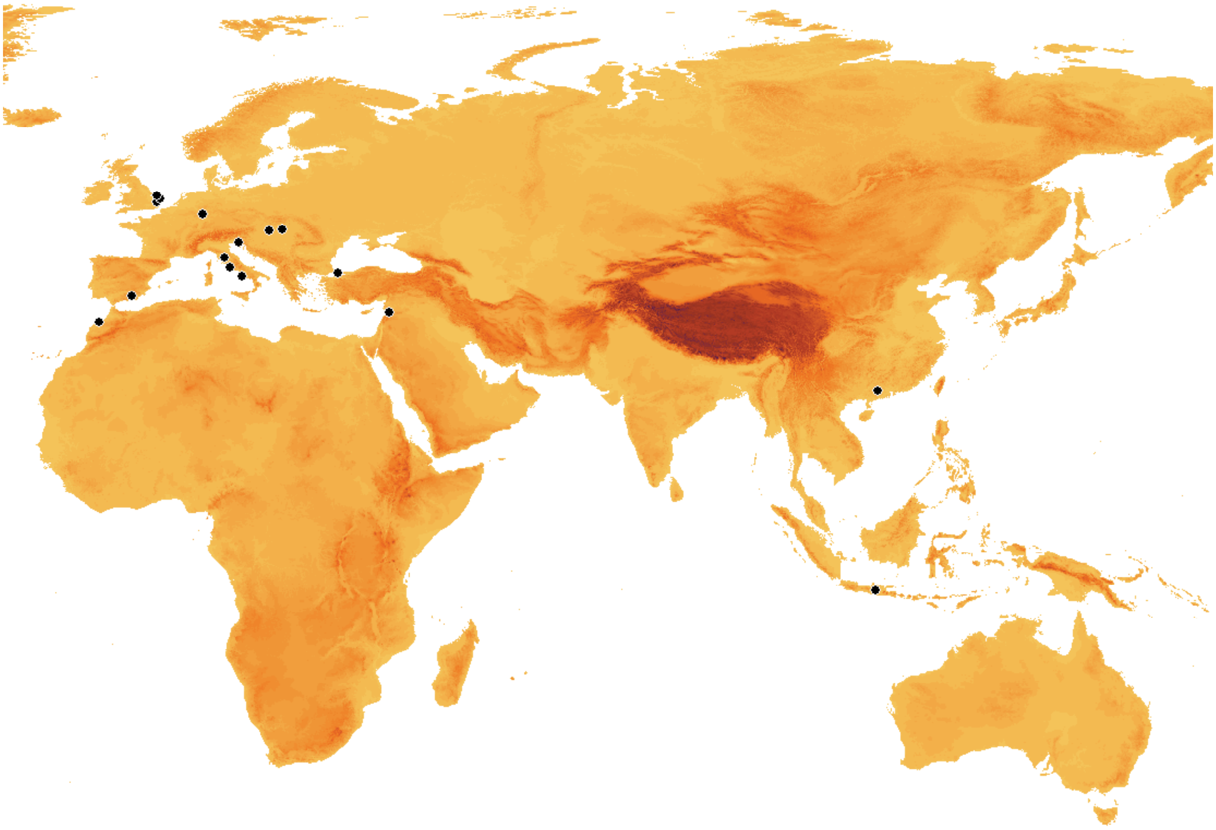


Figura 22. Yacimientos del Pleistoceno Medio con presencia de hiena manchada (780.000-120.000 años BP (Before Present))

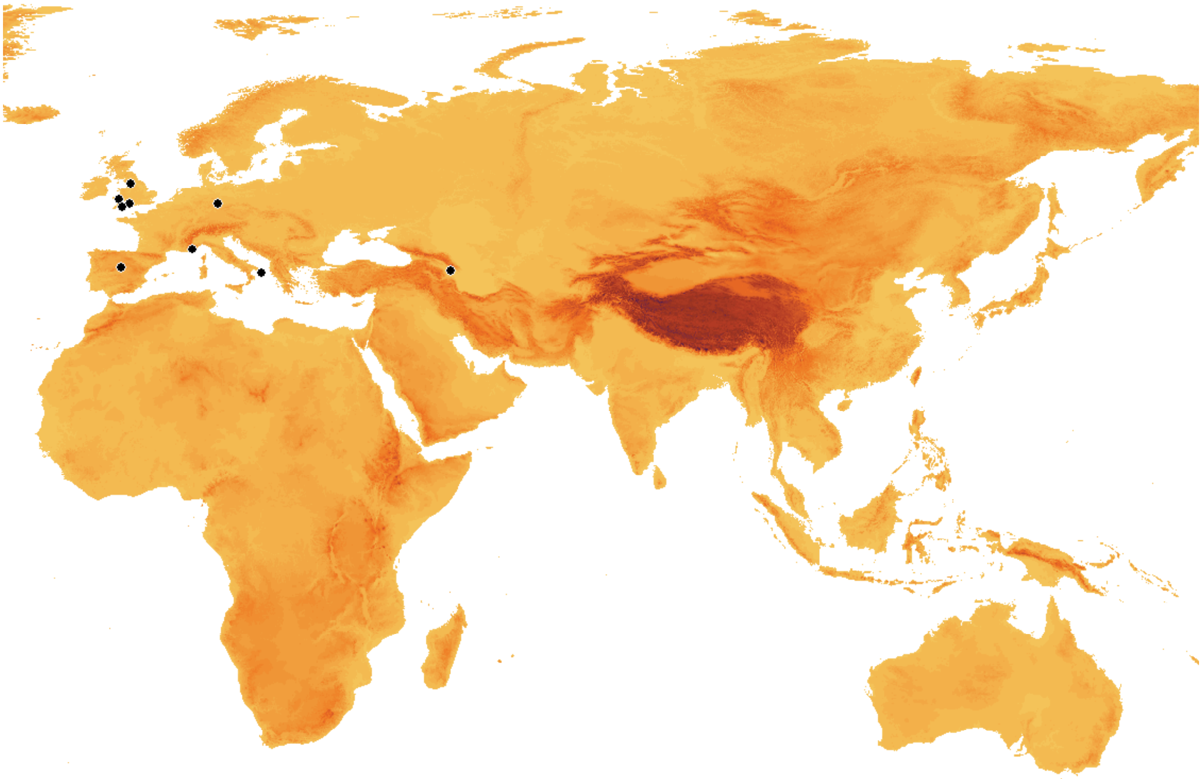


Figura 23. Yacimientos del último interglaciar (OIS 5) con presencia de hiena manchada (hace 120.000 años)

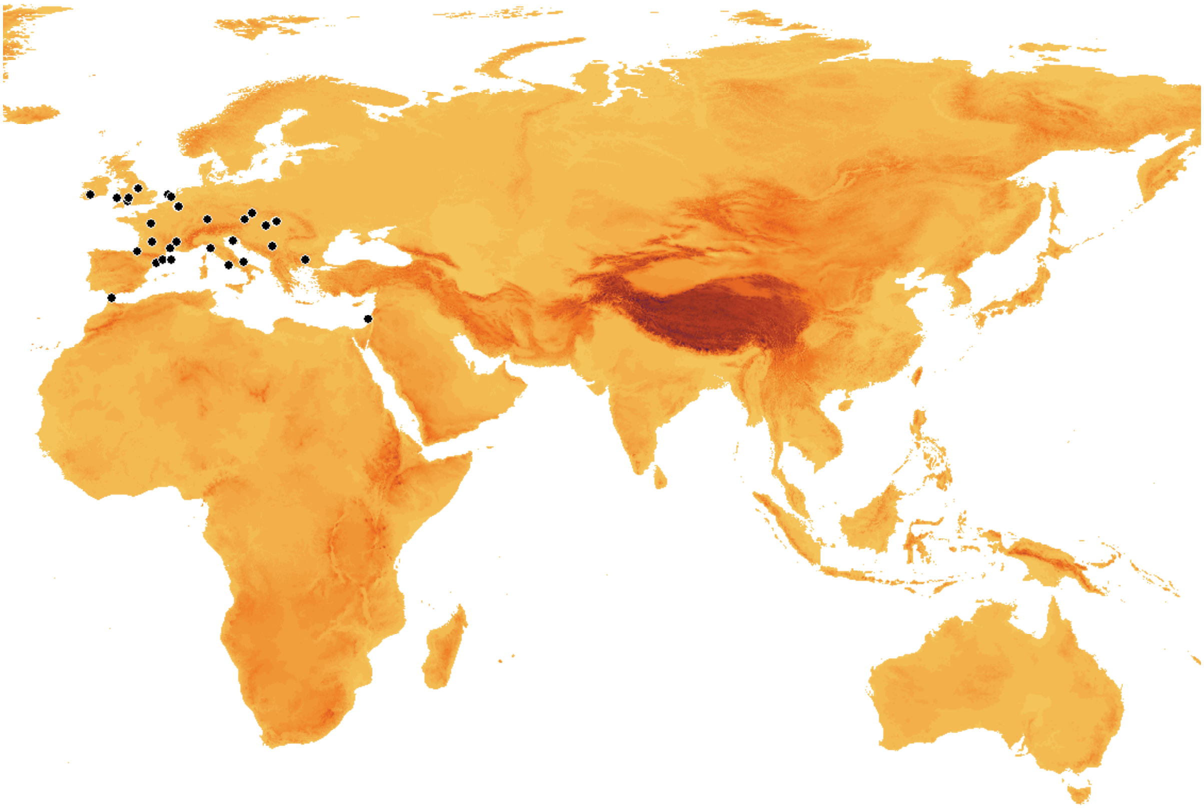


Figura 24 Yacimientos del OIS 4 con presencia de *Crocuta crocuta* (~40.000 años BP)

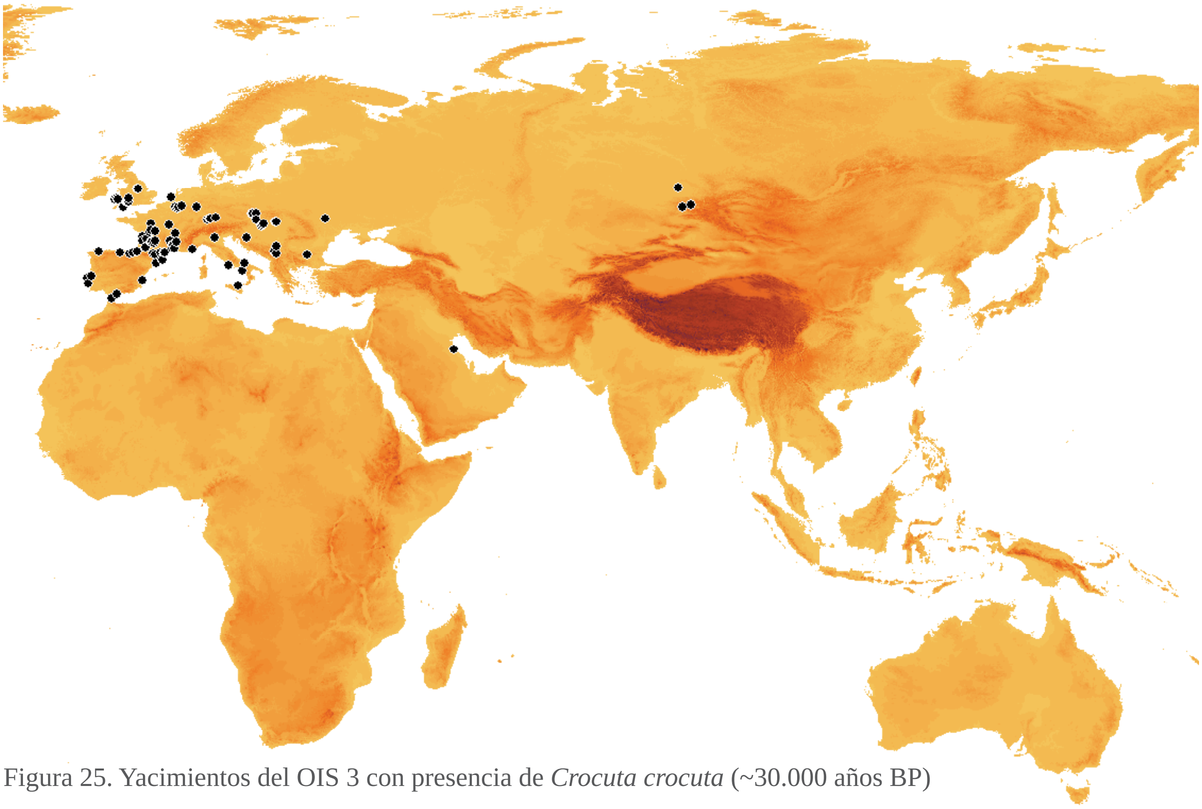


Figura 25. Yacimientos del OIS 3 con presencia de *Crocuta crocuta* (~30.000 años BP)

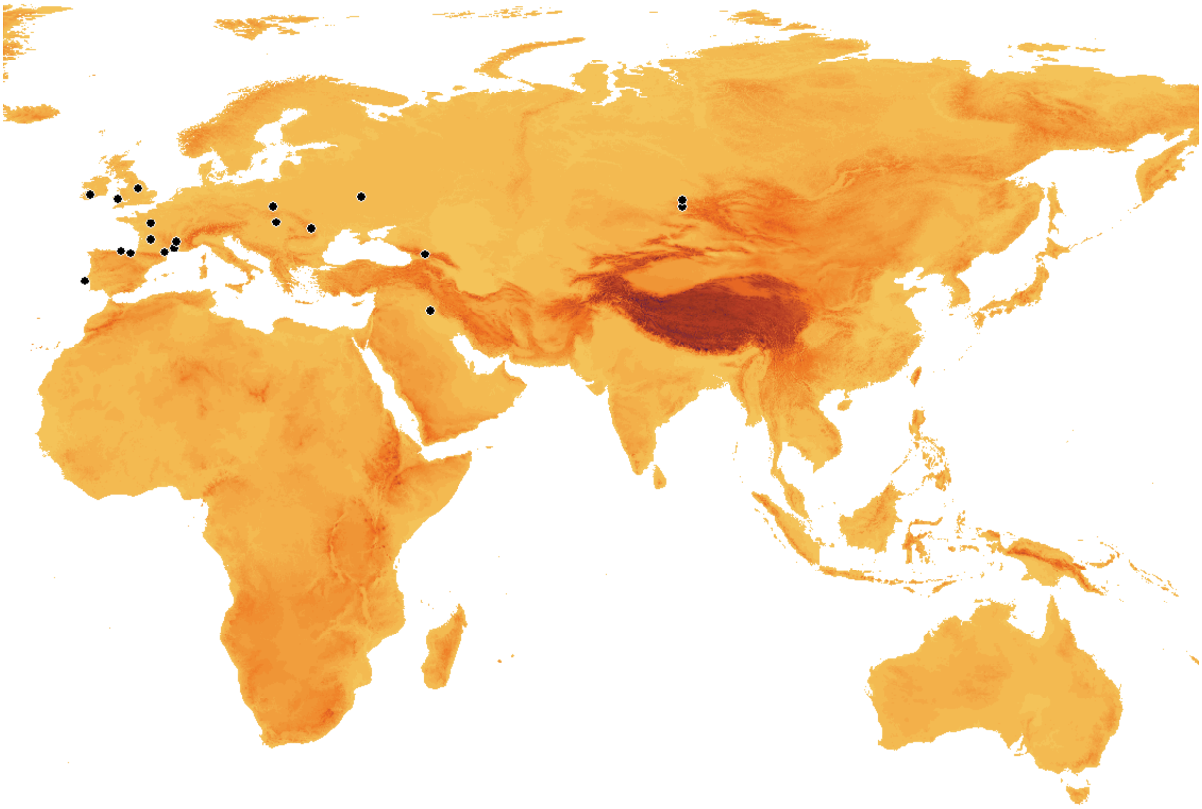


Figura 26. Yacimientos del OIS 2 (útimo máximo glaciar, ~21.000 años BP) con presencia de *Crocuta crocuta*.

4.- Evolution and Biogeography of *Crocuta crocuta*:

The spotted hyena, *Crocuta crocuta* (Erxleben, 1777), belongs to the Family Hyenidae, Order Carnivora. Hyenas have a long evolutionary story. The first species of the family was a civet-like hyena which lived during the Eocene. The diversity of the Family Hyenidae reached its maximum during the Miocene (5 m.a.), with more than 100 species of hyenas (Werdelin et al., 1991). However, after the climatic crisis of the Miocene and the associated global faunal turnover, only 5 species of hyenas survived (Fig 12, 13, 14, 15). Hyenas have not reached the same levels of diversity since then, and the family has not not diversified again (Mills, 1998). The oldest skeletal remains identified as *Crocuta crocuta* are located in Africa and date to 3 m.a. (Turner et al., 2008). Spotted hyenas live under a wide variety of environmental conditions and their feeding requirements are very varied (Hofer & East, 1993a; Owen-Smith & Mills, 2008). Spotted hyenas are opportunistic carnivores, capable of changing their behavior in response to the circumstances. Besides, they are intelligent and live in complex social structured clans of up to 70 individuals (Smith et al., 2008; Graf et al., 2009).

Although the geographic distribution of the spotted hyena is currently restricted to the African continent, the fossil record indicates that during the Pleistocene it covered a wide area of Eurasia. These data point out that, concerning Europe, there has been at least one migration/expansion event and one migration/extinction event. The aim of this work is to study in detail the distribution of the European spotted hyena fossils across time to understand the processes behind the observed geographic pattern. In order to do that, this thesis includes a compilation of published fossil remains (Fig. 21-26), historical records and current occurrences of the species. These data have been analyzed and the factors that could have caused species distribution range shifts, biotic and abiotic, have been discussed.

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Capítulo 2:

Influencia de los cambios climáticos en la extinción de la hiena manchada (*Crocuta crocuta* (Erxleben 1777)) en la Península Ibérica

1.- Resumen

La distribución de la hiena manchada se ha modificado de manera sustancial desde el Pleistoceno hasta nuestros días, de forma que aunque existen registros fósiles de la presencia de la especie en Eurasia a partir del Pleistoceno Inferior, en la actualidad su rango geográfico se restringe únicamente al continente africano. Circunscribiendo el área de estudio a la Península Ibérica, España y Portugal cuentan con datos que prueban la presencia de hienas manchadas (restos fósiles de su esqueleto, coprolitos, marcas de mordeduras en los huesos acumulados en sus cubiles, etc.) desde hace 800.000 YBP (Years Before Present) (García, 2001; Garcia *et al.*, 1999) hasta finales del Pleistoceno Tardío (Carrion *et al.*, 2001). Este estudio tiene como finalidad profundizar en el conocimiento de las causas que pudieron haber provocado la extinción de esta especie en el continente europeo, y en particular en la Península Ibérica. Para ello se analizará la influencia del clima en la distribución y supervivencia de las poblaciones ibéricas de *C. crocuta* durante el Pleistoceno Tardío.

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2.- ABSTRACT

The spotted hyena geographic distribution has changed in the last 120.000 years, from a broad geographic range that covered the Palaeartic and the Palaeotropical regions, to its current distribution, restricted to the African continent. The presence of the species in the Iberian Peninsula has been confirmed by fossil bones, coprolites, bite marks, bone accumulations, etc., from 800.000 YBP (Years Before Present) (García, 2001; Garcia et al., 1999), until the end of the Late Pleistocene (Carrion et al., 2001). The aim of this paper is to explore the role of Pleistocene climatic changes in the geographic distribution of the species in Eurasia and particularly, their influence on the extinction of the Iberian spotted hyena populations. We train a model using past and present spotted hyena distribution data, and we project this model into different Late Pleistocene climatic scenarios. Our results suggest that the Iberian Peninsula climatic conditions remained favourable for the presence of the species during the last 126.000 years. Therefore, our work suggests that the local extinction of the last European populations of hyenas, located in the Iberian Peninsula, is not related to the climatic changes.

3.- INTRODUCCIÓN

A finales del Pleistoceno Tardío se produjo un cambio global en la estructura de las comunidades de mamíferos que poblaban la mayoría de los continentes en ese momento (Rodríguez, 2004). Un elevado número de especies de gran talla desaparecieron para siempre, mientras que otras modificaron sus rangos geográficos, como es el caso de *C. crocuta* (Werdelin et al, 1991; Barnosky et al, 2004). Este evento, conocido como la extinción de la megafauna, ocurrió en diferentes oleadas, la última y más intensa de las cuales se ha datado hace unos 50.000-10.000 años (MacPhee *et al.*, 2002; Koch *et al.*, 2006). A grandes rasgos, esta datación coincide con dos eventos singulares: el último máximo glaciar (21.000 YBP) y la expansión de *Homo sapiens* (datada en torno a los 50.000-20.000 YBP, dependiendo del continente (Mellars, 2004)). Por este motivo, la mayoría de los estudios que analizan las extinciones de finales del Pleistoceno adoptan una o ambas hipótesis (cambio climático y/o competencia con *H. sapiens*) como los factores causales que han podido desencadenar este evento global (Miller *et al.*, 1999; Nogués-Bravo *et al.*, 2008). En este artículo hemos utilizado las condiciones climáticas de las localidades con presencia de C. crocuta, tanto en el Pleistoceno Europeo como en la actualidad (África), para crear un modelo que identifique las áreas con condiciones favorables para la presencia de la especie en Europa. Este modelo lo hemos extrapolado en el tiempo, para así poder

Crocuta crocuta. Fotografía Sara Varela

comprobar si la extinción de las poblaciones ibéricas de hiena manchada estuvo determinada por una pérdida de hábitat favorable como consecuencia de los cambios climáticos de finales del Pleistoceno.

4.- *Crocuta crocuta*

La hiena manchada, junto con *Hyena hyena*, *H. brunnea* y *Proteles cristatus*, constituyen la familia Hyenidae, incluida dentro del orden Carnivora (Mills *et al.*, 1998). Estas cuatro especies son los únicos hiénidos que han sobrevivido a las grandes extinciones que afectaron a los mamíferos y, en particular, a la diversa familia Hyenidae, durante el Plioceno y el Pleistoceno (Werdelin *et al.*, 1991). La hiena manchada es una especie carnívora de gran tamaño, cuyos individuos miden entre 95 y 150 cm y pesan entre 45 y 80 Kg. (Mills *et al.*, 1998). La especie presenta dimorfismo sexual (las hembras son mayores que los machos), y vive en clanes de 3 a 80 individuos (dependiendo de la densidad de presas). Estos clanes están articulados en base a una estructura jerárquica rígida, donde domina una hembra alfa, con unos rangos “sociales” que se heredan de generación en generación (Holekamp *et al.*, 1991). La distribución actual de esta especie se restringe al continente africano, limitada al norte por el desierto del Sahara, en el ecuador por los bosques húmedos de la cuenca del Congo, y en el sur por los ecosistemas desérticos y mediterráneos de Sudáfrica (Mills *et al.*, 1998).

5.- Los restos fósiles del Pleistoceno y su paleodistribución

La identificación de los restos fósiles de hiena manchada no está exenta de la problemática habitual en taxonomía, generada por la aplicación de criterios arbitrarios no estandarizados para establecer las divisiones específicas o subespecíficas. En este sentido, se han propuesto varias clasificaciones atendiendo al tamaño de los individuos y a las proporciones relativas de sus elementos esqueléticos. De este modo, en 1828, de Serres describió la subespecie *C. c.*

Crocuta crocuta. Fotografía Sara Varela *intermedia* a partir del material fósil del yacimiento del Pleistoceno Medio de Lunel-Viel, situado en Francia (Serres *et al.*, 1828). Más tarde, en 1832, Goldfuss añade otra subespecie, *C. c. spelaea*, con la cual se identificarían los individuos de mayor tamaño que habitaron durante el Pleistoceno Superior, bajo condiciones climáticas más severas (Goldfuss, 1832). Por otra parte, Turner propone una hipótesis más conservadora, sugiriendo obviar las diferencias poblacionales e incluyendo a las hienas del Pleistoceno europeo dentro de la especie *C. crocuta* (Turner, 1984). Por ello, en los listados faunísticos de los yacimientos euroasiáticos del Pleistoceno la presencia de restos fósiles de hiena manchada puede aparecer registrada bajo diferentes nombres: *C. crocuta* (Aguirre et alii, 1990), *C. c. intermedia* (Blasco Sancho y Montes Ramírez, 1997), *C. crocuta spelaea* (Nagel *et al.*, 2004; Werdelin *et al.*, 1991), *C. crocuta praespelaea* (Tchernov *et al.*, 1997) o incluso como una especie diferente, *C. spelaea*, clasificación utilizada en por Soergel (1937), Musil (1962) y Markova *et al.* (1995). Recientes estudios de ADN antiguo demuestran que hubo flujo genético entre las poblaciones africanas y euroasiáticas durante el Pleistoceno y, por este motivo, se ha sugerido que las diferencias anatómicas existentes constituirían adaptaciones locales pero que éstas no serían suficientes para concluir la existencia de especies diferenciadas (Rohland *et al.*, 2005). A raíz de estos nuevos datos, hemos estimado oportuno utilizar la propuesta taxonómica más integradora, es decir, considerar a la hiena manchada del Pleistoceno europeo como una subpoblación incluida dentro de la especie *C. crocuta*. El registro fósil de la especie *C. crocuta* aparece distribuido tanto en la región Paleotropical como en la Paleártica. En Europa, como ya se ha apuntado, el primer registro de *C. crocuta* está localizado en el nivel TDW4 de Gran Dolina, Atapuerca (Burgos) y su datación más antigua es de más de 800.000 YBP (Garcia *et al.*, 2001). A partir de este periodo, la presencia de la especie en Eurasia se ha documentado en numerosos yacimientos desde la Península Ibérica hasta los Urales (Testu, 2006). Para este estudio nos centraremos en los registros provenientes de los últimos 126.000 años, periodo durante el cual las poblaciones europeas de *C. crocuta* pasaron de estar ampliamente distribuidas a extinguirse.

6.- El cambio climático

El cambio en las condiciones climáticas ha sido considerado un factor clave a la hora de explicar la distribución geográfica de las especies. De hecho, en la literatura científica abundan los artículos que relacionan la distribución de las especies y los patrones biogeográficos actuales con variables climáticas (Currie, 1991; Bowyer *et al.*, 1998; Geffen *et al.*, 2004). Pero no sólo la ecología y la biogeografía actual defienden la importancia de este factor, desde la paleontología también se recurre frecuentemente a las crisis climáticas para explicar las extinciones o los cambios faunísticos detectados en el registro fósil. De este modo, la crisis Plio-Pleistocénica, la extinción de la megafauna, o los reemplazamientos de especies que se han producido en los ecosistemas a lo largo del Pleistoceno han sido relacionadas con cambios climáticos (Barry *et al.*, 2002; Cardoso, 1996; Coard *et al.*, 1999; Sommer *et al.*, 2005). En estos estudios se asume la existencia de dos tipos de especies, especies propias de climas fríos y especies propias de climas cálidos, que responderían de manera contraria ante las oscilaciones climáticas. Este marco conceptual es una simplificación de la respuesta de las especies al clima, como queda reflejado en los trabajos de Stafford *et al.* (1999), Williams *et al.* (2007) y Stewart (2008). En estos artículos se propone la individualidad en la respuesta de cada especie ante las alteraciones climáticas, constatando la existencia de comunidades Pleistocénicas sin análogos actuales y de distribuciones compartidas que actualmente son disjuntas. De esta manera la respuesta de las especies a las oscilaciones climáticas no tiene por que ser simple, y la división en dos tipos organismos (especies de clima frío y especies de clima cálido) parece una simplificación extrema de la complejidad real de los sistemas naturales. En este trabajo nos proponemos estimar las posibilidades de que la extinción europea de la hiena manchada haya sido provocada por los cambios climáticos del Pleistoceno. Para ello, determinaremos, en primer lugar, el rango climático de las hienas manchadas, basándonos tanto en los datos de distribución actual como en los datos disponibles para los últimos 126.000 años (yacimientos con presencia de *C. crocuta*). Posteriormente, construiremos un modelo orientado a predecir su distribución geográfica potencial de acuerdo a las condiciones climáticas de las localidades en que esta especie está o ha estado presente. El modelo así generado será proyectado a 5 escenarios climáticos diferentes: 126.000 YBP, 42.000 YBP, 30.000 YBP, 21.000 YBP y el presente, a fin de comprobar las diferencias en la distribución climática potencial de la especie en cada momento. Nuestra argumentación es que si los cambios climáticos han sido los principales responsables de la extinción de *C. crocuta* en la Península Ibérica, la distribución climática potencial predicha por el modelo debe reducirse drásticamente en alguno de los escenarios temporales (previsiblemente en el último glaciar, ya que fue en ese momento cuando las condiciones climáticas se hicieron más severas). Si, por el contrario, la representación geográfica de su distribución climática potencial permanece constante o poco variable a lo largo del tiempo, debería descartarse una influencia directa y trascendente del clima en la desaparición de las poblaciones ibéricas de hiena manchada.

7.- MATERIAL

El listado de puntos de presencia actual de la especie en África (Fig.1) se ha obtenido a partir de una búsqueda bibliográfica, considerando aquellas publicaciones que registran la

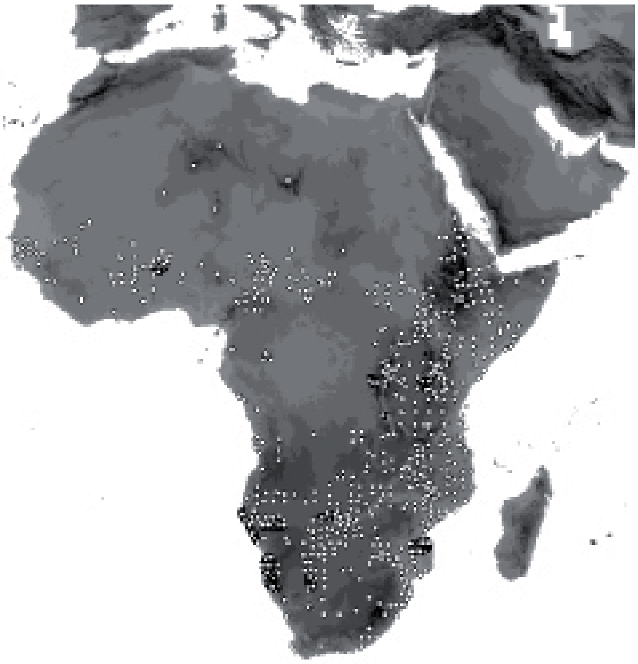

Fig. 1: Localización de los puntos de presencia actual e histórica de *C. crocuta* en África. Los datos de Chad (situados en los sistemas montañosos del interior del desierto del Sahara corresponden a registros de poblaciones actualmente extinguidas). Este mapa ha sido realizado a partir de los muestreos de campo de la IUCN (Mills, G. y Hofer, H., 1998) y de los listados faunísticos de los parques naturales africanos.

presencia de la especie en una determinada localidad o parque natural desde 1900 hasta el presente. De esta forma, se han incluido puntos localizados fuera de su distribución actual, pero contenidos dentro de la distribución histórica de la especie. Entendemos que la extinción en época reciente de estas poblaciones está principalmente relacionada con el impacto que los seres humanos pueden haber causado en ciertos ecosistemas y, por ello, creemos que su inclusión no desvirtúa el análisis sino que lo enriquece, añadiendo registros que mejoran el conocimiento del rango climático apto para la presencia de *C. crocuta*. Las localidades del Pleistoceno Euroasiático (n=79; ver Fig. 2) fueron extraídas de una base de datos que recoge citas bibliográficas

Fig. 2: Situación de los yacimientos seleccionados en este estudio. La inclusión de un yacimiento en el análisis ha estado supeditada al nivel de ajuste entre el intervalo temporal de las dataciones publicadas para el nivel con presencia de C. crocuta y los datos paleoclimáticos. De este modo, se han escogido los yacimientos que se aproximasen, dentro de una horquilla de +/- 3000 años, a las cuatro ventanas temporales de las simulaciones climáticas del modelo GENESIS 2.0.: 126.000 YBP. (círculos negros), 42.000 YBP (triángulos negros), 30.000 YBP (triángulos blancos) y 21.000 YBP (círculos blancvos)

de presencia de la especie en la que se incluyen más de 400 registros. La selección de los yacimientos ha seguido dos premisas fundamentales: primero, el registro debía estar acompañado de una datación fiable (C14, Series de Uranio, etc.), y segundo, la datación del yacimiento debía ajustarse, con un error de +/- 3ky (Nogués-Bravo *et al.*, 2008), a las ventanas temporales de las simulaciones climáticas del modelo GENESIS 2.0. De este modo, el número de localidades incluidas para cada escenario climático es el siguiente: 9 para el máximo interglaciar (126.000 YBP), 33 para 42.000 YBP, 27 para la simulación de 30.000 YBP y 10 para el último máximo glaciar (21.000 YBP). Las variables climáticas consideradas han sido las generadas por el modelo GENESIS 2.0 (Thompson *et al.*, 1995b), para cinco escenarios temporales diferentes: 126.000 YBP, 42.000 YBP, 30.000YBP, 21.000YBP y 0YBP. GENESIS 2.0 es un modelo de circulación global que realiza simulaciones para predecir el clima de la Tierra, tanto en el pasado como en el futuro. Se trata de un modelo complejo, que se articula en torno a diferentes modelos subordinados: un modelo para la circulación atmosférica, otro para la oceánica, además de modelos de suelo, de cobertura de nieve/hielo y de vegetación (Thompson *et al.*, 1995a; Thompson *et al.*, 1995b). Los niveles de dióxido de carbono en la atmósfera se estipulan antes de generar cada simulación, de modo que durante el último interglaciar (126.000 YBP), el valor considerado de Co2 en la atmósfera fue de 345 ppm, mientras que para las simulaciones del oIS 3 y del oIS 2 se fijó en 200 ppm. (Persaram Batra, com. pers.). Los resultados derivados del modelo GENESIS 2.0 coinciden de manera general con las estimaciones obtenidas a partir de datos independientes provenientes de registros polínicos y macrofósiles vegetales (Kaspar *et al.*, 2005). Toda la información biológica y climática se halla en formato digital utilizando un sistema de cuadrículas (o formato ráster) con una resolución de dos grados.

8.- Análisis y modelización

Las variables utilizadas para elaborar el modelo han sido: evapotranspiración real, precipitación anual, precipitación máxima (mensual), precipitación mínima (mensual), temperatura media anual, temperatura máxima (mensual) y temperatura mínima (mensual). Para extraer la información sobre los valores climáticos de los puntos de presencia de la especie en los diferentes escenarios temporales, se utilizó el software Idrisi Kilimanjaro (Clark Labs, 2003), exportando la información de cada píxel a una matriz de datos en Statistica v. 7 (Statsoft, 2001). Los datos climáticos de todas las localidades de presencia sirvieron para calcular el rango de condiciones en el que la especie está o estuvo presente para cada una de las variables consideradas. Esta sencilla aproximación (Busby, 1986), busca predecir la distribución potencial de la especie respecto a las variables utilizadas (Guisan *et al.*, 2000; Beaumont *et al.*, 2005), asumiendo que

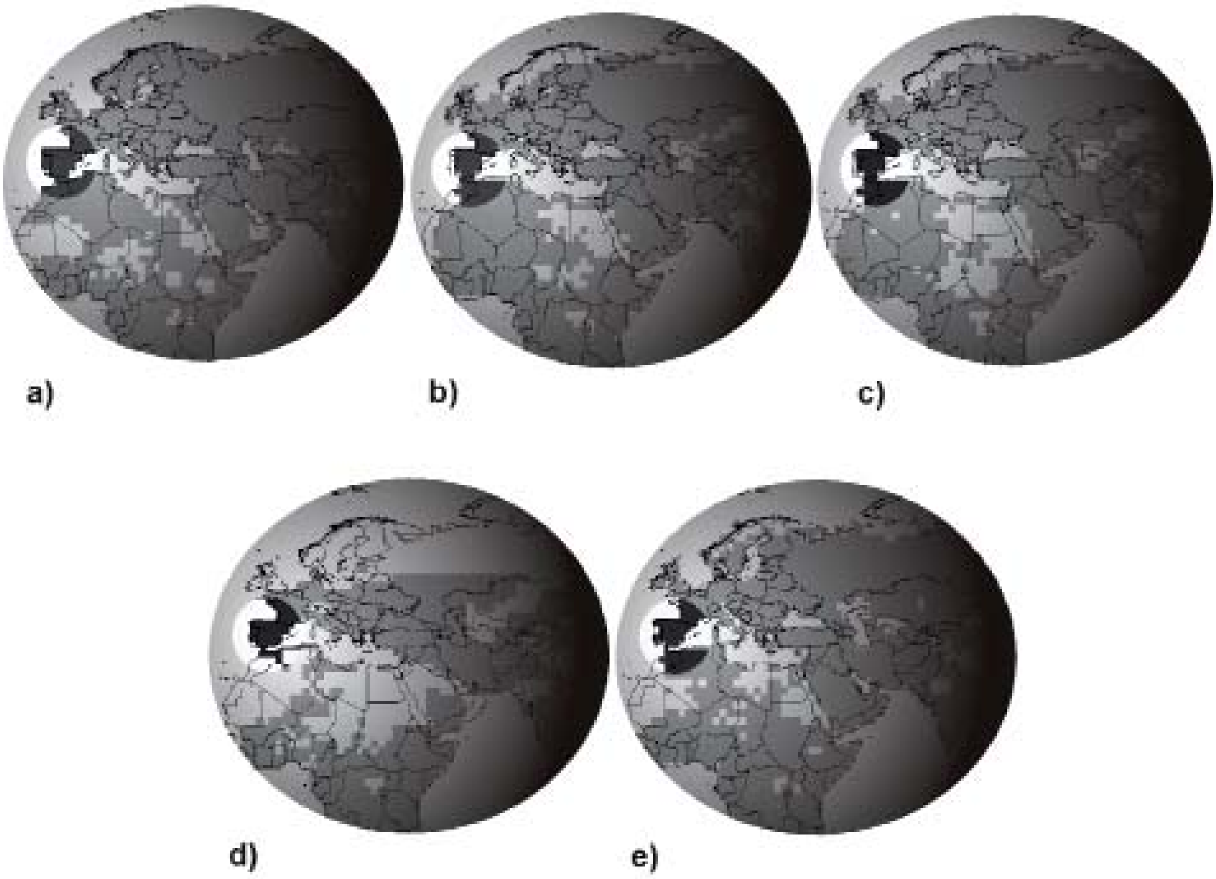

Fig. 3: Resultados de la proyección del modelo en los diferentes escenarios climáticos. a) 126.000 Y.B.P.; b) 42.000 Y.B.P.; c) 30.000 Y.B.P.; d) 21.000 Y.B.P. y e) clima actual. En los mapas, la distribución predicha por el modelo para la Península Ibérica aparece resaltada en color negro. Como se puede observar en la figura, a pesar de las oscilaciones climáticas que sufrió Europa durante el Pleistoceno Superior, C. crocuta contó siempre con condiciones ambientales favorables para su supervivencia en de la Península Ibérica.

las localidades de presencia reflejan, al menos parcialmente, las condiciones climáticas idóneas para la supervivencia de la especie. Una vez estimadas las condiciones climáticas favorables para la presencia de la especie y construido el modelo, éste fue proyectado en los diferentes escenarios climáticos del Pleistoceno y el presente (126.000, 42.000, 30.000, 21.000 y 0 Y.B.P.).

9.- RESULTADOS Y DISCUSIÓN

Si observamos la representación geográfica de los valores climáticos obtenidos para las localidades con registros de C. crocuta durante los últimos 126.000 años (Fig. 3), podemos comprobar que la distribución climática potencial de la especie cubre el total de la Península

Ibérica en cada uno de los escenarios temporales estudiados. Es decir, que desde el inicio del Pleistoceno Superior (el máximo interglaciar, escenario “a”: 126.000 YBP) hasta el presente (Escenario “e”: 0YBP), la hiena manchada parece haber contado siempre con condiciones climáticas similares a las que experimenta o ha experimentado en algún otro periodo. Cabe destacar que durante el máximo glaciar (Escenario “d”: 21.000YBP) la distribución potencial predicha se restringe en el norte de Europa pero que, sin embargo, en ese mismo momento la Península Ibérica aparece como climáticamente favorable para la especie, por lo que podría haber constituido un refugio para las poblaciones de *C. crocuta* europeas. De este modo, a pesar de la oscilación cíclica de las temperaturas (desde un periodo cálido a uno extremadamente frío y, de nuevo, a uno cálido) que ha sufrido la Península Ibérica en los últimos 120.000 años, el área potencialmente habitable por la hiena no disminuye en ningún momento. Estos resultados descartan que los cambios climáticos hayan sido la causa principal y determinante capaz de explicar la extinción de esta especie en la Península Ibérica e incluso en Europa. La desaparición de un hábitat apropiado es una de las principales hipótesis que se manejan para explicar la extinción de megafauna al final del Pleistoceno (Koch *et al.*, 2006). Recientemente Nogués-Bravo *et al.* (2008) aplicaron un proceso de modelización relativamente similar al utilizado en este trabajo para el caso de mamut lanudo (Mamuthus primigenius). Los resultados de esos autores sugieren que, a diferencia de lo que se observa para la hiena manchada, el cambio climático jugó un papel importante en la extinción del mamut lanudo. A expensas de realizar un estudio sobre la influencia de los distintos métodos de modelización en el papel diferencial asignado a los procesos antrópicos o climáticos, parece que la extinción de megafauna sería un fenómeno complejo, en el que los distintos factores implicados (cambio climático, desestructuración de la comunidades biológicas, influencia antrópica…) pueden haber pesado de manera diferente para cada especie. Nuestra opinión es que, para entender la extinción de la megafauna se precisa una aproximación detallada capaz de analizar individualmente la respuesta de cada especie y los factores que han determinado su extinción o supervivencia.

10.- CONCLUSIONES

Las proyecciones de nuestro modelo para los diferentes escenarios climáticos del Pleistoceno indican que la Península Ibérica ha contado siempre con condiciones climáticas a priori favorables para la presencia de la especie. De este modo, las oscilaciones climáticas que sufrió el continente europeo durante el Pleistoceno no parecen haber sido el principal factor causal capaz de explicar la extinción de esta especie, por lo que se deberá seguir indagando en las razones últimas de la desaparición de las poblaciones más septentrionales de *C. crocuta*.

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Capítulo 3:

Were the Late Pleistocene climatic changes responsible for the disappearance of the European spotted hyena populations? Hindcasting a species geographic distribution across time

1.- ABSTRACT

This article examines the role of the Late Pleistocene climatic changes in the disappearance of the European populations of spotted hyenas. A species distribution model was built using both current and past environmental requirements of the species. Model projections were made with climatic scenarios provided by the GENESIS 2.0 General Circulation Model (126 ka, 42 ka, 30 ka and 21 ka). Those projections indicate (1) that during the Late Pleistocene warm scenarios spotted hyenas should have been widespread in Europe, and (2) that during the last glacial maximum their potential climatically suitable geographic distribution diminished in size. The decrease in the potential climatic distribution was strictly restricted to Northern Europe. Climatic conditions in Southern Europe during the Late Pleistocene remained within

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the spotted hyena climatic tolerance. Hence, climate changes could have directly affected the Northern distribution of the species during the last glaciations. However, climate change alone is not sufficient to have caused the disappearance of the spotted hyena populations in Southern Europe. That is, other factors, such as prey abundance or human ecological impacts, in addition to climatic change, are needed to completely account for extinction of the European spotted hyena.

2.- INTRODUCTION

At the end of the Pleistocene (approximately 50-10 KYBP (Kilo Years Before Present)), a worldwide extinction, called the megafauna extinction, affected many of the larger species of mammals (Beck, 1996; Alroy, 1999; MacPhee *et al.*, 2002; Forster, 2003; Barnosky *et al.*, 2004; Louys *et al.*, 2007). In the western Palaearctic region, more than one third of mammalian megafauna genera went extinct (Barnosky *et al.*, 2004), and several widespread and charismatic species disappeared at that time, including *Mammuthus primigenius* (the woolly mammoth), *Homo neanderthalensis* (the Neanderthals), *Megaloceros giganteus* (the Irish Elk), *Coelodonta antiquitatis* (the woolly rhinoceros) and *Crocuta crocuta* (the spotted hyena) (Stuart *et al.*, 2007). The Pleistocene was characterised by an unstable climate with frequent oscillations between ice ages and warmer interglacial climates (Jackson *et al.*, 2000). The megafauna extinction coincided temporally with two major events: (1) the last glacial period and the climatic amelioration of the beginning of the Holocene, and (2) *Homo sapiens*' expansion out of Africa (dated from 45 to 50 KYBP (Mellars, 2006)). Therefore, the late Pleistocene extinction is generally considered a regionally contingent event generated by the combined effect of climate changes and human impacts (Barnosky *et al.*, 2004). In the case of Eurasia, climate change would have caused range shifts (Huntley, 1991) that, together with the increase in human populations, could have negatively and severely impacted large mammal populations (see Nogués-Bravo *et al.*, 2008). *C. crocuta* (the spotted hyena) is one of the large mammals that became extinct in Europe at the end of the late Pleistocene. Prior to their extinction, spotted hyenas were present in Europe for at least 1 million years (Garcia *et al.*, 1999; Carrión *et al.*, 2001). Fossil remains of the species suggest that during the Pleistocene they were present all over the continent from the Iberian Peninsula to the Urals (Testu, 2006). Some authors have assigned the European spotted hyena fossil remains to a subspecies of the African spotted hyenas (*Crocuta crocuta spelaea*, *Crocuta crocuta intermedia*; see Kurtén, 1957, 1968;Werdelin *et al.*, 1991), while others consider them a distinct species (*C. spelaea*; Soergel, 1937; Musil, 1962; Markova *et al.*, 1995). Recently, the taxonomic status of the Pleistocene European spotted hyenas was revised using ancient DNA. That analysis confirmed the existence of genetic flow between the African and Eurasian populations during the Pleistocene (Rohland *et al.*, 2005). Thus, similar to the situation for plants, it appears that the dominant response of mammal species during Quaternary climatic oscillations was extinction or range shift, not evolutionary change (Willis *et al.*, 2004). In this paper, we considered the European spotted hyena fossil remains as belonging to *C. crocuta* following Rohland *et al.* (2005). First, we estimate the climatic niche of this species from distributional data (the set of a priori favourable climatic conditions for the species) using the climatic information generated by the GENESIS 2.0 General Circulation Model (Pollard *et al.*, 1997). Second, we geographically projected this estimated niche in Europe for five temporal scenarios (126 KYBP, 42 KYBP, 30 KYBP, 21 KYBP and present) to ascertain the possible role of Pleistocene climatic changes on the potential distribution of European spotted hyenas. Climate is frequently considered a key factor in explaining the geographical distribution of species at large spatial and temporal scales (Bowyer *et al.*, 1998; Geffen *et al.*, 2004). Macroecological and biogeographical studies based on current data support the hypothesis that climate controls or at least strongly contributes to explaining the distributions of species (Currie, 1991), and many paleontological analyses also highlight the relevance of climate. For example, the Plio-Pleistocene crisis (Kostopoulus *et al.*, 2007) or species replacements during the Pleistocene are usually related to climatic changes (Cardoso, 1996; Barry *et al.*, 2002; Coard *et al.*, 1999; Sommer *et al.*, 2005). In this article, we address the question of whether climatic change alonewas sufficient to account for the extinction of spotted hyenas in Europe. We test whether extinction of the spotted hyena in Europe was related to a decrease in climatically favourable area during the Pleistocene. Finally, we discuss methodological influences on model predictions when using paleontological data.

3.- MATERIALS AND METHODS

3.1.- Spotted hyena data

Spotted hyenas show high morphological plasticity (Klein *et al.*, 1989; Mills *et al.*, 1998). The magnitude or morphological differences among extant populations (Mills *et al.*, 1998; Reynolds, 2007) and across Pleistocene periods is similar (Dockner, 2006). In addition, analysis of DNA from extant populations and from Pleistocene samples (i.e., ancient DNA) indicate that European and African spotted hyenas are the same species (Rohland *et al.*, 2005). Hence, following Rohland *et al.* (2005) we treat the extinct European populations and the extant African populations as different populations of the same species. Location data on the

Crocuta crocuta. Photography: Sara Varela

current occurrence of *C. crocuta* in Africa came from different sources, including the "IUCN Hyena Status Survey and Conservation Action Plan" (Mills *et al.*, 1998) and the African National Parks fauna lists, which collectively constitute 655 presence records (Fig. 1a). European Pleistocene fossil sites were chosen from a database that comprises published records of the species during the Late Pleistocene in Eurasia (see Varela *et al.*, 2009). We used two criteria for including location data for the Pleistocene. First, fossil localities had to be adequately dated (radiocarbon dates were calibrated into calendar years using the CalPal 2005 SFCP application including 95% confidence intervals). Second, these fossil localities with adequate dating and GENESIS 2.0 scenarios had to overlap (a temporal error of _3 ky was arbitrarily stipulated following Nogués-Bravo *et al.* (2008) and Banks *et al.* (2008a)). After applying these two criteria, more than 400 spotted hyena fossil sites were discarded. The number of selected locations was as follows: 9 points for the 126 KYBP scenario, 33 points for the 42 KYBP scenario, 27 points for the 30 KYBP scenario and 10 fossil sites for the 21 KYBP scenario (Fig. 1b). See Varela *et al.* (2009) for more information on the sources used.

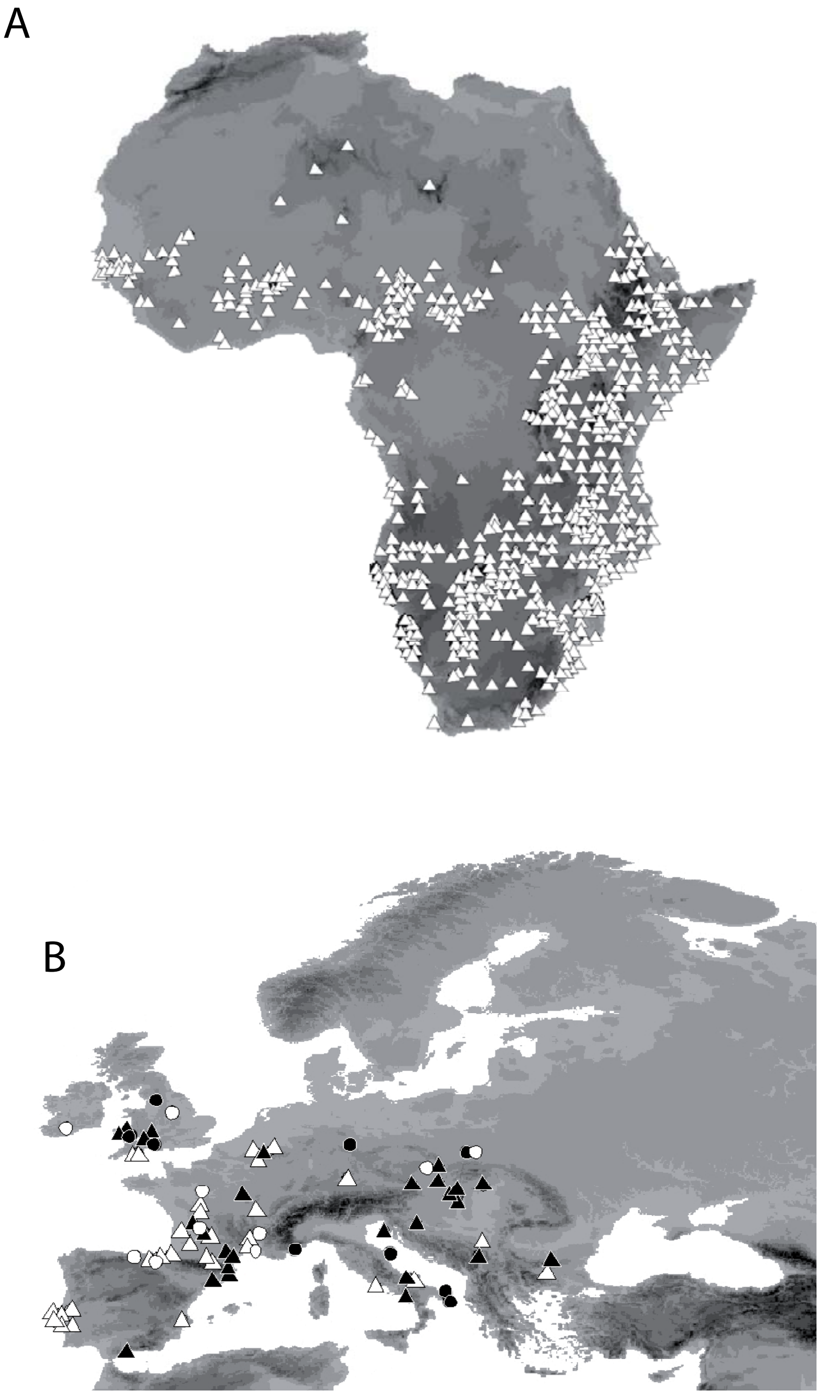

Figure 1. a) Current presence records of the spotted hyena, and b) location of the Pleistocene presence sites included in the analysis, dated from 126,000 YBP (black circles), 42,000 YBP (blck triangles), 30,000 YBP (white triangles) and 21,000 YBP (white circles).

3.2.- *Climatic data*

The climatic conditions at each location were estimated using variables from the General Circulation Model (GCM) GENESIS 2.0. GENESIS 2.0 combines an atmospheric model derived from the NCAR CCM1, a surface model, multilayer models of soil, snow and sea-ice, a slab mixed layer ocean model, and vegetation models (Thompson *et al.*, 1995a, b; Pollard *et al.*, 1997; Cosgrove *et al.*, 2002). There are other climatic simulations restricted to Europe (Banks *et al*., 2008a, b), but GENESIS 2.0 GCM was used because it has different simulations for the global climate of the late Pleistocene, including the last interglacial (126 KYBP). The GENESIS 2 model has been widely used in paleoclimate studies (e.g. Levis *et al.*, 1999; Doherty *et al.*, 2000; Barron *et al.*, 2002). When simulating past climates it performs in the middle of a range of a paleoclimate models (Kohfeld *et al.*, 2000), and it reproduces past climates reasonably well (Harrison *et al.*, 1998; Harrison *et al.*, 2003). Five different scenarios were used: a simulation for a warm climatic event, dated 126 KYBP, which corresponds to the Marine Isotope Stage 5 (MIS 5); two different scenarios for the MIS 3, dated 42 KYBP and 30 KYBP, representing two different periods of cold and dry conditions (Geraga *et al.*, 2005); the last glacial maximum scenario, dated 21 KYBP, corresponding to an extremely cold period during which the northern ice sheet reached middle Europe (MIS 2) (Bowen, 1995), and a climatic simulation of the present climate. The present-day GCM simulation was used to estimate the current climatic conditions in Africa that correspond with where the species is found. Carbon dioxide levels were specified at 200 ppm for MIS 2 and MIS 3, within the range of what was found in the Byrd and Vostok ice cores (Raynaud *et al.*, 1993). For MIS 5, 345 ppm was used (Vavrus, 2001), somewhat higher than the top Vostok value of 300 ppm For MIS 2, we used ICE-4 G paleotopography (Peltier, 1994). For MIS 3, ice sheet and topographic boundary conditions were the same as those detailed in Barron *et al.* (2002). The Last Interglacial reconstruction uses prescribed vegetation, and MIS3 and MIS 2 simulations use the BIOME4 vegetation model. Simulated paleoclimates in Eurasia show reasonable agreement with paleoclimates inferred from pollen and plant macrofossils (Batra, 2003; Kaspar *et al.*, 2005). All climatic information was available at a resolution of 2x2º grid cells. Downscaling methodologies were discarded. As different vegetation or ice-core geographic distribution may modify the atmosphere circulation at global and local scales (Gornitz, 1995) and the atmospheric circulation of the Pleistocene scenarios could be different from the current one (Bowen, 1995), we prefer not to use current local atmospheric circulation nomalies to downscale the coarse output of the past GCM simulations.

3.3.- *Species distribution modelling*

The set of environmental conditions associated with those localities in which the species may have a positive intrinsic growth rate constitutes a partial representation of the fundamental niche (Soberón, 2007). But the fundamental niche can only be completely determined by experimental or physiological studies (Kearney, 2006). Hence, the environmental conditions associated with the occupied area (the geographic distribution of the species) would be a subset of those constituting the fundamental niche due to the effects of biotic interactions or dispersal limitations, as well as the available environmental space (Jackson *et al.*, 2000). Thus, if we aim to generate an appropriate geographical representation of the species' niche using distribution data, we must use simple techniques and the most complete set of data (see Peterson *et al.*, 2007; Jiménez-Valverde *et al.*, 2008). We use a simple climatic envelope (Busby, 1986) to estimate the potential climatic distribution of the species in the different temporal scenarios, basing our model in the climatic requirements of a multitemporal presence data set. The climatic envelope model represents the minimal rectilinear envelope for the sampled multidimensional climatic requirements of the species, according to the available distributional information for the different Pleistocene periods and the present (Guisan *et al.*, 2000; Beaumont *et al.*, 2005). Thus, binary presence-absence maps were created based on the multidimensional envelope that includes the range of climatic conditions in which the species was observed. We also built a continuous geographic representation, using the Mahalanobis distance (Farber *et al.*, 2003) as a measure of climatic favourability. This measure differs from the Euclidean distance in that it takes into account the dependence among variables and is scale-invariant (i.e., the variables have the same weight independently of their variance). To emphasise the role of environmental limits (Huston, 2002) as well as to avoid the effect of bias in current and past fossil distribution data, we used amplitude ([maximum -minimum]/2þminimum) to calculate the central point of the n-dimensional climatic values for all past and present known presence cells. Thus, optimum climatic niche conditions would be equidistant from the extremes of the climatic values present in all known Pleistocene and current localities. This method avoids the bias generated by the use of central tendency measures (mean, mode or median) when estimated on a biased set of data (in this case, there are over 10 times more distributional localities of the spotted hyena in present climatic conditions than there are for all considered past times). Niche climatic envelopes also depend on the type and number of predictor variables used in their estimation (Beaumont *et al.*, 2005). Due to this, a necessary first step should be the selection of the predictor variables with a higher likelihood of being relevant to the distribution of species. We used ecological-niche factor analysis (ENFA) to identify the major climatic requirements of the spotted hyena (Hirzel *et al.*, 2002; Basille *et al.*, 2008; Calenge *et al.*, 2008; Calenge *et al.*, 2008). This exploratory analysis (see Hirzel *et al.*, 2002 for a detailed explanation of the method) allows the identification of those variables that explain both marginality (the difference between the conditions inhabited by the species and the regional average conditions) and the specialisation of the species (i.e., the tolerance of the species to the climatic gradient in the study area). Five separate ENFA analyses were carried out: four in Europe for past time simulations and one in Africa using present day climatic simulations. Those variables with factor loadings >0.33 for the marginality or specialisation axes in any one of the ENFA analyses were selected. In total, seven climatic variables from the complete set of GENESIS variables were retained and used in modelling procedures: actual evapotranspiration, annual precipitation, maximum monthly precipitation, minimum monthly precipitation, annual mean temperature, mean temperature of the warmest month, and mean temperature of the coldest month.

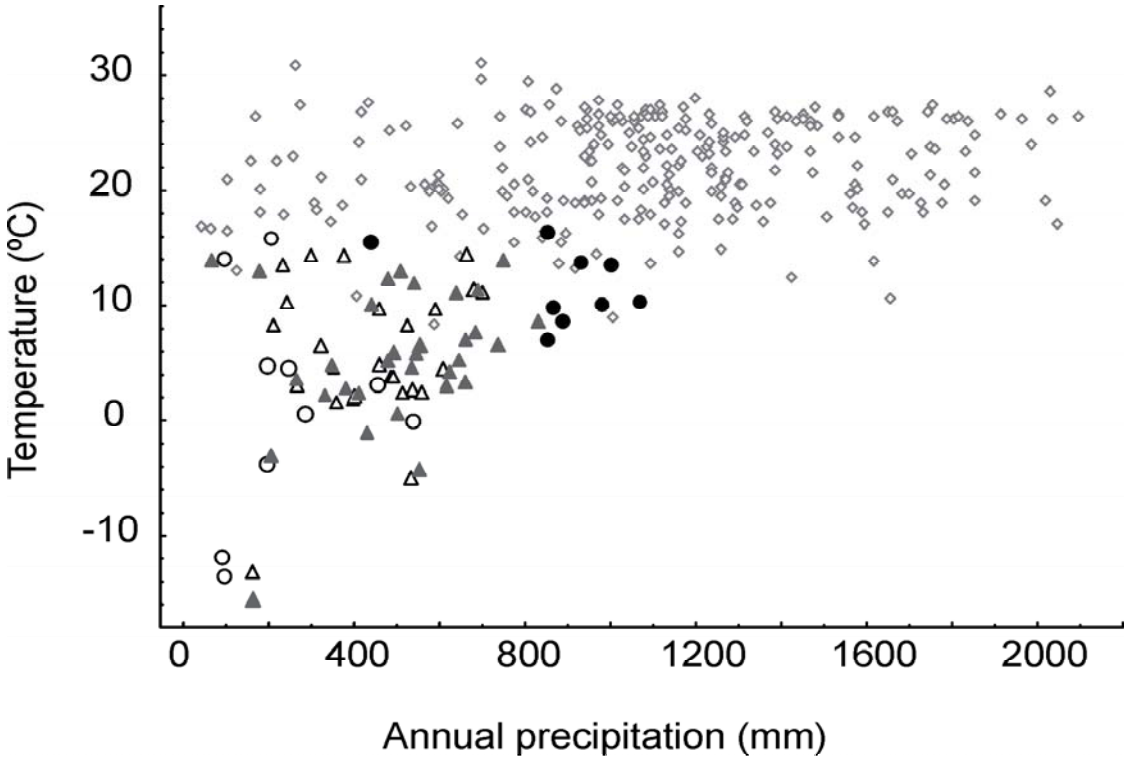

Figure 2. Mean temperature and precipitation values of the spotted hyena presence sites for the different considered temporal data sets: 126 KYBP (black circles), 42 KYBP (black triangles), 30 KYBP (white triangles), 21 KYBP (white circles) and present (grey rhomboids).

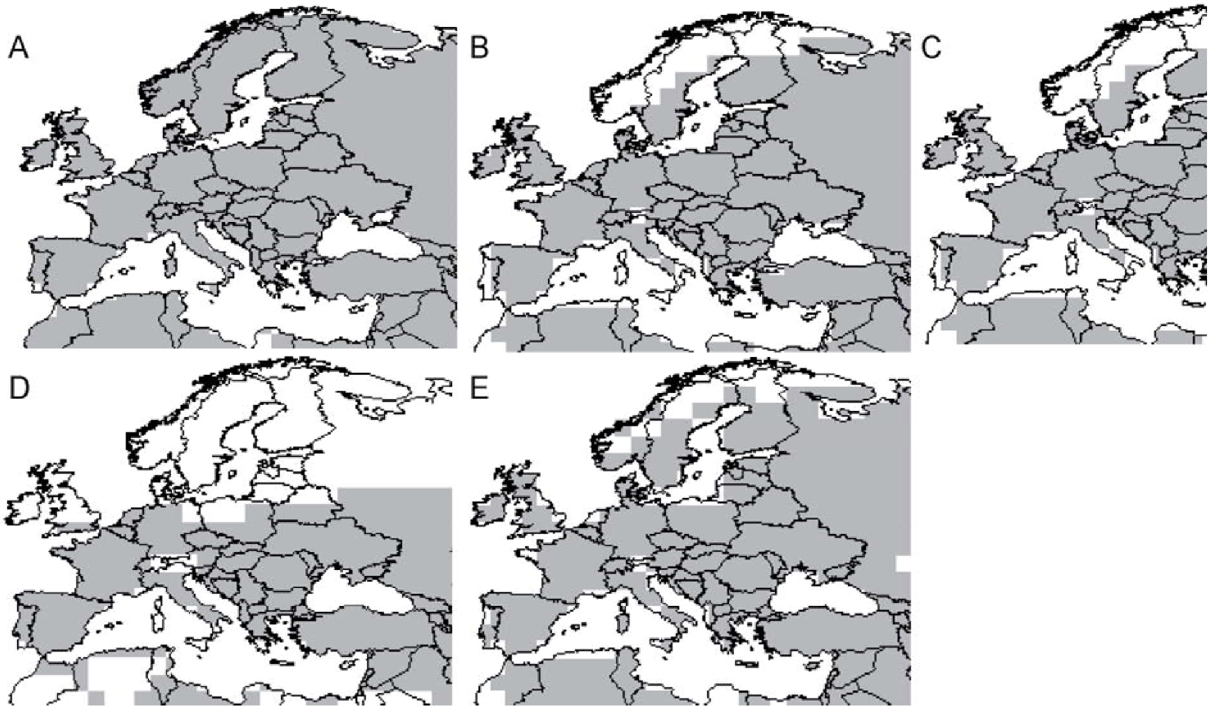

Figure 3. The projection of the entire climatic envelope model for the different temporal scenarios considered: a (126 KYBP), b (42 KYBP), c (30 KYBP), d (21 KYBP) and e (present). Only during the Last Glacial Maximum (d) did the predicted distribution of Crocuta crocuta species appear to be climatically restricted to southern and central Europe.

4.- RESULTS

Spotted hyenas inhabit a wide range of annual precipitation and mean temperature conditions, although Pleistocene European localities appeared to have lower temperatures and, to a lesser extent, lower precipitation than current African localities (Fig 2). Presence data for Europe during the warm/wet conditions of the Pleistocene 126 KYBP scenario had different climatic conditions than those from the cold/dry conditions of the last glaciation. The geographical projections of the climatic niche derived from all fossil and current data indicated that C. crocuta had suitable climatic conditions in Europe during the last 126 KYBP (Fig. 3). The potential climatic distribution of the species covered Europe in the last interglacial age (Fig. 3a), when the climatic conditions were similar to current ones. Model predictions suggested geographic range was reduced by 8% for the MIS3 for both the 42 KYBP and 30 KYBP simulations and by more than 30% for the last glacial maximum (Fig. 3d). The present-day simulation (Fig. 3e) predicted an increase in the potential climatic distribution of the species similar to the MIS3 estimates, although the species went extinct during the Pleistocene-Holocene transition

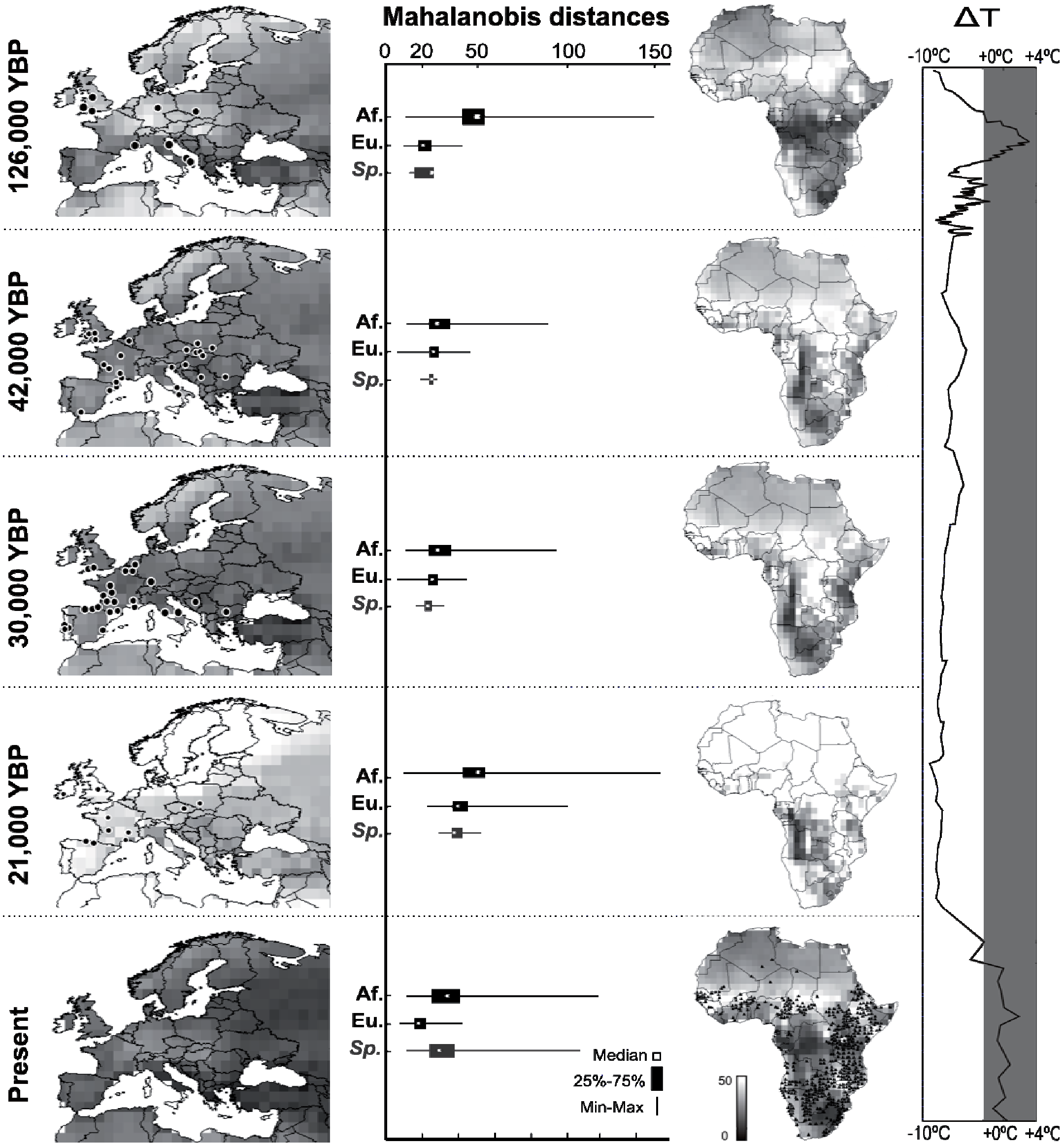

Figure 4. Mahalanobis distance maps representing the climatic distance of each 2º x 2º European and African grid cell from the central point ([maximum – minimum]/2 + minimum) of the n-dimensional climatic values considering all past and present known presence cells of *C. crocuta* for the five different temporal scenarios considered. The grey scale goes from the minimum distance (black), which indicates suitable conditions for the spotted hyena, to the 90th percentile of the data set (white), which indicates extremely unfavourable climatic conditions for the species (Mahalanobis distance = 50). The middle graph represents the dispersion of the Mahalanobis distances. Median, 25%-75% quartiles (black bars) and minimum-maximum values (lines) were plotted both for all of the African (Af) and European (Eu) grid cells, as well as for those grid cells in which *C. crocuta* fossil or current presence data were available (sp). A temperature curve is also provided (modified from Petit *et al*., 1999).

(Carrión *et al.*, 2001). Continuous Mahalanobis predictions indicated that *C. crocuta* had suitable climatic conditions in Europe during all of the Late Pleistocene. Most of European territory is located at short distances from the estimated central climatic niche conditions (Fig. 4), although these distances differed significantly among periods, both in the case of all European cells (Kruskal-Wallis test: H ¼ 2755.64, p< 0.0001, df ¼4, N¼ 4427) and in the case of cells with C. crocuta presences (H ¼ 77.25, p <0.0001, df ¼ 4, N¼338). Thus, although the climatic suitability distances of the spotted hyena presences during the last glaciation overlap with the estimated values in all other periods (Fig. 4), our analyses suggested a significant decrease in the area with very favourable conditions. Interestingly, Africa generally harboured more unstable and less suitable average climatic conditions than Europe in all periods. Furthermore, during the last glaciation, the geographical separation between the favourable areas in Africa and Europe increased substantially (Fig. 4).

5.- DISCUSSION

The geographical representations of the climatic envelope model indicate that the European extinction of the spotted hyena populations could not be related directly to the Pleistocene climatic changes. Our results suggest that the extreme cold conditions prevailing during the Last Glacial Maximum (LGM) would have diminished the extent of the climatically suitable European territory, but even under this apparently extreme climatic scenario, a high proportion of southern and central Europe would remain habitable for *C. crocuta.* Other evidence also supports the view that climate was probably not the most crucial and decisive factor in explaining the extinction of *C. crocuta* in Europe. First, many cold periods occurred during the Pleistocene (Allen *et al.*, 1999) and they did not cause extinction in Europe. Considerable fossil evidence demonstrates that the spotted hyena was present in Europe during Pleistocene glacial conditions. During these time the spotted hyena, coexisted with species such as the woolly rhinoceros and the woolly mammoth (Werdelin *et al.*, 1991; Testu, 2006). Furthermore, our resultsshowthat the distances from the estimated climate optimum are even higher on the continent in which *C. crocuta* still survives (Africa) than in Europe during the last 126,000 years. Late Pleistocene climatic changes could not be linked directly to the final extinction of the spotted hyena. European Pleistocene fossil records of *C. crocuta* are characterised by their location near the cold extreme of the full temperature range. Thus, assuming that our methodological procedure correctly approximated the climatic optimum of the species, our results also suggest that most of the southern European territory possessed low suitability values during the LGM. More importantly, the existence of wide areas with low suitability values separated the climatically favourable areas of Africa and Europe. However, the relevance of the climatic variables highly depends on our methodological procedures. In particular, the selection of the climatic optimum is a key step in this process that may greatly affect the results. For example, in the case of the woolly mammoth, this optimum was estimated using a central tendency measure over the entire set of available climatic data, and the results suggested that climate was the main factor driving both the extinction and the decrease in distribution (Nogués-Bravo *et al.*, 2008). According to our results, during the LGM the spotted hyena could have suffered climatic stress and fragmentation of their potential distributional area in both Europe and Africa, although the consequences of these possible range contractions may have been different in each continent. If the complete geographic range and the probability of recolonization diminished during this cold period, other factors, such as the number of available prey or the competitive interaction with humans could have acted synergistically to precipitate the Holocene extinction of European spotted hyenas. In addition, the plant fossil records of the Palaearctic indicate that there were several short-term vegetation changes, supposedly linked to sharp climatic shifts that affected the general glacial cycles (Li *et al.*, 2006;Wagner *et al.*, 2009). These short-term climatic waves could have played an important role in the disappearance of the European spotted hyena populations. Three aspects of our methodology could have substantially influenced our results and hence our biological interpretations. They are: (i) the temporal and spatial extent of the data used, (ii) the selection of the relevant climatic variables and (iii) the previously mentioned estimation of the species climatic optimum. Some studies on Quaternary mammalian faunas relate species changes to the glacial/interglacial cycles and assume that there were cold-adapted and warm-adapted species. In these analyses, cold-adapted species expand their ranges during glacial periods, while warm-adapted species migrate or disappear (Martínez-Meyer *et al.*, 2004). The spotted hyena is considered to be a warm-adapted species because it is currently living in Africa, and consequently, LGM climatic conditions have been interpreted to be a threat for the species (Jacobi *et al*., 2006). However, we think that the general framework of classifying organisms as warm or cold adapted based on their current realised climatic niche is an oversimplification of the potential climatic requirements. In addition, this assumption could lead to incorrect conclusions about the biological response to the environmental changes. As with other European mammals (Stewart *et al.*, 2003), the past and present geographic distribution of the spotted hyena reflects different parts of their potential climatic niche. In our opinion, the species niche should be determined using both past and present species occurrences because the estimated climatic niche depends critically on the temporal and geographic scope of the data that are analyzed (Varela *et al.*, 2009). It can be inaccurate to estimate the complete potentially suitable climatic requirements of a species using only a single temporal or spatial scenario. Each partially realised distribution does not cover the entire potential climatic tolerance of the species. Therefore, only when the most complete set of distribution data (from more than one different temporal scenario) is used will we best estimate the climatic niche of the species. This apparently simple factor has profound consequences for the discussion on the comparative roles of niche stability factors and niche evolution factors (Holt, 1996). Using distributional information of species, some authors suggest the existence of niche stability because climatic data on species presence sites remain unaltered (Martínez-Meyer *et al.*, 2004; Martínez-Meyer *et al.*, 2006; Peterson *et al.*, 2008; Pearman *et al.*, 2008a). In contrast, niche shift is frequently assumed when climate conditions derived from data coming from different periods or regions do not coincide (Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Urban *et al.*, 2007; Pearman *et al.*, 2008b; Steiner *et al.*, 2008). The climatic conditions prevailing in presence localities cannot provide a reliable picture of the species niche due to the contingent effect of some factors preventing the colonisation of climatically favourable areas. Thus, we advocate the use of as much distributional data as possible. We also suggest caution when deriving niche measures from distribution data, mainly when these data do not completely cover the temporal and spatial spectrum of conditions inhabited by the species. Other important technical decisions that can greatly change the conclusions of these kind of studies are the selection of explanatory variables and the method used to determine the most probable location of the species optimum. Niche modelling results are highly dependent on the quantity and type of variables used (Beaumont *et al.*, 2005). A large number of variables result in more restricted potential distributions and niche estimations. Thus, we recommend the use of an exploratory analysis, such as ENFA, to identify a minimum set of relevant variables that explain to the greatest extent possible the climatic tolerance and marginality of species (Basille *et al.*, 2008; Calenge *et al.*, 2008; Calenge *et al.*, 2008). On the other hand, the correct estimation of the environmental niche is hindered by the frequent biases and scarceness of distributional information (Hortal *et al.*, 2008). In the case of paleontological data, these biases are not only generated by the uneven distribution of the collection effort, but also by the patchiness of the locations of places capable of producing fossils. Although the estimation of the environmental limits may be affected by these biases, they may principally influence the calculation of the climatic optimum. That is, central tendency measures, such as mean, mode or median, might yield optimum values close to the climatic conditions prevailing in the most surveyed locations or in those where the occurrence of fossils is more frequent. To minimize this effect, we suggest that the calculation of continuous suitability measures, such as those provided by the use of the Mahalanobis distance, be based on an optimum derived from the amplitude of the climatic values for all presence data. As these central climatic niche conditions would be located in an equidistant position from the observed climatic extremes, such a procedure assumes that the distribution of climatic values is symmetrical (that is unskewed). Apart from the previously described methodological questions, a few other caveats

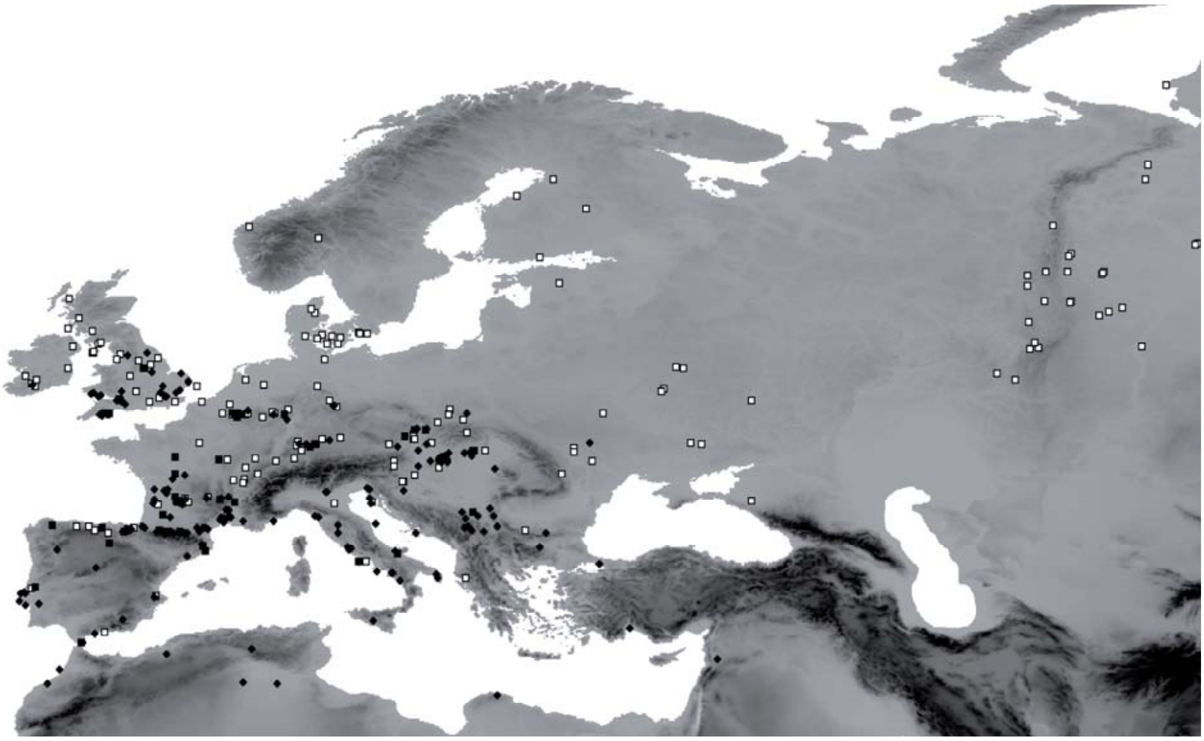

Figure 5. General picture of the location of Pleistocene fossil sites for *C. crocuta*. There is a geographic pattern in the spotted hyena fossil record, and although there are Pleistocene fossil sites located in northern Europe (white), spotted hyena fossil remains have been recorded purely in the South (black).

should be mentioned with respect to the interpretation of our results. In recent African spotted hyena populations, two separate clades with limited geographic overlap near the equator are recognised. These two clades are probably a consequence of colonisation from Pleistocene glacial refugees (Rohland *et al.*, 2005). In contrast, analysis of ancient DNA analysis indicates that European fossil records from the Pleistocene and current African populations could be part of the same species (Nagel *et al.*, 2004; Rohland *et al*., 2005). In addition, the high morphological plasticity detected by Klein *et al.* (1989) and Mills *et al.* (1998), might reflect their capacity to inhabit a wide range of climatic conditions. Plasticity is an inherent property of species, and changes in phenotype through space and time should be expected (Holt, 2003; Shai *et al.*, 2003; Kurtén,1973; Smith *et al.*, 1995, 1998). In this paper, we assumed that both present and ancient morphological or genetic variability did not substantially affect their potential response of *C. crocuta* to climatic conditions. When estimating the factors that determine a species distribution, the variables should be measured at the scale they interact with the target species. To do this, a species' home range could be used as an indicator of the ideal spatial resolution of the climatic variables used to build the model. Spotted hyena territories can reach 1000 km^2, and the mean distance away hyenas will go outside or their territory in search of prey their territory is 40 km, although that distance can be as large as 80 km (Mills *et al.*, 1998). Therefore, the maximum species geographic home range may cover around 10,000 km^2. However, the available climatic scenarios for the Pleistocene have a coarse resolution, and we had to use a 2x2 degree grid cell to build the model (Pollard *et al.*, 1997). Furthermore, the areas of these cells vary with the latitude. The northern species presence cells are 28,300 km^2 while those cells located near the equator are 39,500 km^2. These rough calculations indicate that the grid cells for climate modelling could be two, three or even four times larger than the spotted hyena home range. Species distribution models based on low resolution variables tend to predict larger areas than those constructed using high-resolution grid cells (Seo *et al.*, 2009). Therefore, because there were no high-resolution world climatic scenarios available for the Pleistocene, this was the most accurate approach we could take to estimate the range size and shift of the spotted hyena during the Pleistocene. Finally, the potential distribution that we estimated covers the northern areas of Eurasia both for the 126 KYBP warm scenario and 42 KYBP or 30 KYBP cold events of the MIS3. This result is interesting, because all the spotted hyena European fossil sites were located south of 55º N (Markova *et al.*, 1995) (Fig. 5). This pattern could be explained by a geographic bias in the data sample or because the model is missing some relevant non-climatic factor(s) related to the dispersal/survival capabilities of the species in northern latitudes. Because there are many fossil sites located in northern latitudes without *C. crocuta* remains (Fig. 5), we believe that a taphonomic bias is highly improbable. We recommend that future in niche modelling studies include other non-climatic factors to explain the species' lack of ability to colonize northern Europe. One nonclimatic factor that warrants further analysis is prey diversity and abundance during the Pleistocene because prey diversity and abundance is apparently fundamental to explaining the current distribution of large carnivores (Hayward *et al.*, 2007). Another factor that should be included is the possibility of direct competition between humans and European spotted hyenas, both in their trophic preferences and in their shelter requirements. Similarly, as spotted hyenas use caves to den, we hypothesise that the absence of karstic systems in northern Europe could have been a species specific methological factor that constrained the northern distribution of this species during the Pleistocene. These hypotheses will be deeply discussed in future papers.

6.- CONCLUSIONS

First, our analysis indicates that past climatic changes could have isolated Late Pleistocene *C. crocuta* populations in two different areas: Africa and Europe. The model suggests that the extinction of the European spotted hyena and the prevalence of the African populations cannot be explained solely as a function of climate. Consequently, future research should explore the importance of factors, such as human impacts or herbivore abundance, to test whether these factors may help explain the disappearance of the spotted hyenas from Europe. Second, our model predicts that the spotted hyena European distribution should cover Northern Europe during the warm periods of the Late Pleistocene. The absence of *C. crocuta* fossil records from these areas could be related to the limited number of Northern European interglacial fossil sites. New fossil records in this zone would give further opportunities for model evaluation.

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Capítulo 4:

¿Las extinciones de herbívoros a finales del Pleistoceno están relacionadas con la desaparición de las hienas manchadas?

1.- Resumen

El objetivo de este trabajo es describir los cambios que se produjeron en las comunidades de mamíferos herbívoros a lo largo del Pleistoceno para dilucidar si estas variaciones pudieron haber afectado a la supervivencia de las poblaciones de hiena manchada que habitaban la Península Ibérica. Para comprobar esta hipótesis nos servimos del actualismo, comparando el comportamiento trófico que presenta *Crocuta crocuta* en el presente con las presas potenciales que habitaban la Península Ibérica antes y después de su extinción. Los estudios sobre las poblaciones africanas de hiena manchada indican que esta especie selecciona a sus presas en función de su tamaño, depredando preferentemente sobre herbívoros de talla media. Cuando aplicamos este criterio a las faunas del Pleistoceno, nos encontramos que durante el último millón de años han existido siempre unas comunidades de mamíferos excepcionalmente diversas, con diferentes especies de presas potenciales dentro del rango de tamaños preferido por las

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hienas. Sin embargo, es necesario señalar que después del último máximo glaciar, coincidiendo con los registros de *C. crocuta* más recientes, las comunidades de mamíferos de la Península se empobrecen de una manera drástica quedando solamente una presa (*Cervus elaphus*) dentro del rango de tamaños óptimo para la especie. Por este motivo, hemos realizado un último análisis, examinado la posibilidad de que un ecosistema Mediterráneo de la transición Pleistoceno-Holoceno pudiese haber mantenido una población estable de hiena manchada. Nuestros resultados sugieren que, al igual que en el caso de los cambios climáticos, las profundas modificaciones en la composición de las comunidades de herbívoros que ocurrieron a finales del Pleistoceno no parecen haber sido un factor trascendental que, por sí solo, explique la desaparición de esta especie.

2.- ABSTRACT

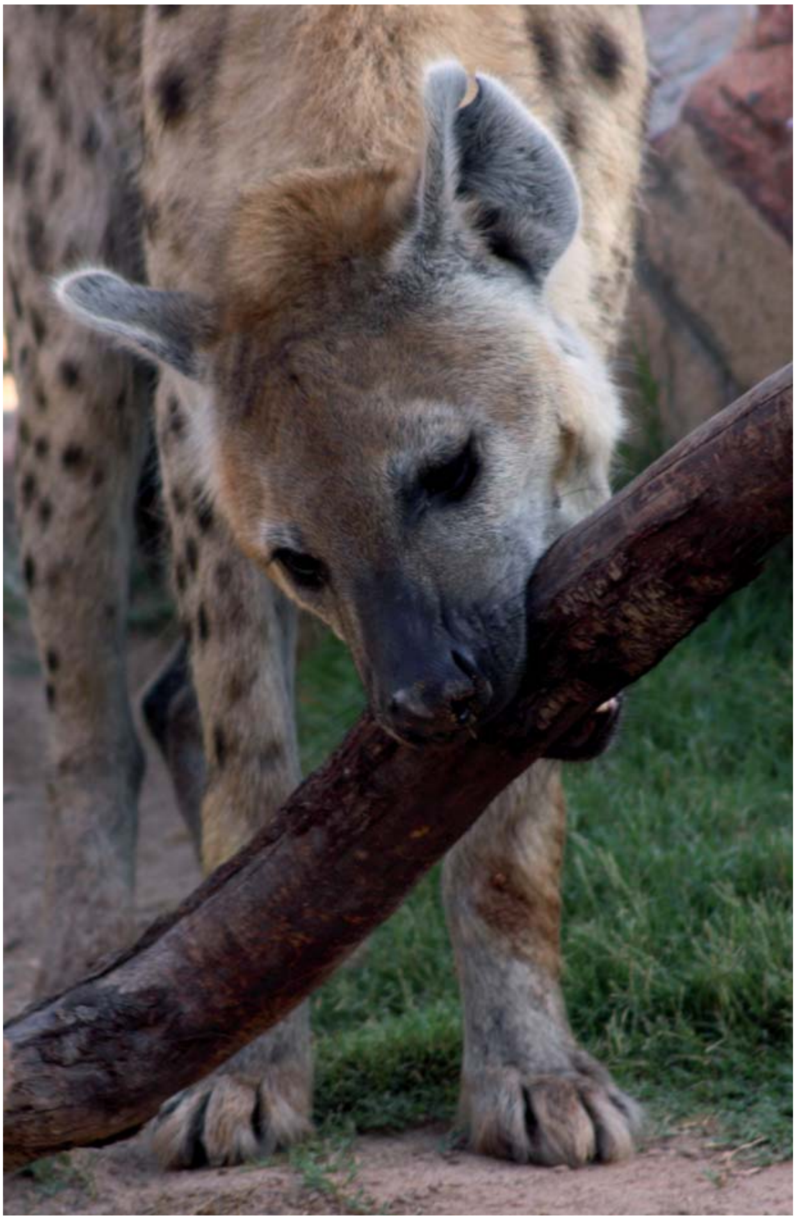
This investigation aims to test whether the extinction of the latest spotted hyena populations could have been related to the prey availability. We describe the compositional changes in the herbivore mammal fauna throughout the Pleistocene in order to elucidate how fauna variation could have affected persistence of the spotted hyena population in the Iberian Peninsula. In order to do this, we analyze the current trophic behaviour of *Crocuta crocuta* in Africa, examining the type of available and consumed preys. Subsequently, we compare the results against the prey communities that were present tin he Iberian Peninsula during the Pleistocene, after and before the hyena extinction. Current spotted hyena trophic behaviour in Africa indicate that the prey size is the most important selection criteria for this species. The majority of the biomass consumed by *C. crocuta* comes from mesoherbivores. Applying this criterion to the Pleistocene faunas, we have found that there were always different species of mesoherbivores that hyenas could have predated. However, after the Last Glacial Maximum, and coinciding with the latest spotted hyena fossil records found in the Iberian Peninsula, the herbivore communities suffered an important extinction event. Only one species (*Cervus elaphus*) within the optimum prey size of spotted hyenas was left. In order to test whether these impoverished communities of the Pleistocene- Holocene transition could have maintained a *C. crocuta* population, we used an equation proposed by Carbone and Gittleman (2002). This formula relates the carnivore size and the prey biomass with the number of predators expected in the ecosystem. Our results suggest that the profound compositional modifications in herbivore assemblages during this period do not seem to be the determining cause for the extinction of *C. crocuta* in the Iberian Peninsula, as with the analysis of the Pleistocene climatic fluctuations (presented previously in this same volume).

3.- INTRODUCCIÓN

Crocuta crocuta ha modificado su distribución geográfica durante el último millón de años, pasando de ocupar amplias áreas de las regiones Paleártica y Paleotropical durante buena parte del Pleistoceno a poseer actualmente una distribución restringida al continente africano (Werdelin *et al.*, 1991). En los estudios sobre las extinciones de la fauna del Pleistoceno se suele recurrir a eventos globales, como son los cambios climáticos o la expansión de Homo sapiens, para explicar de manera general la desaparición de las especies. Comprobada la hipótesis climática en otro artículo de este mismo volumen, y a expensas de analizar la influencia humana, en este trabajo hemos querido individualizar nuestra hipótesis de partida y adaptarla a los requerimientos biológicos (en este caso tróficos) de un carnívoro de gran tamaño como es la hiena manchada. La relación entre la densidad de presas y de predadores ha sido analizada en numerosas ocasiones y sus resultados constituyen uno de los pilares fundamentales de la dinámica de poblaciones (con la famosa ecuación de Lotka-Volterra como punto germinal de partida (Korobenkov *et al.*, 1999)). En el caso de la hiena manchada, la relación entre el número de efectivos de esta especie y la abundancia de presas de mesoherbívoros de los ecosistemas africanos actuales es lineal (Grange *et al.*, 2006). Además, la dinámica poblacional de *C. crocuta* parece responder rápidamente a los cambios en la abundancia de sus presas, como sugiere un estudio realizado en el cráter del Ngorongoro, Tanzania (Höner *et al.*, 2005). En este estudio se presentan los resultados de un muestreo llevado a cabo durante 43 años, en el que el número de individuos de hiena manchada se redujo a la mitad en un periodo de 36 años debido a la escasez de presas, para posteriormente duplicar su tamaño en 7 años una vez recuperadas las poblaciones de ungulados. Esta fuerte dependencia de los recursos tróficos nos ha llevado a plantear si el empobrecimiento de las comunidades de herbívoros sucedidas a finales del Pleistoceno pudo haber actuado como un factor desencadenante de la desaparición de las poblaciones ibéricas de esta especie. Para ello, revisaremos primero la gama de presas consumidas por *C. crocuta* en África, estimando el peso óptimo de las preferencias tróficas de esta especie. Seguidamente, estudiaremos la composición y el tamaño de las posibles presas existentes durante todo el Pleistoceno, utilizando para ello los datos de un conjunto amplio de yacimientos fósiles. Finalmente, considerando los cálculos existentes sobre la biomasa de herbívoros necesaria para mantener una población de predadores, trataremos de comprobar si la densidad de las especies de herbívoros presentes a finales del Pleistoceno sería capaz de sustentar una población de hiena manchada.

4.- El comportamiento trófico actual

Valverde (1967) señaló que el tamaño, combinado con la presencia de estructuras o comportamientos de defensa, es el factor principal que determina qué especies son las presas preferidas por un mamífero predador. El predador tiende a preferir presas de un tamaño similar al suyo ya que de esta forma se establece un equilibrio entre la cantidad de energía que obtiene el predador consumiendo la presa y la que consume intentando capturarla. Las presas demasiado grandes son muy costosas, cuando no imposibles de abatir, y las muy pequeñas tienen un índice de apetencia bajo pues proporcionan muy poca energía (Valverde, 1967). En este caso, el comportamiento trófico de *Crocuta crocuta* en la actualidad se caracteriza por una enorme versatilidad. Las hienas manchadas seleccionan a sus presas en función de su tamaño y abundancia, adoptando una estrategia de caza en grupo o en solitario según el tipo de presa (Hayward, 2006). El consumo de carroña es ocasional y oportunista y, normalmente, no representa un porcentaje elevado dentro de su dieta. A modo ilustrativo, el estudio del comportamiento trófico de un clan de la reserva de Masai Mara mostró que la ingesta de carroña en este grupo suponía sólo un 5% de la biomasa consumida a lo largo del año (Cooper, 1990). En lo que respecta a la selección de tamaños de presa, el 47.7% de la biomasa consumida en esta población procedía de ñus (*Connochaetes taurinus*), cuyo peso medio es de 180 kg, el 21.8% de cebras (*Equus burchellii*), con un peso aproximado de 250 kg y el 16.8% de topis (*Damaliscus lunatus*), animales de 160 kg. Esto significa que más del 85% de la biomasa consumida por esta población provenía de presas comprendidas entre los 160 y los 250 kg, lo cual sugiere que existe una selección basada en el tamaño dirigida, preferentemente, hacia los herbívoros de talla media. Este resultado está apoyado también por el hecho de que las hienas de esta población rechazaban consumir gacelas de Thomson (*Gazella thomsoni*), un herbívoro de tamaño pequeño (20 kg) pero muy abundante en el medio. Di Silvestre et alii (2000) en su trabajo sobre el comportamiento trófico de *C. crocuta* en el Parque Nacional de Niokolo Koba (Senegal), afirman que las hienas poseen una clara preferencia por las presas de más de 100 kg. En este caso, búfalos (*Syncerus caffer*) con un peso entre 300 y 900 kg en edad adulta, bubales (*Alcelaphus buselaphus*) con un peso aproximado de 135 kg, y facóqueros (unos 70 kg) son consumidos con una frecuencia mayor de la esperada en relación a su abundancia. Henschel y Skinner (1990) apuntan que los búfalos (*Synceros caffer*), aunque son una parte importante de la dieta de las hienas manchadas, no suelen ser cazados sino que éstas se limitan a carroñear sus restos, mientras que kudus (*Tragelaphus* sp.), impalas (*Aepyceros melampus*) y facóqueros (*Phacochoerus* sp.), todos ellos presas con pesos comprendidos entre los 50 y los 220 kg, son depredados frecuentemente. Este último estudio concluye que las hienas manchadas dependen fundamentalmente de ungulados con pesos comprendidos



Crocuta crocuta. Fotografía: Sara Varela

entre los 130 y los 350 kg. Por otro lado, Hayward (2006), en un estudio bibliográfico que resume 17 publicaciones sobre la dieta de la hiena manchada, menciona que habitualmente las presas cazadas tienen un rango de peso de entre 56 y los 182 kg, con un pico en los 102 kg, y que las especies mayores (elefantes, jirafas, búfalos, etc.) están generalmente representadas en la dieta por juveniles y neonatos, cazados de manera oportunista, por lo que su aportación en la dieta sería marginal. En resumen, los estudios sobre el comportamiento trófico de *C. crocuta* en África indican claramente que las poblaciones actuales de esta especie dependen fundamentalmente de presas de tamaño mediano (entre los 50 y los 250 kg), despreciando generalmente las presas de menor talla (aunque éstas presenten poblaciones abundantes) y carroñeando de manera oportunista las presas mayores. Para este trabajo hemos compilado 22 listados faunísticos de otros tantos Parques Nacionales o áreas protegidas africanas con presencia de hiena manchada (Tabla 1) a fin de estimar el rango de presas disponibles en la actualidad para esta especie. La adscripción de cada una de las especies a las distintas categorías (presa "ocasional", "frecuente" o "consumo no registrado") se ha efectuado teniendo en cuenta la información procedente de un buen número de publicaciones sobre el comportamiento trófico de C. crocuta (ver Tabla

Localidad	Long.	Lat.	Referencia
Augabries Falls (South Africa)	20.21	-28.35	Rautenbach *et al* (1971)
Basse Casamance (Senegal)	-16.00	12.45	Dupuy (1973)
Etosha (Namibia)	15.42	-18.56	MAB
Kahuzi Biéga (Democratic Rep. Congo)	28.45	2.31	MAB
Kalahari Gemsbok N. P. (South Africa)	20.37	-25.68	MAB
Lac Kivú (Democratic Rep. Congo)	28.30	-2.00	Rahm *et al* (1963)
Lake Manyara (Tanzania)	35.60	-3.30	MAB
Mahale (Tanzania)	29.40	-6.12	MAB
Mamili (Namibia)	23.38	-18.23	MAB
Mlawula (Swaziland)	32.00	-26.00	MAB
Mount Kenya (Kenya)	37.19	0.10	Young *et al* (1993)
Namib-Naukluft Park (South Africa)	15.23	-24.37	MAB
Nechisar National Park (Ethiopia)	37.54	6.00	MAB
Parc National d'Odzala (D. Rep. Congo)	14.88	0.80	MAB
Pendjari (Benin)	1.50	11.00	MAB
Queen Elisabeth (Rwenzori)	29.92	0.40	MAB
Serengeti (Tanzania)	35.10	-2.25	Swynnerton (1958)
Skeleton Coast (Namibia)	13.20	-19.27	MAB
Weenen Game Reserve (South Africa)	30.40	-28.70	Bourquin *et al* (1995)
West Caprivi Game Reserve (Namibia)	22.37	-17.55	MAB
West Coast NP (South Africa)	18.13	-33.17	Avery *et al* (1990)
Zinave (Mozambique)	33.3	-21.15	Dalquest (1965, 1968)

Tabla 1: Relación de las localidades Africanas con presencia de *Crocuta crocuta* utilizadas para construir el listado faunístico de los mamíferos con los que cohabita esta especie (presas potenciales). MAB (Programa Man And Biosphere) es el acrónimo de la Base de Datos de la UNESCO sobre reservas de la Biosfera, accesible en la dirección http://www.ice.ucdavis.edu/bioinventory/bioinventory.html

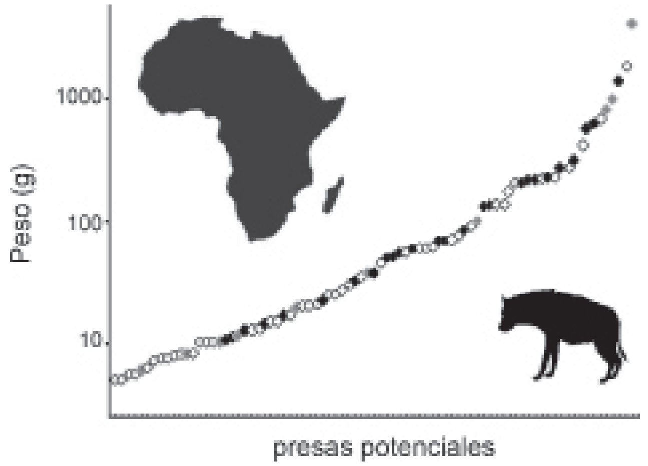


Figura 1: Patrón de consumo de presas por parte de *C. crocuta* en relación a los mamíferos existentes en el medio. La información para construir este gráfico proviene las referencias bibliográficas citadas en la tabla 1 y 2. Las especies han sido ordenadas en función de su tamaño y la escala del eje de ordenadas se ha transformado logarítmicamente para que las variaciones de la talla sean más patentes, como en los cenogramas propuestos por Valverde (1967). Las presas habituales aparecen señaladas en negro, las esporádicas en gris y los mamíferos de los cuales no se tienen datos que confirmen su consumo pero que están presentes en el medio están representados por rombos blancos. En la figura se puede comprobar como las hienas no seleccionan cualitativamente a sus presas, sino que pueden depredar sobre mamíferos de muy diferente talla.

2). Es importante señalar que, dada su gran flexibilidad trófica, una especie identificada como “habitual” en una localidad puede no ser presa común para otra población si en su territorio existe otro recurso más apetecible. El resultado de esta primera aproximación muestra que el espectro trófico de la hiena manchada en relación a las presas disponibles en el medio es realmente amplio (Fig. 1), pudiéndose alimentarse tanto de pequeños mamíferos como de grandes herbívoros. De esta manera, C. crocuta no parece seleccionar a sus presas en relación a su tamaño, por lo menos de manera cualitativa. Sin embargo, si analizamos la frecuencia de caza o la cantidad de biomasa aportada (Fig 2), entonces, tal y como sugiere la bibliografía, las presas de tamaño medio adquieren una importancia relevante. En la figura 2 se presentan como ejemplo las proporciones relativas de biomasa aportada por las especies consumidas en dos ecosistemas diferentes, una sabana (Masai Mara) y un desierto (Namib). En esta figura puede apreciarse que, cuantitativamente, las hienas de estas dos poblaciones dependen de presas comprendidas entre 160 y 270 kg, siendo presas habituales los ñus, cebras, topis y oryx (ver Hayward, 2006). De este modo, aunque el comportamiento oportunista de este carnívoro amplíe su espectro trófico, las presas preferenciales que conforman la base de su dieta en la actualidad están sesgadas hacia los tamaños medios. Este dato ha sido utilizado en el siguiente apartado para comprobar la variación temporal de la fauna de mesoherbívoros a lo largo del Pleistoceno, es decir, de las especies que conformarían la dieta de *C. crocuta* en ese tiempo.

Especie	Frecuencia	Peso (kg)	Referencia
Acinonyx jubatus	Accidental	50	Kamler *et al* (2007)
Aepyceros melampus	Frecuente	52	Hayward (2006)
Alcelaphus buselaphus	Frecuente	135	Breuer (2005)
Antidorcas marsupialis	Ocasional	37	Hayward (2006)
Cephalophus natalensis	Frecuente	14	Hayward (2006)
Cephalophus rufilatus	Frecuente	11	Breuer (2005)
Chlorocebus aethiops	Ocasional	6	Breuer (2005)
Civettictis civetta	Ocasional	12	Silvestre *et al* (2000)
Colobus guereza	Ocasional	10	Breuer (2005)
Connochaetes taurinus	Frecuente	215	Nowak (1999)
Damaliscus lunatus	Frecuente	133	Nowak (1999)
Diceros bicornis	Ocasional	1000	Nowak (1999)
Equus burchellii	Frecuente	315	Nowak (1999)
Equus zebra	Frecuente	273	Tilson *et al* (1980)
Erythrocebus patas	Accidental	8	Silvestre *et al* (2000)
Gazella thomsonii	Frecuente	22	Hayward (2006)
Gazella granti	Frecuente	55	Hayward (2006)
Genetta genetta	Ocasional	2	Silvestre *et al* (2000)
Genetta tigrina	Ocasional	2	Silvestre *et al* (2000)
Giraffa camelopardalis	Ocasional	825	Nowak (1999)
Hippopotamus amphibius	Frecuente	1425	Hayward (2006)
Hippotragus equinus	Frecuente	270	Breuer (2005)
Hystrix cristata	Frecuente	13	Breuer (2005)
Kobus kob	Frecuente	70	Silvestre *et al* (2000)
Kobus ellipsiprymnus	Frecuente	206	Breuer (2005)
Loxodonta africana	Ocasional	4250	Salnicki *et al* (2001)
Lycaon pictus	Accidental	25	Kamler *et al* (2007)
Oreotragus oreotragus	Ocasional	12	Hayward (2006)
Oryx gazella	Frecuente	225	Tilson *et al* (1980)
Ourebia ourebi	Frecuente	17	Breuer (2005)
Panthera pardus	Accidental	50	Silvestre *et al* (2000)
Papio hamadryas	Frecuente	32	Breuer, (2005)
Phacochoerus aethiopicus	Frecuente	70	Silvestre *et al* (2000)
Phacochoerus africanus	Ocasional	100	Breuer (2005)
Potamochoerus larvatus	Frecuente	60	Hayward (2006)
Raphicerus campestris	Frecuente	11	Hayward (2006)
Redunca redunca	Frecuente	50	Breuer (2005)
Sylvicapra grimmia	Ocasional	20	Hayward (2006)
Syncerus caffer	Frecuente	625	Breuer (2005)
Taurotragus oryx	Accidental	575	Salnicki *et al* (2001)
Tragelaphus scriptus	Frecuente	38	Breuer (2005)
Tragelaphus angasii	Accidental	85	Hayward (2006)
Tragelaphus strepsiceros	Frecuente	215	Hayward (2006)

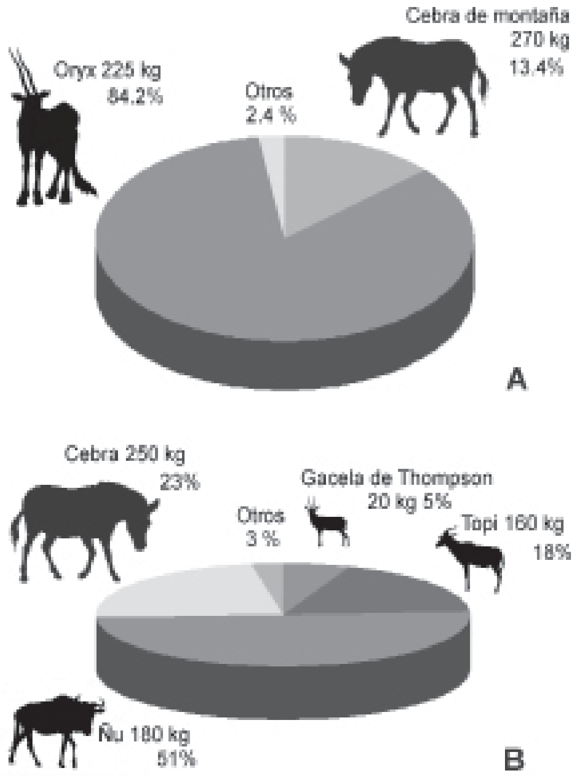


Tabla 2 (izquierda): Relación de las especies depredadas por la hiena manchada. En la tabla se indica la frecuencia de consumo, su peso y la referencia bibliográfica de la cual se ha obtenido la información.

Figura 2 (derecha): Aporte relativo de las diferentes presas a la dieta de las hienas en a) Masai Mara (de Cooper *et al*, 1999) y b) Namib (Tilson *et al*, 1980). En este gráfico se puede observar como la biomasa consumida por las hienas proviene, en más del 97%, de especies de tamaño medio.

5.- LAS COMUNIDADES DE HERBÍVOROS DEL PLEISTOCENO

Uno de los aspectos diferenciales de las comunidades de mamíferos del Pleistoceno ibérico respecto a los ecosistemas actuales es su gran diversidad, con un rango de tallas extremadamente amplio, como se puede comprobar en la figura 3. En este gráfico, elaborado a partir de la propuesta taxonómica de Van der Made (2005), se resumen las faunas de herbívoros que habitaron la península en el último millón de años, ordenadas según categorías de peso. Para tener una visión más detallada de las especies presentes en los diferentes periodos hemos examinado los listados faunísticos de los mamíferos registrados en 9 yacimientos ibéricos del Pleistoceno Inferior, 28 del Pleistoceno Medio y 148 del Pleistoceno Superior, resumiendo la información obtenida en la figura 4. En el gráfico superior (Fig. 4A) aparecen las especies que habitaron durante el Pleistoceno Temprano, momento en el cual se ha datado presencia más antigua de *C. crocuta* (García, 2001). La figura 4B muestra un escenario de mediados del Pleistoceno Medio, y la 4C es el resultado de la compilación de los registros faunísticos de finales del Pleistoceno Tardío. En todas ellas se puede comprobar como siempre ha existido un

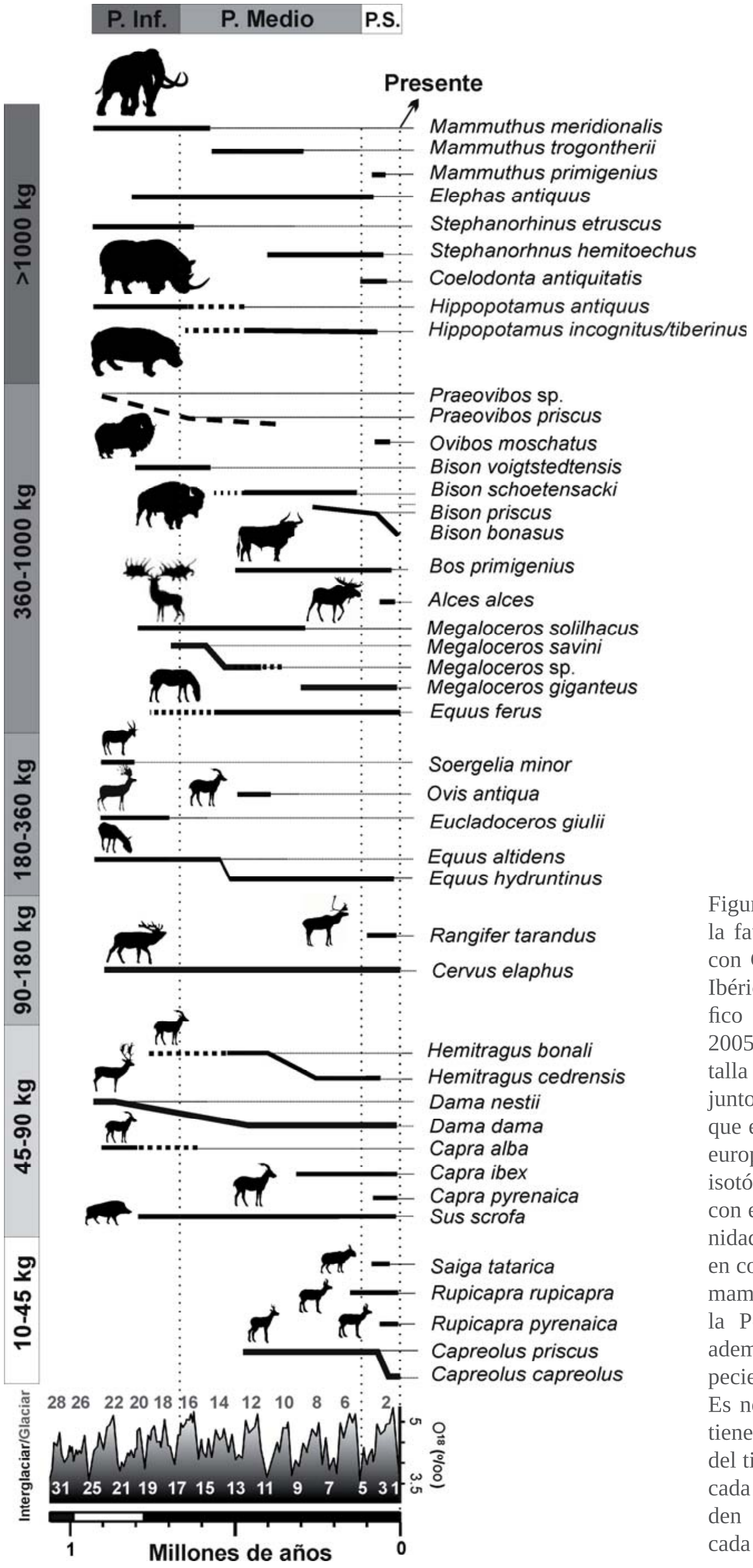


Figura 3: Distribución temporal de la fauna de herbívoros que cohabitó con Crocuta crocuta en la Península Ibérica durante el Pleistoceno (gráfico modificado de Van der Made, 2005). En la figura se representa la talla aproximada de cada especie, junto con el intervalo temporal en el que estuvo presente en el continente europeo y su relación con los estadios isotópicos del oxígeno (y por lo tanto con el clima). Se trata de unas comunidades excepcionalmente diversas en comparación con las comunidades mamíferos que actualmente pueblan la Península Ibérica, que destacan además por el elevado número de especies de mamíferos de gran tamaño. Es necesario señalar que las siluetas tienen un papel ilustrativo, indicando del tipo de mamífero representado en cada línea evolutiva, y que no pretenden ser ilustraciones fidedignas de cada especie.

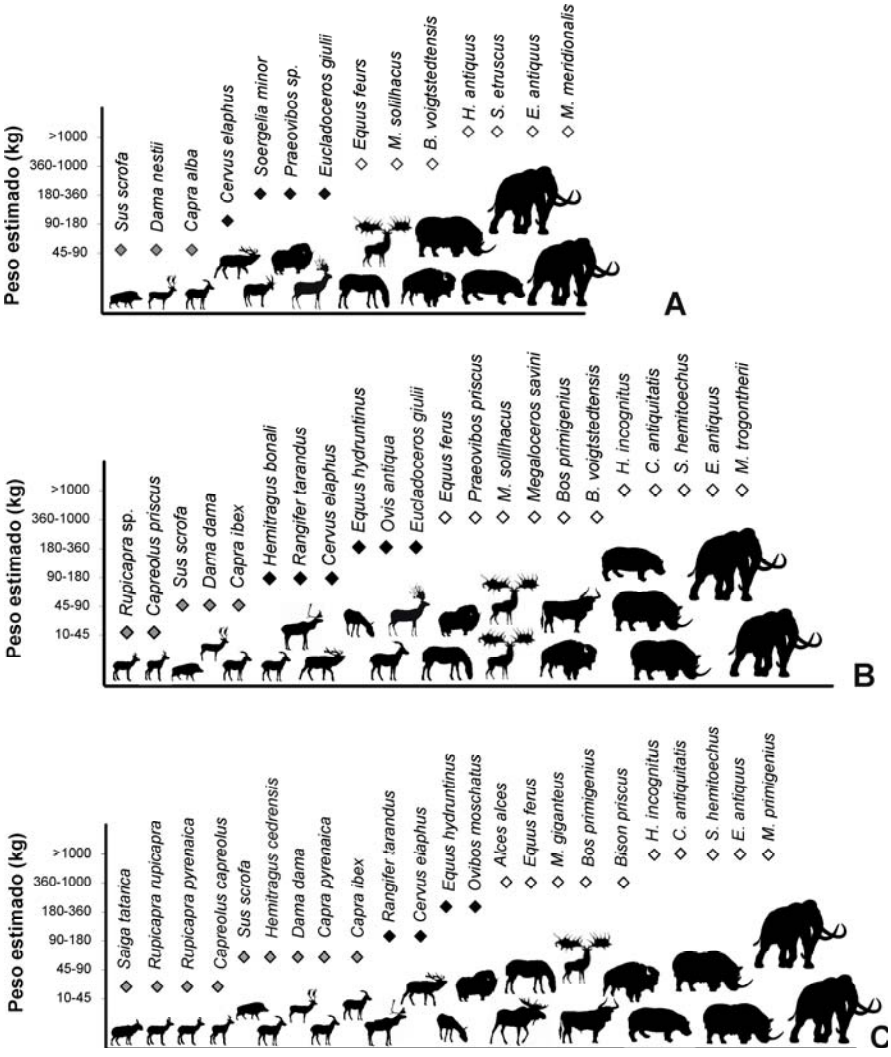


Figura 4: Distribución de tamaños de las especies registradas en Europa durante a) el Pleistoceno Temprano, b) mediados del P. Medio y c) principios del Pleistoceno Tardío. La riqueza de las comunidades de mamíferos del Pleistoceno europeo es mucho mayor que la que existe hoy en día. De esta manera, la hiena manchada contaría con 4 especies de talla óptima (señaladas con un rombo negro) durante el P. Temprano, 6 en el P. Medio y 4 en el P. Tardío. Además, en todo momento existe una diversa fauna de megaherbívoros (señalada con rombos blancos) que podría haber utilizado como recurso esporádico a través del carroñeo oportunista o de la caza de inmaduros, así como mamíferos de menor talla.(señalados rombos grises) Las siluetas de los tipos de mamífero se han empleado para visualizar la riqueza y composición ecotípica de cada escenario.

buen número de presas potenciales dentro del rango de tamaño comprendido entre los 90 y los 360 kg (señaladas con un rombo negro), que sería el rango de tallas que incluye a las presas que las hienas seleccionan preferentemente en la actualidad. Además de estas especies, habría también una gran variedad de animales de mayor talla (señaladas con un rombo blanco) y de especies pequeñas de ungulados (rombos grises). Al mismo tiempo, se puede visualizar como las especies que conformarían la base de la dieta de la hiena habrían ido cambiando en el tiempo. Durante el Pleistoceno Temprano existirían 4 especies dentro del rango óptimo (*Cervus elaphus*, *Soergelia minor*, *Praeovibos* sp. y *Eucladoceros giulii*). En el Pleistoceno Medio este número asciende a 6 (*Hemitragus bonali*, *Eucladoceros giulii*, *Cervus elaphus*, *Equus hydruntinus*, *Ovis antiquia* y *Rangifer tarandus*, esta última especie restringida al norte peninsular (Van der Made, com. per.), mientras que durante el Pleistoceno Tardío disminuye otra vez a 4 (*Rangifer tarandus* (en el norte), *Cervus elaphus*, *Equus hydruntinus* y *Ovibos mostachus*). A estas especies hay que añadir la variedad de animales de talla pequeña, que también habrían sido presas potenciales para las hienas. Además, durante todo este intervalo temporal las hienas habrían dispuesto de más de una docena de especies de megaherbívoros (>400 kg) que podrían haber utilizado como recurso esporádicamente, bien mediante una caza oportunista, bien a través del consumo de carroña. Si restringimos la ventana temporal de análisis y nos centramos en las presas disponibles durante el estadio isotópico 2, es decir, durante el último máximo glaciar, podemos observar como el número de especies dentro del rango de tamaños óptimo sigue siendo 4 (las mismas que a comienzos del Pleistoceno Tardío), y que aun persiste una diversa fauna de megaherbívoros (Fig. 5A). Para la realización de esta figura nos hemos basado en los listados faunísticos de 71 yacimientos de la Península Ibérica data- dos dentro del estadio isotópico 2. Además hemos realizado una pequeña aproximación para describir el espectro trófico de las hienas en ese momento, basándonos en los registros provenientes de dos yacimientos interpretados como cubiles; Labeko Koba, niveles VII y IX (Arrizabalaga Valbuena *et al.*, 2000; Altuna *et al.*, 2000) y Grota do Caldeirao, niveles musterienses (Davis, 2002). Las especies que aparecen en estos dos últimos yacimientos muestran que el patrón de tamaños de las presas presumiblemente consumidas por las hienas era considerablemente diverso (sus siluetas aparecen en gris en la figura), lo cual concuerda con el espectro de presas depredadas por *C. crocuta* en la actualidad. Entre las especies identificadas en estos cubiles, las que se incluyen en el rango de tamaños óptimo actual (90-360 kg) serían, dos cérvidos (*Cervus elaphus* y *Rangifer tarandus*) y un équido (*Equus hydruntinus*). Por lo tanto, si recurrimos al actualismo para interpretar estos datos, se podría proponer una hipótesis trófica en la que estas tres especies conformarían la base de la dieta de estas dos poblaciones de hienas, mientras que el resto de los mamíferos registrados serían consumidos de manera esporádica en función de las oportunidades del medio. Si continuamos avanzando en el tiempo y analizamos los listado faunísticos de finales del Pleistoceno (10000-14000 B.P.), momento en el cual se ha datado el último registro de hiena peninsular (Carrión *et al.*, 2001), podemos observar que el número de presas dentro del rango de tamaño óptimo disminuye drásticamente (ver Fig. 5B). Ya sólo existe una especie (*Cervus elaphus*) dentro del rango de tallas seleccionado por las hienas actualmente, y, debido a su gran porte, *Equus ferus* y *Bos primigenius*, aun presentes en el ecosistema, debieron haber sido consumidos preferentemente antes de alcanzar la edad adulta. La información sobre la ocurrencia

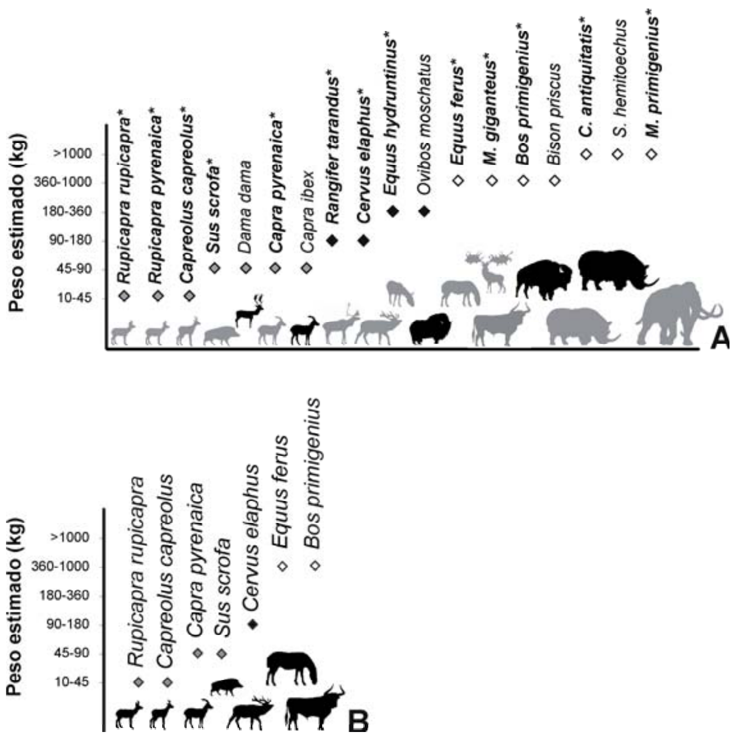


Figura 5: a) Distribución de tamaños de mamíferos durante el estadio isotópico 2. Las especies dentro del rango de tamaños apropiado para las hienas aparecen señaladas con un rombo negro, las de talla mayor con uno blanco y las menores con un rombo gris. Además se han resaltado con un asterisco los nombres de las especies registradas en dos yacimientos identificados como cubiles de hienas (los niveles VII y IX de Labeko Koba (Altuna y Mariezkurrena, 2000) y los niveles musterienses de la Gruta do Caldeirao (Davis, 2002)). Al mismo tiempo, la silueta de estas especies es gris, para diferenciarlas de las especies ausentes en estos yacimientos pero presentes en el medio (en negro). A partir de esta figura podemos suponer, en base al actualismo, que las poblaciones de hiena manchada que habitaban estas dos cuevas podrían haber basado su dieta en 3 especies, Cervus elaphus, Rangifer tarandus y Equus hydruntinus. b) distribución de tamaños los ungulados que poblaban la Península Ibérica a comienzos del Holoceno (hace 10.000 años). En este último escenario, la única especie dentro del rango de tamaños óptimo para la hiena manchada es el ciervo (rombo negro). Es patente como las extinciones de finales del Pleistoceno han empobrecido de manera drástica los ecosistemas peninsulares, quedando solamente una pequeña submuestra de la gran diversidad de herbívoros que habrían poblado estas latitudes durante más de un millón de años.

de estas dos últimas especies en la península una vez iniciado el Holoceno es incierta, por este motivo hemos considerado su posible extinción, optando por el escenario más adverso para la supervivencia de un gran carnívoro. Ciertamente, teniendo en cuenta su carácter oportunista, las hienas podrían haber ampliado su espectro de presas hacia tamaños más pequeños tras la desaparición de la fauna de megaherbívoros, e incluso podrían haber depredado sobre el ganado doméstico. Sin embargo, esta última hipótesis debe ser descartada, ya que la introducción de la domesticación en la Península Ibérica no se produjo antes de la segunda mitad del octavo milenio B.P. (Esquembre *et al.*, 2008). Por otro lado, de las cuatro presas potenciales de tama-

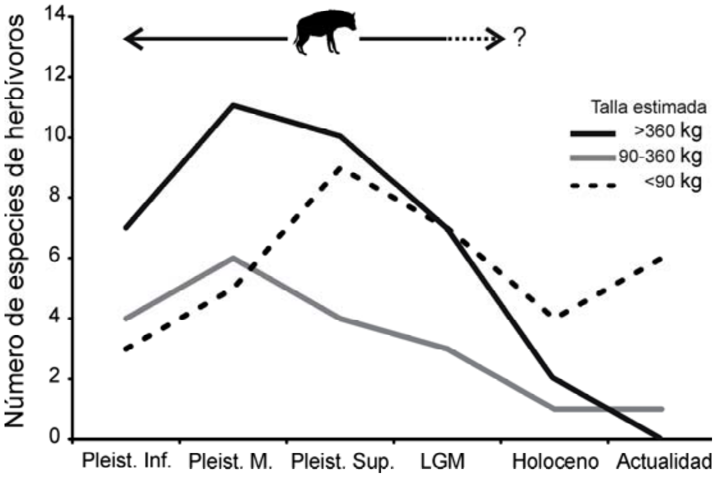


Figura 6: Relación entre el número de especies de herbívoros (divididos en tres tallas: pequeños, medianos y megaherbívoros) y el tiempo. En esta figura se puede comprobar como los últimos registros de C. crocuta (Carrion et alii, 2001), coinciden en el tiempo con un empobrecimiento en las faunas de ungulados peninsulares. El acrónimo LGM, Last Glacial Maximum, se refiere al último máximo glaciar.

ño comprendido entre los 30 y los 90 kg, dos (*Rupicapra rupicapra* y *Capra pyrenaica*) están adaptadas a la vida en alta montaña. Finalmente, conviene recordar que el gamo (*Dama dama*) y el muflón (*Ovis musimon*), especies que habitan la Península Ibérica en la actualidad, son especies introducidas en tiempos históricos y que, por lo tanto, no estarían presentes a mediados del Holoceno (Mitchell-Jones *et al.*, 1999). Por tanto, las únicas presas de las que dispondría una hipotética población relicta de esta especie que hubiese sobrevivido durante el Holoceno serían el ciervo, el corzo y el jabalí. A modo de resumen en la figura 6 se recopila de forma esquemática la información sobre el número y tamaño de las especies presentes en la Península Ibérica a lo largo del Pleistoceno y hasta el presente. En ella se puede observar que la diversidad de herbívoros de talla media y grande aumenta durante el Pleistoceno Medio y como a partir de ese momento el número de especies cae de manera continuada hasta llegar a la situación actual, en la que no existen especies de megaherbívoros y solamente hay un ungulado de talla media (*Cervus elaphus*). La riqueza de especies de tamaño pequeño sigue un patrón diferente, alcanzando su máximo en el Pleistoceno Medio, descendiendo hasta el Holoceno, y aumentando su número en el presente, consecuencia en parte de la naturalización de especies introducidas por los humanos (ej. *Dama dama*, *Ovis musimom* (Mitchell-Jones *et al.*, 1999)). En esta figura se puede visualizar claramente como la desaparición de la hiena coincide con un descenso generalizado del número de especies de presas, por ello cabe preguntar- se si la escasez de recursos tróficos podría haber sido la causa de su extinción.

6.- ¿UN ECOSISTEMA MEDITERRÁNEO ACTUAL SERÍA CAPAZ DE MANTENER UNA POBLACIÓN DE C. CROCUTA?

Para comprobar si un ecosistema mediterráneo con una densidad normal de herbívoros pudo haber mantenido una población de *C. crocuta* hemos aplicado la función propuesta por Carbone y Gittleman (2002). Estos autores identificaron una relación directa entre el número (N) y el peso (P) de los predadores que mantiene un sistema ecológico por unidad de biomasa de presas (10000 kg) de modo que:

N = 89.1 x P-1.05

De acuerdo con esta fórmula, son necesarios 10000 kg de biomasa de presas para sustentar cerca de 90 carnívoros de talla pequeña (1 kg), o un solo gran carnívoro (de alrededor de 90 kg). De esta manera, nos hemos servido de los datos de densidad de *Cervus elaphus* en el Parque Natural de la Sierra de Baza, situado en la provincia de Granada, como modelo representativo de un ecosistema mediterráneo. Este entorno natural cuenta con una importante población de ciervos: 1800 ejemplares en un área de 523 Km2, es decir, una densidad aproximada de 3.5 ind/km2, cifra que está dentro del rango normal para esta especie (Granados *et al.*, 2001), con un peso medio de 137.5 kg. De este modo, la biomasa de presas disponible en el Parque Natural de la Sierra de Baza es de 247500 kg. Además hemos utilizado el peso medio de las hienas sudafricanas (70 kg), que son las que actualmente tienen individuos de mayor talla (Reynolds, 2007), a fin de ajustar los cálculos a las estimas que predicen un tamaño relativamente mayor que el actual para las hienas del Pleistoceno europeo, relacionado con las oscilaciones climáticas (Klein *et al.*,1989). A partir de estos datos, hemos aplicado la fórmula de Carbone y Gittleman modificando el exponente según su intervalo de confianza al 95% (entre -1.250 y - 0.854). De este modo, el total de individuos de *C. crocuta* predichos para este ecosistema mediterráneo tipo oscilaría entre 11 y 58 ejemplares, con una estima para el valor medio de 25 ejemplares. Es decir, a pesar del empobrecimiento de las faunas, un ecosistema mediterráneo con una densidad de cérvidos como la existente en el Parque Natural de la Sierra de Baza podría mantener, potencialmente, una población de hiena manchada promedio de 25 ejemplares. Este inesperado resultado nos llevó a plantearnos una segunda cuestión. ¿Qué pasaría si las hienas hubiesen tenido que competir por los recursos con otro depredador? ¿Sería la competencia interespecífica un factor plausible para explicar de la extinción de esta especie? Para comprobar esta hipótesis añadimos una especie más al análisis, el lobo (*Canis lupus*), único carnívoro de gran tamaño que persiste en la península, con un peso medio de 30 kg (Palomo *et al.*, 2005). Asumiendo un reparto equitativo de la biomasa de presas disponibles en la Sierra de Baza entre ambas especies

Capacidad de carga de un ecosistema mediterráneo de 523 km2

A: sin competencia
(BM presas disponible = 247500 kg)

límites de confianza	BM potencial de predadores de 70 kg	*C. crocuta*
Max. (95%)	4100.5 kg	58 indiv.
Medio	1783.19 kg	25 indiv.
Min. (95%)	762.39 kg	11 invid.

B: con competencia
(BM presas disponible para cada especie = 123750 kg)

límites de confianza	BM potencial de predadores de 70 kg	*C. crocuta*
Max. (95%)	2050.25 kg	30 indiv.
Medio	891.59 kg	13 indiv.
Min. (95%)	381.19 kg	5 indiv.
límites de confianza	BM potencial de predadores de 30 kg	*Canis lupus*
Max. (95%)	1811.68 kg	60 indiv.
Medio	930.17 kg	31 indiv.
Min. (95%)	471.13 kg	16 indiv.

Tabla 3: Resultados de la aplicación de la ecuación de Carbone y Gittleman (2002) para el Parque Natural de la Sierra de Baza (Granada), simulando dos escenarios diferentes, uno sin competencia (A) y otro en el *Crocuta crocuta* y *Canis lupus* comparten los recursos tróficos (B). En este territorio de 523 Km2 la densidad de *Cervus elaphus* (137.5 kg) es de 3.5 ind/km2, por lo que la biomasa (BM) potencial de presas disponibles para la hiena manchada será de 247500 kg en el escenario A y de 123750 kg en el B. Tanto si consideramos un escenario en el que la hiena manchada fuese el único carnívoro (situación A), como compartiese los recursos con otro predador, *Canis lupus* (situación B), *Crocuta crocuta* podría sobrevivir y mantener una población de 11-58 hienas habitando en solitario, o de 5-30 hienas y 16-60 lobos si ambos predadores tuviesen que competir por los mismos recursos.

(123750 kg), después de aplicar la ecuación con los nuevos valores para los parámetros, y, a pesar de la influencia de un competidor, el resultado sigue siendo favorable para la presencia de la hiena manchada. En este segundo escenario tendríamos un número mínimo de 5 ejemplares de *C. crocuta*, y un máximo de 30 (valor medio=12), cohabitando con una población de entre 16 y 60 lobos (valor medio=31) (Tabla 3). El tamaño de las manadas de hiena manchada actuales oscila entre los 3 y los 54 individuos (Mills *et al.*, 1998), mientras que los lobos ibéricos forman manadas de 5 a 10 individuos y tienen territorios de 100 a 500 km2 (Palomo *et al.* , 2005). Es decir, aun en el caso de que las hienas tuvieran que competir con los lobos y ambos dependieran completamente de las poblaciones de ciervos, una densidad de *C. elaphus* como la existente en el Parque Natural de Sierra de Baza en la actualidad podría sustentar una manada de cada una de estas especies. Conviene recordar que los restos fósiles del Pleistoceno europeo de *C. crocuta* muestran que la especie ha variado de tamaño a lo largo del tiempo dependiendo de las condiciones climáticas (Klein *et al.*,1989) y que para estos cálculos se ha utilizado un sólo peso (70 kg), asumiendo que las poblaciones actuales de mayor tamaño tendrían una talla similar a las hienas de finales del Pleistoceno. En este sentido, aumentar o disminuir el peso estimado de las poblaciones de hiena manchada del Pleistoceno significaría una variación cuantitativa en la capacidad de carga predicha para nuestro ecosistema, lo cual podría afectar al principal resultado de este artículo. Para resolver este conflicto se ha calculado el peso necesario para que el número mínimo de individuos de *C. crocuta* predicho sea menor de tres, que es el tamaño mínimo registrado como grupo estable por la IUCN (Mills *et al.*, 1998). El resultado es de 200 kg para el escenario sin competidores y 115 kg en el caso de compartir el ecosistema con *C. lupus*. Las medidas craneométricas sitúan a las hienas europeas de 30000 YBP en el extremo superior del rango de tamaño actual, pero dentro de los límites de la varianza de las poblaciones africanas (Dockner, 2006). Por este motivo, las estimas de peso que llevarían a la especie a la extinción por falta de recursos (200 y 115 kg) parecen demasiado elevadas para ser realistas. Además, en nuestros cálculos no hemos incluido la presencia de otros herbívoros (como podrían ser el corzo o el jabalí), los cuales acrecentarían la biomasa disponible en el ecosistema con el consecuente aumento de las posibilidades de supervivencia de cualquier predador.

7.- CONCLUSIONES

Nuestras estimas están basadas, inevitablemente, en una interpretación regida por el actualismo biológico, pero sugieren que el número de presas potenciales disponibles para la hiena manchada en la Península Ibérica se mantuvo relativamente estable a lo largo del Pleistoceno Medio y Superior, y que éste disminuyó drásticamente a finales del Pleistoceno. No obstante, nuestros cálculos demuestran que, aun así, esas comunidades de herbívoros empobrecidas podrían haber sostenido poblaciones estables de hiena manchada, aunque el tamaño de sus individuos estuviese sesgado hacia el extremo superior del rango actual. De este modo, un ecosistema de tipo mediterráneo, en el cual se encontrasen las especies que sobrevivieron hasta el Holoceno, podría mantener poblaciones de *Crocuta crocuta*, considerando incluso la presencia de un competidor como *Canis lupus*. Estos sencillos cálculos sugieren que, al igual que los cambios climáticos (Varela *et al.*, 2010), la disminución de la diversidad de ungulados a finales del Pleistoceno no parece haber sido un factor de relevancia capital para explicar la extinción de la hiena manchada en la Península Ibérica. ¿Por qué desaparecieron entonces las poblaciones de *C. crocuta*? Ciertamente, la fuerte dependencia de una sola presa, *Cervus elaphus*, podría haber contribuido a extinguir unas poblaciones relictas y fragmentadas. Pero probablemente la respuesta a esta pregunta necesita del concurso sinérgico de varios factores, entre los cuales sería adecuado incluir también el efecto de Homo sapiens como competidor.

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Capítulo 5:

Is current climatic equilibrium a guarantee for the transferability of distribution model predictions? A case study of the spotted hyena

1.- ABSTRACT

The transferability of species distribution models requires that species show climatic equilibrium throughout their entire distribution area. We test this assumption for the case of the spotted hyena, *Crocuta crocuta*, a large carnivore that has shifted its distribution over the last 100,000 years from a widespread Eurasian and African range to its current geographical distribution, restricted to the Sub-Saharan areas of the African continent. The current realized distribution of *C. crocuta* was estimated using presences and reliable absences as well as climatic, land-cover and anthropic variables as predictors. The potential distribution was estimated using presences and a set of pseudo-absences selected from localities outside climatically suitable localities, with only climatic variables serving as predictors. The current potential distribution was transferred to the Last Interglacial period (126,000 yr bp) using the palaeoclimatic data yielded by the GENESIS 2 general circulation model, and validated with European fossil

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data. Generalized linear models were used on all occasions. Our results indicate that the climatic variables are able to predict the current distribution of the species with high accuracy. The geographical projection of this model indicates that the species is distributed over almost all of its potential suitable area, which allows us to suppose that the current distribution of this species is in climatic equilibrium. However, the time transference of model predictions for the western Eurasian region reveals almost no suitable conditions for hyenas, despite the widespread presence of *C. crocuta* fossil remains on this continent during the Last Interglacial period. Therefore, even when model results suggest a climatic equilibrium for a species distribution, the time transferability of such models does not necessarily provide realistic results. This occurs because the current geographical range does not allow estimations of all of the environmental requirements of a species. Therefore, any model trained with current data risks underestimating the potential suitable environmental and geographical range for species in a new area or time period.

2.- INTRODUCTION

Distribution is a dynamic characteristic of species that depends on a wide variety of environmental and contingent processes operating at different spatial and temporal scales (Maurer *et al.*, 2002). Despite the difficulties involved in deriving causal processes from correlations, the available data on distribution are frequently related to a variety of explanatory variables in order to identify probable influential factors (Rahbek *et al.*, 2001), generate distributional hypotheses for changing scenarios (Araújo *et al.*, 2005), or establish hypotheses about the current geographical range of a species when presence data are scarce (Guisan *et al.*, 2000). One of the most common sources of uncertainty in species distribution models (SDMs) derives from the lack of reliable absence information. Species may be absent from modelpredicted favourable places owing to factors such as biotic interactions, dispersal limitation, extinctions, or historical processes (Pulliam, 1988, 2000; Ricklefs *et al.*, 1993; Hanski, 1998). On a geographical scale, most species are unable to colonize all potentially suitable areas. The inability to recolonize former distributional ranges after the Pleistocene glaciation events (Svenning *et al.*, 2007) and range-size contractions as a consequence of human activities (Channell *et al.*, 2000) are two well-established examples of the roles played by these restrictive forces in preventing the full geographical filling of environmentally suitable areas. Fortunately, this drawback apparently does not invalidate one of the main abilities of SDMs: to construct potential distribution hypotheses capable of estimating the total territory that can be inhabited by a species according to a set of predictor variables (see Soberón *et al.*, 2005; Peterson, 2006; Soberó n, 2007; Chefaoui *et* *al.*, 2008; Jiménez-Valverde *et al.*, 2008). This approach is useful for suggesting the likely future distribution of invaders (Peterson, 2003), for estimating the degree of species equilibrium with current environmental variables (Svenning *et al.*, 2004), and for suggesting probable distribution shifts that might occur under a changing climatic scenario (Jiménez-Valverde *et al.*, 2007a). However, these potential distribution models have two main drawbacks. First, they constitute simulations that cannot be validated using real distributional data, since it is always possible to find a favourable place in which the species is absent (i.e. the absence in a favourable place cannot be used to test the accuracy of these potential model predictions). Second, as potential distribution models are parameterized with data from the species' native range, which is influenced by biotic or historical constraints, they may actually underestimate the potential range of a species. This happens because SDMs are built with the implicit assumption that the species occurs in all environmentally suitable localities; that is, in equilibrium with the environmental conditions (Brereton *et al.*, 1995; Dormann, 2007; Jiménez-Valverde *et al.*, 2008). These two drawbacks hinder both the evaluation and the transferability of potential distribution simulations to different areas and time periods, especially if predictions are based on explanatory variables lacking a functional basis (Austin, 2002; Dunne *et al.*, 2004; Kearney *et al.*, 2004; Kearney, 2006; Vanreusel *et al.*, 2007). In this paper we examine the accuracy of SDMs when transferred. For that purpose, we build two different distribution models, one to estimate the realized distribution of the spotted hyena, *Crocuta crocuta* (Erxleben, 1777), and to test whether its current distribution is in equilibrium with climatic conditions, and another to identify potential environmentally suitable areas outside its current African distribution, specifically in the Western Palaearctic region, through geographical extrapolation of model results. The accuracy of these representations of potential distribution was evaluated by examining the past distribution of the spotted hyena in Europe during the Last (Eemian) Interglacial period (126,000 yr bp), the most recent period with similar climatic conditions to the current ones. The potential distribution model calibrated with current distribution and environmental data was transferred to the Last Interglacial period by using the climatic variables derived from the general circulation model (GCM) GENESIS 2 (Thompson *et al.*, 1997; Vavrus, 2001). By projecting a model fit with current environmental data onto past data, we assessed whether it is possible to predict the past distribution reliably when the current distribution apparently shows equilibrium with the environment, a basic assumption for the transfer of model predictions (Guisan & Thuiller, 2005). The specific objectives of this study were: (1) to discern the main variables accounting for the current known distribution of *C. crocuta*; (2) to perform a simulation of the climatic potential distribution of this species for the Afrotropical and Western Palaearctic regions, as well as one for the realized distribution in Africa (taking into account relatively reliable absence data); and (3) to test the accuracy of the potential model distribution predictions when they are transferred in time and space. The obtained results are used to discuss the necessary precautions needed in transferring model predictions and the frequent inability to assess the equilibrium state when the predicted distributions are based exclusively on current distribution data.

3.- MATERIALS AND METHODS

3.1.- Basic information on the target species

The spotted hyena (*Crocuta crocuta)* is an opportunistic hunter and scavenger, preying mainly on ungulates (see Cooper *et al.*, 1999; Trinkel *et al.*, 2004 or Hayward, 2006). The current geographic distribution of C. crocuta is constrained to the Sub-Saharan area of the African continent (Mills *et al.*, 1998), where it prefers inhabiting open and dry habitats, though a few individuals can be found in the rain forests of Equatorial Guinea (Frank *et al.*, 1995; Mills *et al.*, 1998). *Crocuta crocuta* appeared in the African fossil record around 4 Myr BP (Turner, 1990), in Asia at 1.4 Myr BP (Dennell *et al.*, 2005), and reached Europe around 1 Myr BP (Werdelin *et al.*, 1991; Mills *et al.*, 1998; García *et al.*, 2001). *C. crocuta* was a ubiquitous carnivore during

Crocuta crocuta. Photography: Sara Varela

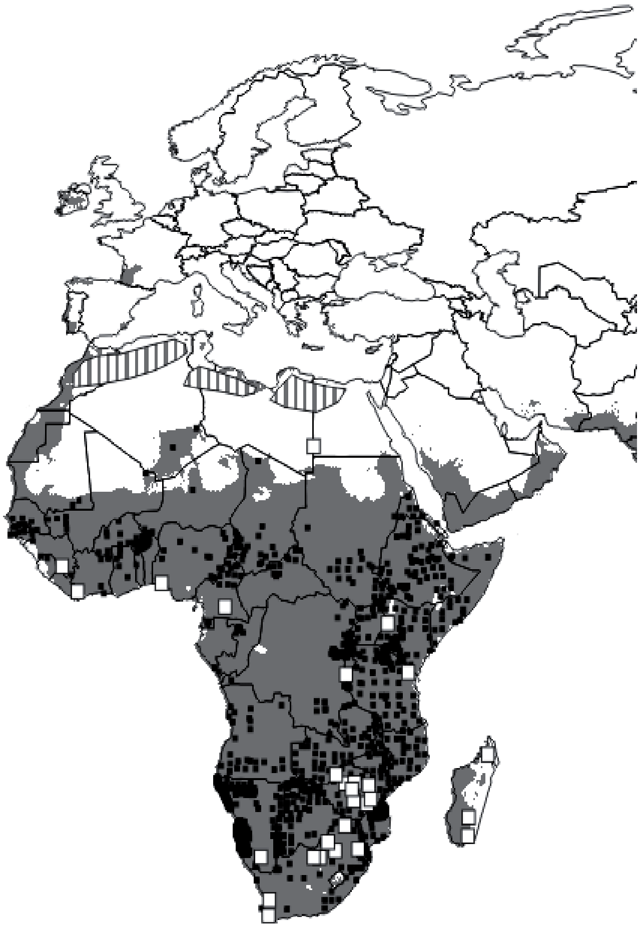

Figure 1 Presence and absence data locations for *Crocuta crocuta*. Presence data are plotted as black squares, and absences as white squares and as three striped polygons located in northern Africa. Pseudo-absences were selected randomly outside the multidimensional climatic envelope model (grey area).

the European Pleistocene and has been recorded at hundreds of palaeontological sites, from both cold and warm periods (Bologna et al., 1994; Altuna & Mariezkurrena, 2000; Testu, 2006). DNA studies have shown that African and Eurasian spotted hyena populations were connected on several occasions during the Pleistocene (Rohland *et al*., 2005). The most recent fossil evidence suggests that the European spotted hyena population went extinct at the beginning of the Holocene (10 kyr BP), with the last occurrence sites located near the Pyrenees Mountains (Brugal, 1981; Carbonell *et al*., 1996; Muñoz *et al*., 1997; Nadal *et al*., 1997) and also in England (A. Currant, pers. comm.).

3.2.- Data origin

Presence data for *C. crocuta* were selected from faunal lists of African National Parks and from the IUCN Conservation Plan for Hyenas (Mills *et al*., 1998), the GBIF database and other specific studies in the literature (see Fig.1). The climatic information in the associated presence localities can vary considerably depending of the resolution of the used data used. Because of this, we select the appropriate resolution (cells of approximately 100 km2) according to the amount of territory necessary to obtain self-sustained populations (between 13 and 1095 km^2; see Trinkel *et al*., 2006). For presence data derived from National Parks, all the cells in-

Last Interglacial fossil sites	Longitude	Latitude	Reference
Bacon Hole	-4.07	51.56	Currant *et al*, 2001; Gilmour, 2007
Burtle Beds	-2.42	50.99	Currant, 2004
Cava Nuzzo	18.27	40.13	Bologna et al, 1994
Grotte de l´Observatoire	7.42	43.73	Testu, 2006
Malarnaud	14.17	43.52	Dufour, 1989
Taubach	11.38	50.95	Von Koenigsvald et al, 2000
Victoria Cave	-2.29	54.06	Gilmour, 2007
Bynagady	48.00	40.50	Markova, 1995
Dziadowa Skala Cave	19.50	50.50	Kowalski, 1959

Table S1: List of the European Last Interglacial localities with fossil data of *Crocuta crocuta* and bibliographical sources from which these data were extracted.

cluded in the polygon of this territory were used as presence points. Reliable absences were also extracted from fauna lists of African National Parks and from the IUCN project “Conservation Plan for Hyenas” (Mills *et al*., 1998). As *C. crocuta* is a conspicuous and large mammal that is easy to identify, we assume that the lack of observations of this species in a territory strongly validates the correctness of these absences. Three North African polygons were also drawn outside the recent distribution of spotted hyenas described in the IUCN “Conservation Plan for Hyenas” project, and in countries with no evidence of species presence. In total, 2814 cells of 0.08 x 0.08 were selected as presences and 13,727 cells of 0.08 x 0.08 as absences from a total of 766,452 cells (Western Palaearctic and Africa; see Fig. 1). The fossil dataset was collected from bibliographic sources, using only those accurately and strictly dated for the Last Interglacial period (126,000 ± 3000 yr BP) see table S1.

3.3.- Current explanatory variables

Nineteen current bioclimatic variables derived from the WorldClim interpolated map database (version 1.4, http://www.worldclim.org; Hijmans et al., 2005) were used as climatic predictors: annual mean temperature, mean diurnal range, isothermality, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter. Furthermore, to consider the relevance of non-climatic factors, 14 land-cover features (woodland, evergreen needleleaved forest, deciduous needleleaved forest, mixed forest, evergreen broadleaved forest, deciduous broadleaved forest, open shrubland, closed shrubland, wooded grassland, grassland, bareground, cropland, water, and urban), two measures of anthropic environmental impact, and one simple binomial variable (Barrier) were included to represent the likely barrier effect of the Sahara Desert. The used anthropic variables were distance to populated areas (places with more than 200 inhabitants/km2) and distance to wilderness areas (those lacking anthropic impact). They were created from the Gridded Population of the World project of the Center for International Earth Science Information Network (version 3; see http://sedac.ciesin.org/gpw) and the World Wilderness Areas data set of the UNEP/GRID (see http://www.grid.unep.ch). They represent the distance between either the populated or the wilderness areas to other pixels of the map. The Idrisi Kilimanjaro GIS software was used in all these calculations (Clark Labs, 2003). Lastly, a simple binomial variable (Barrier) was included to represent the likely barrier effect of the Sahara Desert. This dummy variable has a score of one for all of the African cells except for those located from the southern boundary of the desert to the Mediterranean coast. This boundary was defined as the cells with less than 100 mm of annual precipitation and calculated with the Idrisi Kilimanjaro GIS software (Clark Labs, 2003). All variables (except the binary land-cover variables and the barrier) were standardized to means of zero and standard deviations of one to eliminate the effect of varying measurement scales.

3.4.- Palaeoclimatic data

Palaeoclimatic data were downloaded from the GENESIS 2 GCM experiments (http://ccr.aos.wisc.edu/). The Last Interglacial climate simulation was performed by Vavrus (2001) with the GENESIS 2 GCM (Thompson *et al.*, 1995). The simulation uses a mixed-layer slab ocean with dynamic sea ice, carbon dioxide levels are prescribed at 345 p.p.m. (Persaram Batra, pers. com.). Simulated past temperatures in Eurasia show reasonable agreement with palaeotemperatures inferred from pollen and plant macrofossils (Kaspar *et al.*, 2005). Two explanatory variables were used as predictors in these models according to previous results on the relevant variables able to explain the current distribution of the species: annual temperature range and annual precipitation. Annual temperature range was calculated as the difference between the January and August atmospheric temperature of the lowest two meters (absolute value), while annual precipitation was the result of the sum of the monthly precipitation values. In this case we use both current and past GENESIS 2 GCM climatic data at a resolution of 4.5ºx7.5º cells.

3.5.- Modelling methods and statistical analysis

Many different techniques are currently available to model species distributions (see Guisan *et al*., 2000; Scott *et al*., 2002), either considering only presence data (niche envelope models) or considering also absence data (group discrimination techniques). In general, group discrimination methods seem to offer more accurate predictions (Hirzel *et al*., 2001; Brotons *et al*.., 2004; Segurado *et al*., 2004), although the type of absence data used to calibrate the model strongly influences the type of distributional simulation obtained (see Soberón *et al*., 2005; Peterson, 2006; Chefaoui *et al*., 2008). If the aim of a study is to generate distributional simulations to reflect the potential climatic distribution of a species (the set of environmentally suitable areas in which the species could occur according to a group of environmental variables), the absence information used must be located outside those environmentally suitable localities in which the species does not occur as a result of historical factors, biotic interactions, or dispersal limitation (Pulliam, 1988, 2000; Ricklefs *et al*., 1993; Hanski, 1998). Including absences from a priori environmentally favourable localities will inevitably diminish the predicted range size (see Chefaoui *et al*., 2008; Lobo *et al*., 2008). Two types of models were generated with the available information for *C. crocuta*: (1) one for the Western Palaearctic and Afrotropical regions, using all available presence information (n = 2814) and 10 times more pseudo-absences (n = 28,140) selected outside the climatic conditions existing in the presence localities; and (2) another for the Afrotropical region, in which the same presences were used, but only previously well-determined absences were considered (n = 13,727). The first approach allowed us to obtain a simulation of the potential climatic distribution of C. crocuta across the two biogeographical regions in which the species has been present since the beginning of the Pleistocene. The second approach offered a simulation of the realized distribution on the continent currently inhabited by this species (Africa). Pseudo-absences were selected by first tabulating each of the 19 climatic variables' maximum and minimum values for the observed distribution localities, in order to estimate the multidimensional envelope defined by the values of the locations where the species was observed (see Busby, 1986). The pseudo-absence cells were then randomly selected from the area falling outside this envelope; that is, within the generally inappropriate environmental conditions for the species according to the observed presence points (see Engler *et al*., 2004 or Lobo *et al*., 2006). Presences and absences (or pseudo-absences) were logistically regressed against continuous and dummy explanatory variables using generalized linear models (GLMs; Crawley, 1993), an extension of linear models that allows for nonlinearity in the data and also a range of independent non-normal variable distributions. Recent studies recommend the use of simple GLM techniques that do not overfit when good-quality species data are used (Meynard *et al*., 2007) and when model results are transferred to different regions and environments (Randin *et al*., 2006). We first related the dependent variables separately to each predictor variable in order to identify the most relevant predictors. To consider possible curvilinear relationships, we selected the linear, quadratic or cubic function of each variable that accounts for the most important change in deviance with significant terms (Austin, 1980). Next, we built a complete model using all of the formerly detected statistically significant variables, selecting between competing models by a forward–backward stepwise selection procedure. The purpose of this complete model is not to estimate the parameters of each explanatory variable correctly, but to obtain a reliable model able to forecast the distribution of the species throughout the entire territory. The statistica 6.0 software package was used for these computations (StatSoft, Inc., 2003). The stability of the final model results was examined by a cross-validation procedure in which the original data were partitioned 10 times in training (75% of total data) and testing (25% of data) sets, and model accuracy measures were calculated for these testing data. Continuous probabilities derived from GLM results were converted into a presence–absence variable using the recommended threshold that minimizes the difference between sensitivity and specificity (Jiménez-Valverde *et al*., 2007b). Sensitivity (the ratio of correctly predicted presences to the total number of presences, or true-positive rate), specificity (the true-negative rate), and the receiver operating characteristic curve (ROC; Zweig *et al*., 1993) were used to estimate model accuracy. The area under the ROC curve (AUC) provides a single performance measure across all possible ranges of thresholds (Fielding *et al*., 1997). This score can be used to estimate the accuracy of distribution-model predictions, provided that they are carried out on the same species and extent (Lobo *et al*., 2008). A similar procedure was used to derive the potential distribution of the species using current climatic layers from the GENESIS 2 GCM in order to transfer the predictions to the conditions characterizing the Last Interglacial period (the GENESIS 126,000 yr bp climatic scenario).

	Coefficients	SE	Wald	p-values
Intercept	9.68	0.86	127.64	<0.00001
Isothermality	3.34	0.45	55.11	<0.00001
Mean Temperature of Wettest Quarter	-7.22	1.01	51.45	<0.00001
Mean Temperature of Wettest Quarter^2	2.95	0.50	34.50	<0.00001
Mean Temperature of Coldest Quarter	-121.36	8.78	191.00	<0.00001
Mean Temperature of Coldest Quarter^2	25.03	2.90	74.44	<0.00001
Minimum Temperature of Coldest Month	29.64	2.94	101.38	<0.00001
Minimum Temperature of Coldest Month^2	-3.09	1.27	5.92	0.01
Annual Mean Temperature	75.39	7.13	111.86	<0.00001
Annual Mean Temperature^2	-9.54	1.43	44.62	<0.00001
Mean Temperature of Warmest Quarter	-9.04	2.17	17.39	0.00003
Precipitation of Wettest Month	8.16	1.29	40.24	<0.00001
Precipitation of Wettest Month^2	-2.86	0.47	36.90	<0.00001
Precipitation of Wettest Month^3	0.19	0.06	11.55	0.0007
Precipitation of Wettest Quarter	-9.39	1.25	56.24	<0.00001
Precipitation of Wettest Quarter^2	5.01	0.52	91.66	<0.00001
Precipitation of Wettest Quarter^3	-0.39	0.06	43.21	<0.00001

Table S2.- Parameter estimates (± standard error; SE) from the final generalized linear model (GLM) of Crocuta crocuta in Africa and Eurasia. Pseudo-absences were selected outside the environmental range defined by all these climatic variables (potential distribution). Wald statistic scores test the significance of regression coefficients.

4.- RESULTS

4.1.- Current potential distribution

The complete model included eight explanatory variables accounting for 96.5% of the total deviance (see coefficients in Table S2). Accuracy measures for this model are remarkably high (AUC = 0.999; sensitivity and specificity = 0.994), whereas cross-validation values (mean ± 95% CI) are 0.9990 ± 0.0004 for the AUC; 0.9936 ± 0.0007 for sensitivity; and 0.9936 ± 0.0005 for specificity. Examination of the individual environmental variables indicated (Table 1) that those related to annual temperature variability (isothermality and temperature seasonality) explained the highest percentage of total deviance (around 80% and 70%, respectively). The probability of *C. crocuta* presence increased when isothermality values (a measure of the annual temperature range experienced on a daily basis) were higher as well as when temperature seasonality was low. In general, temperature variables seemed to be more relevant to explaining the potential species distribution than precipitation variables. In Africa, the species had high probabilities of occurrence in almost all Sub-Saharan territories, including in some high-precipitation and xerothermic localities (Fig. 2a). Using only the two most important detected climatic variables (isothermality and temperature seasonality), a selection of pseudo-absences outside the climatic conditions existing in the presence localities generated a similar potential distribution.

	Function	Sign	Deviance	Change in deviance	Percentage change in deviance
Full model			18,859.41		
Isothermality	cubic	+-+	3817.35	15042.06	79.76
Temperature Seasonality	quadratic	--	5577.58	13281.84	70.43
Mean Temperature of Wettest Quarter	cubic	+--	10835.28	8024.13	42.55
Temperature Annual Range	quadratic	--	11173.01	7686.41	40.76
Mean Temperature of Coldest Quarter	cubic	+-+	11667.75	7191.66	38.13
Mean Temperature of Driest Quarter	cubic	+-+	12001.04	6858.38	36.37
Minimum Temperature Coldest Month	quadratic	+-	12102.89	6756.53	35.83
Annual Mean Temperature	cubic	+-+	13375.04	5484.37	29.08
Precipitation Seasonality	cubic	+--	14212.21	4647.20	24.64
Mean Temperature Warmest Quarter	cubic	+--	15242.14	3617.27	19.18
Maximum Temperature Warmest Month	cubic	+--	15906.70	2952.71	15.66
Precipitation of Wettest Month	quadratic	+-	16968.52	1890.89	10.03
Precipitation of Wettest Quarter	quadratic	+-	17130.96	1728.45	9.16
Precipitation of Driest Month	cubic	-+-	17184.50	1674.92	8.88
Precipitation of Warmest Quarter	cubic	++-	17438.27	1421.14	7.54
Precipitation of Driest Quarter	cubic	-+-	17480.80	1378.61	7.31
Mean Diurnal Range	cubic	+-+	17687.00	1172.41	6.22
Annual Precipitation	cubic	++-	18060.17	799.25	4.24
Precipitation of Coldest Quarter	quadratic	-+	18262.37	597.05	3.17

Table 1 Deviance and change in deviance from a full model in which the number of parameters is equal to the number of observations for *Crocuta crocuta* distribution in Africa and western Eurasia for each of the explanatory climatic variables used (see Hijmans *et al.*, 2005). The model was computed by selecting pseudo-absences outside the environmental range defined by these variables (potential distribution). The linear, quadratic, or cubic functions of each variable accounting for a significant change in deviance (P < 0.05) were selected.

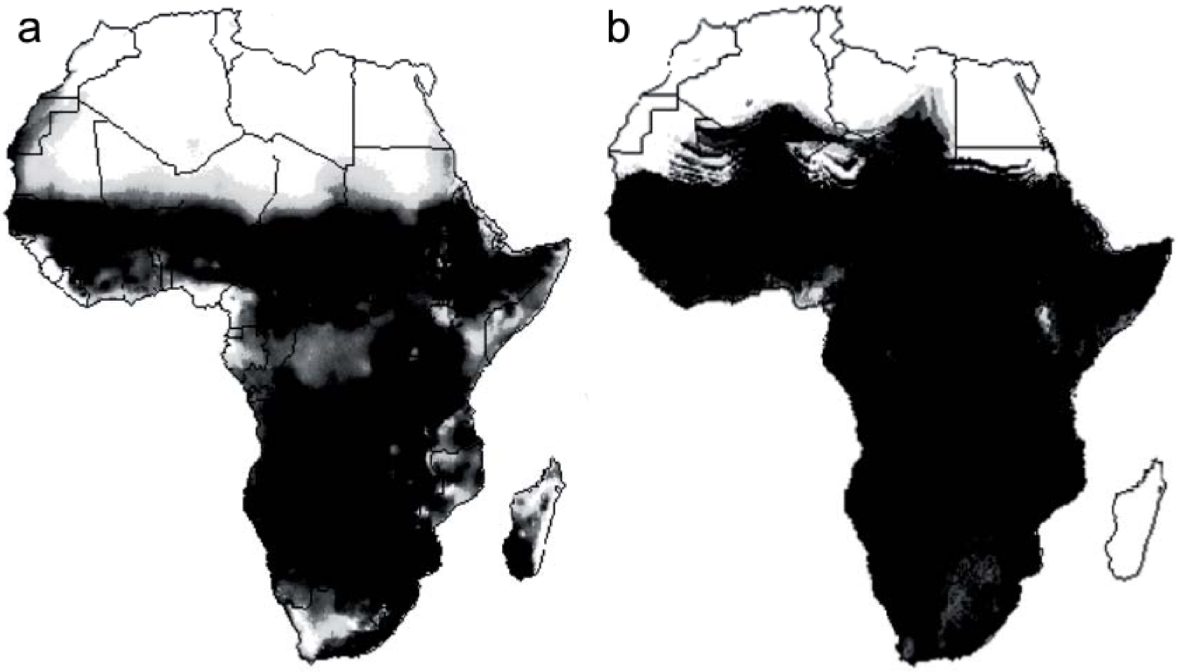

Figure 2 Geographic predicted representations of the (a) potential and (b) realized distributions of *Crocuta crocuta* (see Tables S2 and S3). The probability maps are in a white (0) to black (1) scale. The striped pattern in the north is a consequence of the interpolation procedure used for the seasonal precipitation variable. IUCN estimations of the distribution of the spotted hyena identify Central African evergreen rain forest as an absence area. However, as our dataset includes presence points within evergreen rain forests in Equatorial Guinea, the model does not identify the areas with this type of habitat as potentially unsuitable.

4.2.- Current realized distribution

The climatic variables related to temperature variability were also able to explain a high percentage of the total deviance (see Table 2). The Sahara Desert barrier variable accounted for 92% of the total variability; anthropic variables (distance to populated places and wilderness areas) accounted for 37%; and land cover accounted for 31%. Adding all these significant non-climatic variables to the complete climatic model increased the explained variability by only 1%. Land-cover and anthropic variables did not seem to be particularly relevant for explaining the general pattern of presence and absence on a global scale, although it will be necessary to study the relationship between these variables and the species distribution at a local scale. The complete model generated with all of the former significant variables included nine explanatory variables (see coefficients in Table S3), accounting for 98% of total deviance. Accuracy measures were also high (AUC = 0.979; sensitivity = 0.95; and specificity = 1), and cross-validation values (mean ± 95% CI) were 0.9992 ± 0.0007 for the AUC; 0.9963 ± 0.0010 for sensitivity; and 0.9964 ± 0.0008 for specificity. Apart from the Sahara Desert barrier, the five most important variables were the same as those in the potential climatic model. Again, isothermality and temperature seasonality were the two most explicative variables, accounting for 90% and 83% of total variability, respectively. *Crocuta crocuta* was predicted to be absent when isothermality scores are < 50 (Fig. 3), representing places with a high variation in temperature throughout the year. Thus, mediterranean-type climate and desert areas were not covered by the model (Fig. 2b). Predicted values also declined when isothermality values were around 80, as observed in the Congo and Central African tropical rain forests. In West Africa, coastal areas with high values of precipitation and minimum temperature, from Guinea to Gabon, were predicted as unsuitable for *C. crocuta*, as were the rain forest areas of Gabon and Congo. The mediterranean-type climate areas of South Africa and the areas with low values of isothermality that surround Lake Malawi and the coast of Mozambique, as well as the desert coast of Djibouti and Eritrea, were other areas where the model predicted the species to be absent.

	Coefficients	**SE**	**Wald**	**p-values**
Intercept	12.36	1.69	53.55	<0.00001
Isothermality	-6.79	2.069	10.82	0.001
Isothermality^2	3.29	0.65	25.90	<0.00001
Temperature Annual Range	2.37	0.80	8.89	0.003
Minimum Temperature of Coldest Month	4.31	1.56	7.61	0.006
Minimum Temperature of Coldest Month^2	-17.66	2.34	56.88	<0.00001
Minimum Temperature of Coldest Month^3	10.81	1.14	89.36	<0.00001
Precipitation Seasonality	3.34	0.68	23.98	<0.00001
Precipitation Seasonality^2	-3.73	0.50	40.23	<0.00001
Precipitation Seasonality^3	-1.69	0.39	18.95	0.00001
Barrier	11.75	1.39	70.95	<0.00001
Urban distance	-5.09	0.73	48.68	<0.00001
Urban distance^2	-2.56	0.54	22.23	<0.00001
Wilderness distance	5.67	1.59	12.75	0.0004
Wilderness distance^2	7.47	2.23	11.25	0.0008
Land use-Wooded grassland	0.94	0.35	7.06	0.008
Land use-Croplands	0.74	0.36	4.12	0.04

Table S3: Parameter estimates (± standard error; SE) from the final generalized linear model (GLM) of *Crocuta crocuta* distribution in Africa using reliable presences and absences, performed by a backward stepwise procedure on the variables described in the second table of the main article. Wald statistic scores test the significance of regression coefficients.

	Function	Sign	Deviance	Change in deviance	Percentage change in deviance
Full model			15088.06		
Climatic variables					
Isothermality	cubic	+-+	1440.18	13647.88	90.45
Temperature Seasonality	cubic	-++	2560.68	12527.38	83.03
Temperature Annual Range	cubic	-++	5442.38	9645.68	63.93
Mean Temperature of Coldest Quarter	cubic	++-	5878.14	9209.92	61.04
Mean Temperature of Wettest Quarter	cubic	+--	6520.79	8567.27	56.78
Precipitation of Warmest Quarter	cubic	+-+	6867.08	8220.98	54.47
Minimum Temperature of Coldest Month	cubic	++-	6988.50	8099.56	53.68
Precipitation of Wettest Month	quadratic	++	9532	9327.41	49.46
Precipitation of Wettest Quarter	quadratic	++	9637.34	5450.72	36.13
Mean Temperature of Driest Quarter	quadratic	--	9787.3	9072.11	48.10
Maximum Temperature of Warmest Month	cubic	-+-	9857	5231.45	34.67
Precipitation Seasonality	linear	+	10811.63	4276.43	28.34
Annual Precipitation	cubic	++-	10940.4	4147.64	27.49
Mean Diurnal Range	cubic	-++	12405.08	2682.98	17.78
Mean Temperature of Warmest Quarter	quadratic	-+	12650.82	2437.24	16.15
Precipitation of Coldest Quarter	cubic	-+-	13224	1863.99	12.35
Annual Mean Temperature	quadratic	++	13462.4	5397.01	28.62
Precipitation of Driest Month	quadratic	++	14026.33	1061.73	7.04
Precipitation of Driest Quarter	cubic	++-	14080.4	1007.67	6.68
Non-climatic variables					
Barrier		-	1141.50	13946.56	92.43
Urban distance	quadratic	-+	10420.19	4667.87	30.94
Land use-Bareground		-	12239.09	2848.97	18.88
Land use-Woodland		-	13468.71	1619.35	10.73
Wilderness distance	quadratic	++	13506.22	1581.84	10.48
Land use-Wooded grassland		-	13973.03	1115.03	7.39
Land use-Evergreen broadleaf forest		-	14688.24	399.82	2.65
Land use-Grassland		-	14826.23	261.83	1.73
Land uses-Closed shrubland		-	14944.76	143.30	0.95
Land use-Cropland		-	15058.18	29.88	0.20
Land use-Deciduous broadleaf forest		-	15060.45	27.61	0.18

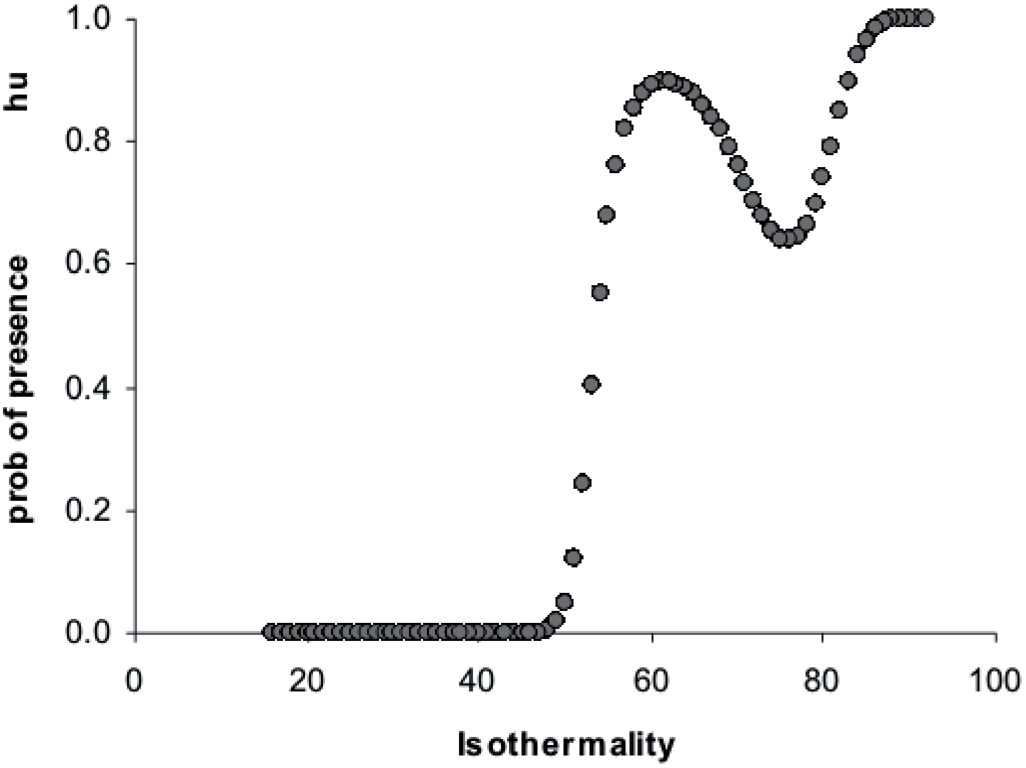

Figure 3 Relationship between isothermality (the ratio between mean diurnal range and temperature annual range) and the predicted probability of presence for the realized distribution. *Crocuta crocuta* has a low probability of occurrence when temperature scores exhibit strong variation throughout the year (deserts and mediterranean-type climate areas); the species has a high probability of occurrence in environments with more stable temperature conditions. The shift in the slope (when isothermality values are around 80) approximately coincides with the evergreen rain forest data points.

Table 2 (left): Deviance and change in deviance from a full model in which the number of parameters is equal to the number of observations for Crocuta crocuta distribution in Africa for each explanatory climatic and nonclimatic variable used (see Hijmans et al., 2005). The model was computed using reliable absences (realized distribution). The linear, quadratic, or cubic functions of each variable accounting for a significant change in the deviance (P £ 0.05) were selected. Land-cover variables came from the Global Land Cover Characterization of the US Geological Survey (version 2; see http://edcsns17.cr.usgs.gov/glcc/), and the distance to populated areas (urban distance) and distance to wilderness areas (wilderness distance) were created from the Gridded Population of the World project (version 3; see http://sedac.ciesin.org/gpw) and the World Wilderness Areas dataset of the United Nations Environment Programme (see http://www.grid.unep.ch).

4.3.- Model transferability

The geographic representation of the aforementioned potential distribution showed that the Western Palaearctic region currently does not seem to exhibit the climatic conditions necessary for the presence of *C. crocuta* (Fig. 4). In spite of the similarity between current and Last Interglacial temperatures, the fossil presence is outside supposedly climatically favourable European areas, as derived from current distribution locations (Fig. 4b). Using current GENESIS 2 GCM climatic variables, we were able to explain 67% of the total deviance. The potential distribution thus generated (Fig. 5a) was transferred to the Last Interglacial without success, since fossil records were located in cells with zero or very low suitability values (mean ± SD; 0.032 ± 0.064; Fig. 5b).

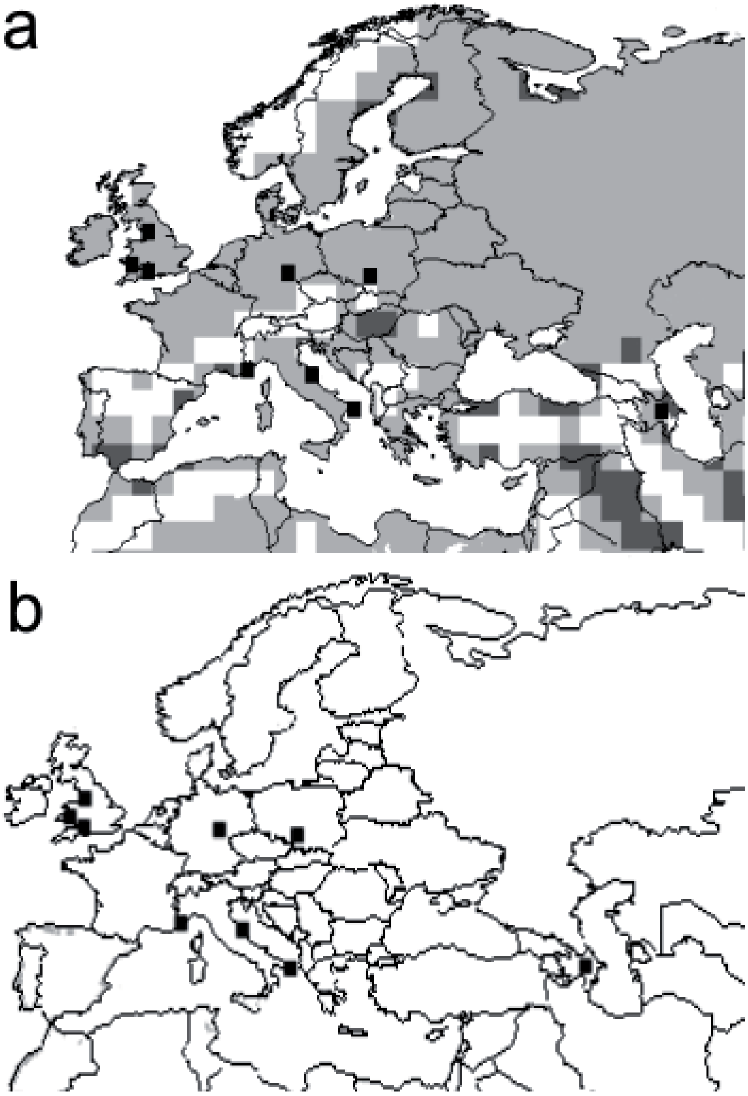

Figure 4 (a) Differences between the Last Interglacial (126,000 yr bp) average annual temperature and the current values for Europe according to three categories: white, current colder temperatures (£ 2C); dark grey, current warmer temperatures (‡ 2C); grey, similar temperatures (± 2C). Climate layers extracted from the GENESIS 2 general circulation model (Thompson & Pollard, 1995, 1997; P. Batra, unpublished data). The correlation between the two temperature values for all 2 cells is statistically significant (r = 0.97; P < 0.0001) with a regression slope of 1.006. Fossil sites are represented as black squares. (b) The predicted suitable area in Europe (in black) according to the potential prediction model generated using current African data. Note that favourable locations are restricted to the coast of the Iberian Peninsula and that fossil sites appear outside the predicted potential distribution.

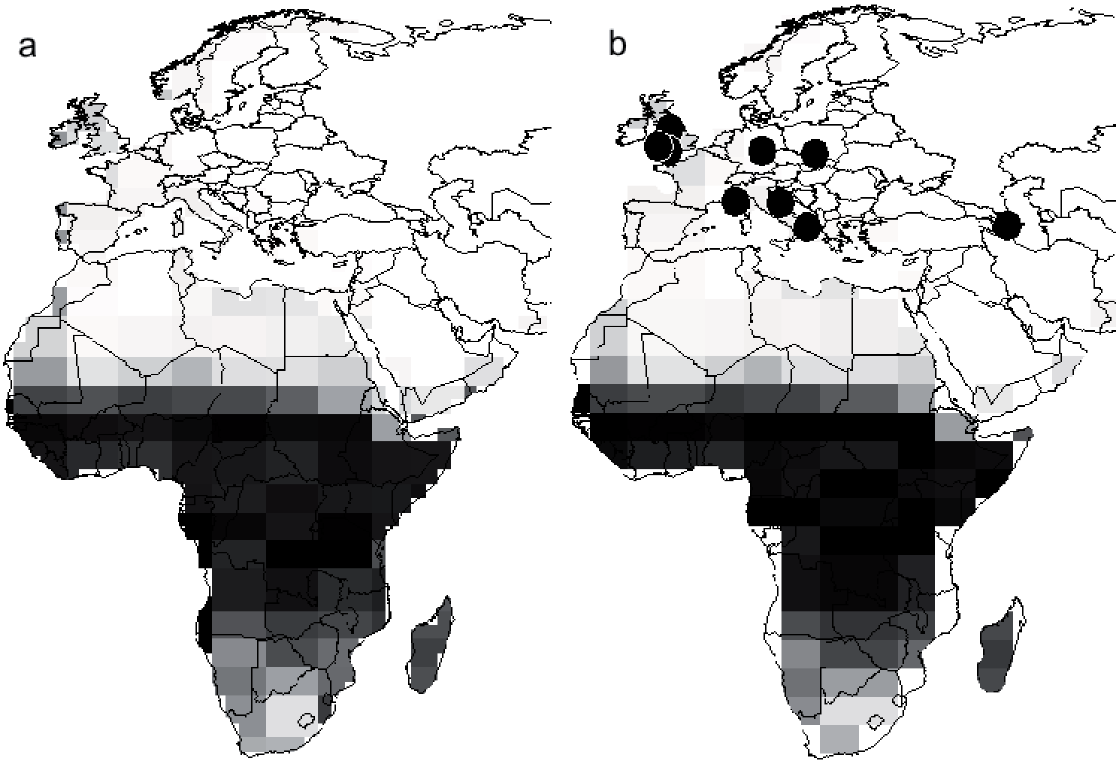

Figure 5 (a) Predicted suitable area for Crocuta crocuta using current data on annual temperature range and annual precipitation derived from the GENESIS 2 general circulation model climatic data (4.5 x 7.5 resolution), and (b) projected potential distribution using the Last Interglacial climate scenario (GENESIS 2 GCM). Western Eurasia is not predicted as a suitable area for the species, and the probability of occurrence differs only slightly from zero in southern Europe. Crocuta crocuta fossil locations during the Last Interglacial (black circles) are located outside the predicted suitable areas for the species. Probabilities oscillate between zero (white) and one (black).

5.- DISCUSSION

5.1.- Ecological implications of model results

Among the climatic variables, those related to temperature stability during the year had the highest predictive capacity in both models. Spotted hyenas seem to avoid areas with regular precipitation throughout the year (evergreen forests) as well as those with high values of temperature seasonality (mediterranean-type climate and desert zones). It is likely that temperature stability is not linked to any physiological constraint, but to the species' response to certain habitat structures (Mills *et al*., 1998). The barrier variable (the Sahara Desert) also had a high explanatory capacity to predict the realized distribution, suggesting that this large desert could be conditioning the current northern dispersal of *C. crocuta*. Interestingly, genetic studies (Rohland *et al*., 2005) indicate that the last connection between the European and African populations occurred during the Last Interglacial, a period of intensified monsoons and increased precipitation. As a consequence of this increase in humidity, 97% of North Africa was covered by vegetation, mainly grasses (van Andel *et al*., 1996; Montoya, 2007). The Sahara Desert also experienced other much less arid periods during the late Pleistocene and Holocene (Issar, 2003; Drake *et al*., 2006). In particular, during the period from 10,300 to 9500 yr bp, when the European population went extinct, the Sahara was significantly more humid than it is at present (Lézine, 2007). Studies on the viability of the spotted hyena metapopulations highlight the possibility that isolation could be a key factor for the extinction of this species (Mills *et al*.,1998). If this is the case, further investigation will be necessary to determine why the African spotted hyena populations failed to spread northwards and rescue the European populations from extinction.

5.2.- Climatic equilibrium and transferability

Both potential and realized distribution models of *C. crocuta* were highly accurate, describing around 96% of the total variability and offering extremely high cross-validation results. According to our model, climate is the main conditioning factor capable of explaining the current distribution of this species. The predicted area for the potential distribution in Africa is only 8% higher than the realized area. Hence, our results suggest that the current *C. crocuta* distribution is highly conditioned by climatic variables and that the species is currently present throughout the major portion of its climatically suitable area. Thus, the assumption of equilibrium with the climatic conditions is apparently not violated, potentially allowing this model to be transferred in space and time. Transferability of the model results to western Eurasia predicts almost no suitable area for the species, and the potential model built using GENESIS 2 climatic layers showed similar results, again excluding western Eurasia as a favourable area for the species during the Last Interglacial period. However, fossil data available for a climatically similar Pleistocene period clearly indicate that this species inhabited regions with climatic conditions very different from those experienced currently. An overwhelming amount of fossil evidence indicates that *C. crocuta* inhabited the European Pleistocene under both glacial and interglacial conditions (Werdelin *et al*., 1991; Testu, 2006), coexisting both with cold-adapted species, such as *Coelodonta antiquitatis* (woolly rhinoceros) and *Mammuthus primigenius* (woolly mammoth) (Altuna*et al*., 2000), and with warm-adapted species, such as *Dama dama* (fallow deer) and *Sus scrofa* (wild boar) (Bologna *et al*., 1994). The failure of the models to predict the palaeodistribution of the species suggests that current distribution data do not represent the entire climatic range where spotted hyenas are able to live. Similar results could be obtained for many other large mammals currently extinct in Europe but present in Africa (Barnosky *et al*., 2004).

When seeking to minimize the difference between the estimated population parameters and the sample statistics, it is universally agreed that the use of statistical methods to draw inferences requires that the sample from which relationships among variables will be inferred be representative of the population described (Zar, 1999). In the case of species distribution models (SDMs), such samples frequently comprise the available information on the presence of the species (i.e. species occurrences), which is a subset of the total number of inhabited localities. The relationships that SDMs aim to infer constitute the ‘niche’ or set of environmental conditions that would allow any species’ population to attain a positive rate of demographic increase in the absence of immigration (Soberón, 2007). The subsequent geographical representation of such an inferred niche could provide reliable hypotheses on the potential distribution of species, provided that the inferred relationships represent all the combinations of environmental conditions where the species can persist. Hence, we sought to determine whether it is possible to attain reliable knowledge of the niche using only distributional information. Darwin (1859, p. 346) himself wrote in the Origin of Species that ‘…neither the similarity nor the dissimilarity of the inhabitants of various regions can be accounted for by climatal and other physical conditions’. That is, the environmental conditions of the localities with data on the presence of the species will not provide information on the whole spectrum of suitable environmental conditions. The distribution of a species is (almost always) the consequence of the interplay of a large number of current and past processes, many of them exerting contingent effects on species populations (Ricklefs, 2004). Most species distributions are not in equilibrium with current environmental conditions (Svenning *et al*., 2004), owing to the impact of past environmental conditions, dispersal limitations and the particular history of regions and organisms. Such a lack of equilibrium hinders the precise estimation of potential distributions/niches from current distribution data (Jiménez-Valverde *et al*., 2008). Recently, the lack of success in the transferability of the results of SDMs has been presented as evidence of niche shifts (Broennimann *et al*., 2007; Fitzpatrick *et al*., 2007). Such an argument neglects both the role played by the phenotypic plasticity of species (Miner *et al*., 2005) and the fact that a species can be predicted to be absent from areas with suitable environmental conditions simply because these conditions do not exist within its native distribution area. On these premises, the transference of the set of suitable environmental conditions inferred from the sample used to another time or region is subject to an unknown degree of uncertainty, even if SDMs are developed using an adequate resolution and the presence data used cover the species’ entire geographical distribution. SDMs developed from current distributional information may underestimate the set of environmental conditions where a species can occur (Dormann, 2007). Extreme caution is thus mandatory if the aim is transferring the results of merely correlative models over both space and time. The apparent equilibrium with climate that might be estimated from current distributional information does not guarantee the transferability of model predictions. Rather, to estimate the potential distributions of species it is advisable to use distributional data coming from different regions and time periods (Mau-Crimmins *et al*., 2006; Nogués-Bravo *et al*., 2008) and/or functional and physiological data (Kearney *et al*.., 2008).

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Capítulo 6:

Data, predictors and species distribution models in Palaeobiogeography

1.- ABSTRACT:

The current technological scenario provides new tools for Palaeobiogeography, allowing to analyze the past from a quantitative and macroecological perspective, and promising a huge advance in our knowledge of the past systems. In this context, species distribution models (SDM) are increasingly used to predict the past distribution of species through an array of different modelling techniques. However, a sound theoretical framework to support these new analyses is yet lacking. Here, we review the main sources of uncertainty while constructing Palaeo-SDM to predict the past distribution of species. We discuss the use of presence/absence data sets to estimate the species' climatic requirements, the methods for selecting the predictor variables and the biological assumptions of the different models. Besides, we review the recent literature, finding that the SDM techniques used to estimate past species distribution ranges are highly heterogeneous and that the choice of technique has been so far arbitrary to some degree. We conclude with a series of recommendations for the use of SDM in palaeobiogeography: include current and fossil data in the training data sets; avoid using absence data to train the models; select the predictors using an independent factorial niche-based analysis (e.g., ENFA); use simple SDM techniques, such as climatic envelopes or Mahalanobis distances (justifying

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the selection of the species climatic optimum). Further, we propose three lines that could help to establish the basis of a sound research in Palaeobiogeography: create a standardized global open access fossil database; implement regional and local climatic models to produce past high-resolution environmental maps; and continue to investigate the relationship between species and climate, to improve SDM and make more accurate and realistic predictions.

2.- INTRODUCTION

Palaeobiogeography is facing a new epoch. The narrative biogeographic descriptions and interpretations of fossil data are starting to be complemented with the use of quantitative statistics and modelling techniques to describe and estimate past species range shifts and extinction events (Rodriguez-Sanchez *et al.*, 2008). The widespread access to GIS information about past and current species distributions, climate, remote sensing products, topography or geology allow researchers to use new data to investigate the past (e.g., *Faunmap*, http://www.museum.state.il.us/research/faunmap; *The Paleobiology Database*, http://www.paleodb.org/cgi-bin/bridge.pl; *GBIF*, http://www.gbif.org; *Stage Three Project*, http://www.esc.cam.ac.uk/research/research-groups/oistage3; *WorldClim*, http://www.worldclim.org/ ; *PMIP*, http://pmip3.lsce.ipsl.fr/; etc.), and new tools permit simulating the geographic consequences of these climatic changes across time (Allen *et al.*, 2006). These advances have allowed to relate the environmental changes of the Pleistocene climatic oscillations with spatial and temporal faunistic turnovers, the location of glacial refugia, the fragmentation of distributional ranges, migration and extinction events, and even speciation processes (Meloro *et al.*, 2008; Stewart *et al.*,2008; Lister *et al.*, 2008; Knowles, 2001).

Species distribution models (SDMs) are a heterogeneous group of techniques used to model species distribution ranges by relating known species presences with the environmental conditions (typically climatic) in these locations (see, e.g., Guisan *et al.*, 2000; Guisan *et al.*, 2005). The relationships identified through these techniques are thought to provide a description of the adequability of each combination of environmental predictors for the maintenance of populations of the studied species, i.e., those areas where the net reproductive rate of these populations would be positive (Soberon, 2007; Soberón, 2010; Soberón *et al.*, 2009). SDMs are amongst the most widely used in biogeography and macroecology (see Lobo *et al.*, 2010), typically to map species ranges, but also to address many evolutionary and ecological questions. In palaeontology SDMs are starting to be used to study the relationship between climate variations and the past distribution of species and/or human cultures (Banks *et al.*,2006; Banks *et al*., 2008), extinction events (Nogues-Bravo *et al*., 2008; Varela *et al*., 2010), or to determine the past location of climatically suitable areas that could have acted as glacial refugia (Jakob *et al*., 2007; Carnaval *et al*.,2008; Schmickl *et al*., 2010). Further, they have been also applied to examine the retention of niche-related ecological traits over time (Martinez-Meyer *et al*., 2006), or to analyze the fingerprints of past climatic changes on current observed genetic patterns (Alexandrino *et al*., 2007). Herein we will refer to the paleontological applications of SDM as Palaeo-Species Distribution Modelling, or PSDM. All these new approaches may enhance our understanding about the determinants of species distributions and their evolution, helping to address some fundamental questions, such as how tight are species' responses to environmental changes; what are the biological consequences of an extreme climatic event; where were the species refugia located in past periods; or whether these refugia are a key factor for explaining current biogeographic patterns.

The generalization of PSDMs as research tools could foster a major step forward for palaeoecology and palaeobiogeography (Nogués-Bravo, 2009). However, for such potential to be fully and soundly taken profit of, it is necessary to establish robust and scientifically based theoretical and methodological frameworks. Unfortunately, the use of PSDMs for estimating the past distribution of species is yet lacking such sound conceptual framework. Here we examine the main methodological and conceptual issues in the application of PSDMs. Specifically, we will discuss: (i) the special relevance of biases and scarceness in the available species distribution data from fossil records; (ii) the influence of the SDM techniques used to select the appropriate causal predictors; and (iii) the inherent difficulty of deriving distributional representations for different time scenarios when the only confident information are species presence data. In addition, we review the different SDM methodologies used to project current data into past scenarios (i.e., hindcasting; see Nogués-Bravo, 2009). Based on the above, we propose future research guidelines, suggesting key gaps of knowledge that need to be investigated before the use of PSDMs is widespread in palaeontology, with the general purpose of stimulating debate and discussion on this novel and potentially fruitful field of research.

3.- METHODOLOGICAL AND CONCEPTUAL ISSUES FOR PALAEO-SPECIES DISTRIBUTION MODELLING

3.1.- The Paleontological data

For describing the past distribution of a species in a context of climatic change, we need a model that accurately identifies the species actual relationship with climate. In other words, a model that provides accurate results when it is geographically projected into any temporal or regional scenario. The ideal dependent variable for training this kind of model would be a measure that reflects the species' response to the climatic changes (e.g. reproductive rate, mortality rate, abundance, physiologic basal cost, etc.) (Kearney *et al*., 2009). However, rather than any of these measures, georeferenced species presence data is commonly the only dependent variable generally available for SDMs. The information about the distributions of species typically presents different biases and deficiencies that seriously undermine the capacity of occurrence data for representing the full spectrum of environmental conditions in which a species may have a net positive demographic rate (Rocchini *et al*. 2011; Hortal *et al*., 2008). The geographical information of fossil data is subject to similar limitations, perhaps even more severe due to their spatiotemporal character. Contrary to recent data, occurrences extracted from fossil data should not be directly interpreted as part of the realized distribution of the species (Fernandez Jalvo, 1996; Chew *et al*., 2009; Barnosky *et al*., 2005). A straightforward interpretation of the data could lead to misleading conclusions about the species-climate relationships (Hadly, 1999) because taxonomic, spatial and temporal fossil data are the consequence of a diverse array processes (climatic and non climatic) that operate at different scales (Fernández-Jalvo *et al*., 2010). Here we summarize the specific biases that should be taken in consideration when building PSDMs from fossil data.

3.1.1.- Spatial, temporal and taphonomic bias

Fossils occur in sedimentary deposits. Therefore, the geographic distribution of the fossil records is biased by the distribution of the sedimentary layers. A general consequence of this bias is that the absence of fossil records does not necessary mean the absence of the species. Rather, the lack of fossil records depends on the high number of physical, chemical and biological processes behind the process of being converted into a fossil. This fundamental characteristic of fossil data adds up to other factors that difficult the extraction of actual absences from distributional data, such as lack of survey effort or species detectability (Mackenzie *et al*., 2005). The latter factors are discussed in detail elsewhere (e.g., Lobo *et al*., 2007; 2010; Hortal *et al*.; 2008; Rocchini *et al*., 2011), so we will only discuss in detail the taphonomic processes that difficult tearing apart actual absences from the fossil record.

Their intrinsic ecological and biological characteristics can either prevent some species from being deposited in a sedimentary area or increase the prevalence of others (Andrews 2006; Davis *et al*., 2007; Reed 2005). In addition, the fossilization of the organic material is a function of their composition and size, in relation to the sedimentary local conditions (Arroyo-Cabrales *et al*., 2007). As an example, fossil data samples are usually biased towards species with large body sizes (Lucas *et al*., 1997; Muñoz-Duran *et al*., 2006). The most extreme implication of this is that small species could be absent in a fossil deposit despite of being present in the moment the deposit was formed. This characteristic of fossil data can also increase the spatial bias, causing the biotas of certain biomes to be either over- or underrepresented in the available distribution data (Nieto *et al*., 2003). For example, many regions of Spain lack sedimentary basins from the Lower Pleistocene (Fig. 1), thus introducing an unavoidable bias in our knowledge on the faunas that inhabited the Iberian Peninsula during this period, and in consequence a bias in the estimation of the environmental conditions occupied for any species at that moment of time. It follows that a taphonomic study about the modifications of the biological remains since the species decease and some knowledge about the specific processes implicated

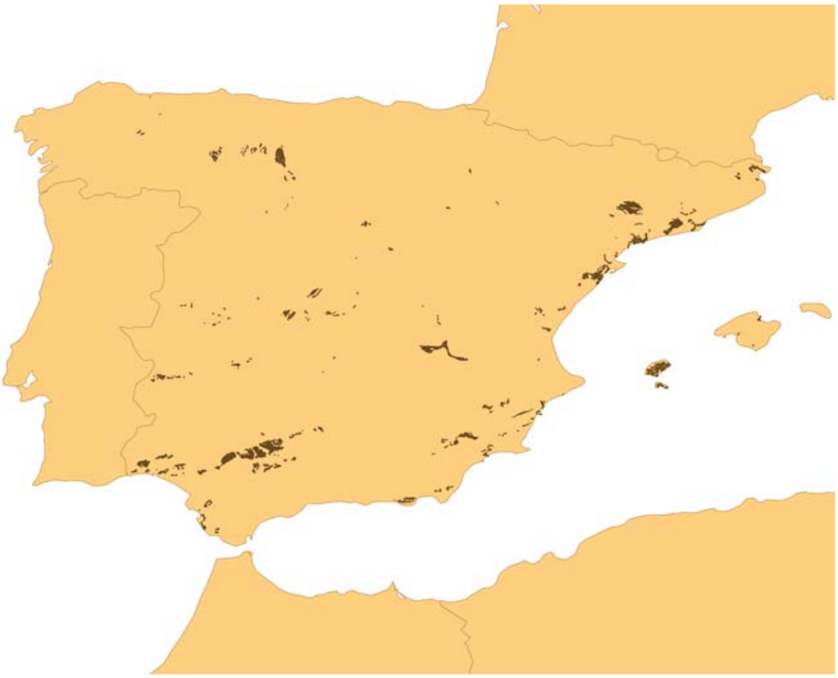

Fig. 1: Geographic distribution of the Lower Pleistocene deposits in Spain.

in the prevalence of the studied species during the fossilization are fundamental to correctly interpret fossil occurrence data sets.

Besides such spatial bias, fossil data are also subject to temporal bias. Certain periods have larger sedimentary areas than others, and therefore the areas that could potentially host fossil records may increase or decrease through time, which ultimately results in a tight influence of these oscillations on the fossil record. This implies that the variations in abundance of fossil records through time should not be interpreted directly as an indicator of the species' population dynamics. To infer or compare population abundances it would rather be necessary to consider the obtained records, the number of fossil sites from the same period and region, and the paleontological survey effort carried out. For example, sedimentary deposits are more abundant in Spain for the Lower Pleistocene than for the Upper or Middle Pleistocene (Fig. 2). As a consequence, the fossil record of the Spanish Lower Pleistocene contains comparatively more rare species, such as the exceptionally rare hominids remains founded in Atapuerca, Burgos (Bermudez de Castro *et al.*, 2008). Temporal bias also depends on the dating methodologies applied to estimate the chronology of fossil records. Given that there are few widespread methodologies to date the fossil records older than 50,000 Years Before Present (YBP), the lower confidence limit of ^{14}C (Magee *et al.*, 2009), Late Pleistocene fossil records have typically accurate dating while Middle and Lower Pleistocene fossils remain undated, which could give the erroneous impression of higher species abundances in the Late Pleistocene.

To summarize, the fossil record is not unevenly distributed either in time or in space (Jass *et al.*, 2010), and therefore presence data gathered from fossil records cannot be used as a direct indicator of the global geographic or temporal distribution and abundance of a species (Chew *et al.*, 2009). These data could be weighted to balance the effects of the biases discussed above (Crampton *et al.*, 2003), but to do this it is first necessary to estimate the geographic and temporal bias in the location of the sedimentary basins and the bias derived from the dating methodologies, in addition to the biases also inherent to the distributional data on recent species.

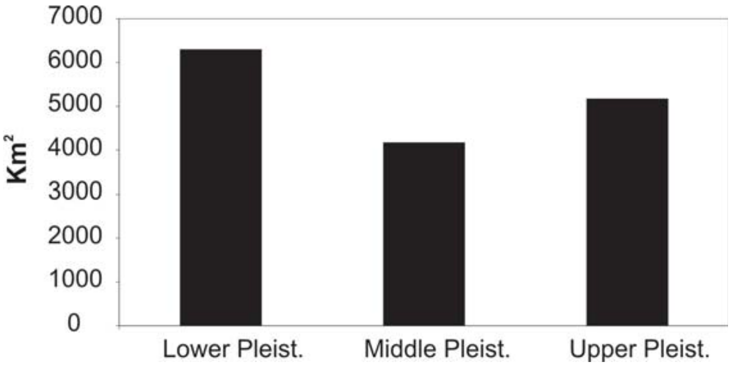

Fig. 2. Pleistocene deposits in the Iberian Peninsula (km^2).

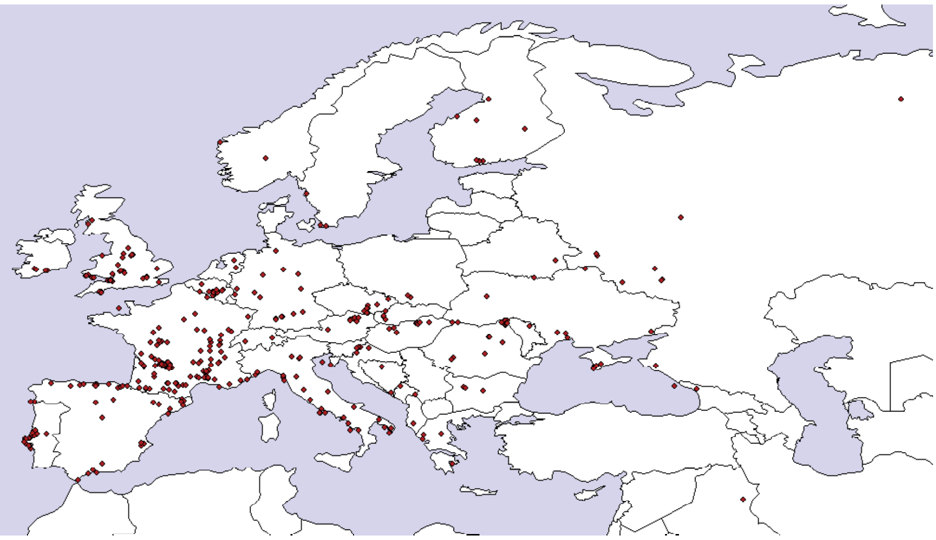

Fig. 3.
Geographic distribution of the European mammal fossil sites during the OIS 3

(Stage 3 Project database; http://www.esc.cam.ac.uk/research/research-groups/oistage3).

3.1.2.- Collectors' bias

Palaeontologist's preferences and their methodological procedures also may bias our knowledge of past distributions. On the one hand, the between-country differences in paleontological tradition generate spatial heterogeneity in survey efforts. The distribution of mammal fossil sites for the European OIS may illustrate this point; the long paleontological tradition in France has resulted in that almost one third of the fossil records during this period being located in that country (Fig. 3). Besides, there are temporal or geographic scenarios that are more interesting for solving certain biological questions. For example the extinction of the Neanderthals in Europe at around 30,000 YBP is explicitly studied addressed by the Stage 3 Project (http://www.esc.cam.ac.uk/research/research-groups/oistage3), which studies the environmental and biotic conditions of this particular period. This has rendered much larger quantity and better quality for the data on this period than for any other moment of time during the European Pleistocene. In the same way, some taxonomic groups are particularly well studied; a search in the ISI Web of knowledge (October 2010) rendered 784 papers using "Pleistocene" and "hominids" as topic keywords, 259 using "Pleistocene" and "large mammal", and 147 using "Pleistocene" and "small mammal". Nevertheless, the excavation methodologies employed can bias the fossil record, typically towards large-sized mammals. Rodents and insectivores are sometimes absent from the species checklist of a fossil site simply because the applied excavation methodology does not consider small-sized species.

Apart from these typical collectors' biases, the taxonomic identification of the fossil remains is highly dependent on the Palaeontologists' interpretation (Lister *et al.*, 2005; Mounier *et al.*, 2009). The classification of living organisms and the discrimination of species is already a complex issue due to the spatial variation in the traits of individuals (both phenotypic and genotypic) (Tobias *et al.*, 2010), but when it comes to fossil species the temporal dimension adds an extra complexity (Escude *et al.*, 2008; Ogino, 2009). The morphological variations observed through time are interpreted by palaeontologists like recent taxonomists interpret geographic variations in current species: depending on the criteria used by the specialist they can be considered to be either morphotypes from the same species, different subspecies, or even distinct species or chronospecies. A direct consequence of such unevenness in the taxonomical standards is that the species lists from different fossil sites are not directly comparable without assessing the eventual differences in the excavating procedures and the taxonomic criteria followed for the identification of the remnants.

The spatial and temporal amplitude used for agglutinating the fossil remnants into discrete species is highly relevant. Species are not indisputable entities (Quintyn, 2009) and their populations have genotypic and phenotypic plasticity, which in turn are spatially and temporally structured (Holliday, 2003). Such variability turns the decision of when to discriminate two different species into an arbitrary exercise, which may seriously condition any results obtained from the resulting taxonomic classification. Fossil remnants are not an exception to this, so any use of the fossil record necessarily implies taking a position on this controversial question (Hlusko, 2004). On the one hand, it could be assumed that all past occurrences of the studied taxon represent different individuals of the same taxonomic entity, even when separated by large periods, such as 1 million years. In this case, we can use all fossil records and current records as training dataset for the selected SDM technique (Varela *et al*., 2010). On the other hand, the decision can be taken to fix the temporal or the spatial dimension, or both. For instance, the geographic extent of the training data can be set up to any species' occurrences within the Iberian Peninsula, independently of the time period (Alba-Sanchez *et al.*, 2010), assuming that the Iberian populations of the studied species behave as a separate and coherent unit in relation to their climatic requirements, and by implication as a distinct species. Both approaches can be correct depending on the context, but the decision of including or excluding species occurrences from each particular analysis needs to be grounded in the particular question addressed, and the reasons for such decision should be explained and discussed in detail.

The combination of all these different collectors' biases leaves a footprint in the fossil record (Fig. 4). As consequence, the relationships between species presence-absence data and the environmental or non-environmental predictors may offer an incomplete or even biased picture of the species' niche. It is fundamental to keep this idea in mind when using SDM techniques to hindcast the past distribution of a species in relation to climatic changes. If we

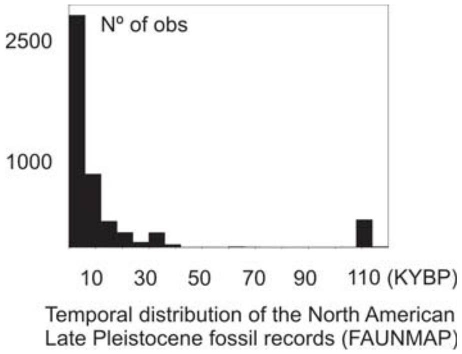

Fig. 4.Temporal distribution of the Late Pleistocene fossil records of North America (FAUNMAP database).

ignore or simply do not take into account the extent and distribution of the biases in the data, the error and/or uncertainty in the estimate of the species' climatic requirements provided by the obtained model will remain unaccounted for and/or unknown, thus failing in predicting the species geographic ranges through time (Elith *et al.*, 2010). It is however possible to take profit of fossil data from an understanding of its limitations. Fossil remnants may be considered extremely long temporal surveys about the geographic distribution of the species in a global scenario of changing climate. Thus, the fossil record provides the most complete knowledge on the responses to environment of many species, better than the one obtained using just their current distributions (Varela *et al.*, 2010). This advantage makes fossil data helpful to understand the processes behind current biogeographical patterns, because analyzing the whole "movie" of the realized distribution of the species through time includes more information than the mere "picture" provided by its current distribution (Varela *et al.*, 2009).

3.2.- The predictors

The accuracy of SDM predictions also relies on the explanatory variables that we use to build the models (Stockwell *et al.*, 2002). Thus, a key step in the construction of a PSDM is how to choose the predictors. The ideal predictors should have the adequate spatial and temporal resolution to describe the response of the studied species, while at the same time be truly causal factors able to determine the species occurrence (Austin, 2002). Unfortunately, the available predictors for Palaeontological data are in general the coarse-grained outputs of the climatic scenarios provided by different General Circulation Models (GCMs; see (Braconnot *et al.***,** 2007) and http://pmip3.lsce.ipsl.fr/ for detailed information). GCMs are mathematical models simulating the general circulation of the atmosphere and ocean of the Earth that, together with sea-ice and land-surface components, can be used to generate climatic forecasts for a particular moment in the future, or hindcasts for a moment in the past (Foley *et al.*, 1998). To do this, they assume certain initial conditions (like CO_2 atmospheric concentration, ice-covered surface, etc.) and they are run a high number of iterations, until they stabilize (Thompson *et al.*, 1995a; Thompson *et al.*, 1995b).

Due to the difficulty of modelling complex climatic processes at small scales, the spatial resolution of GCM-derived maps is typically coarse, from 2º to 60 km in regional models that use GCMs as the boundary conditions to run more detailed climatic simulations (Barron *et al.*, 2002)). Given that coarse variables can lead to coarse (i.e., unprecise) results (Seo *et al.*, 2009), researchers apply diverse procedures to downscale the climatic layers of these simulations (Peterson *et al.*, 2008; Banks *et al.*, 2008; Galbreath *et al.*, 2009), and different algorithms are applied to define the relationship between large and local scale climate variables, deriving past climatic conditions from either current climatic data or indirect data about past climate (e.g., vegetation from pollen cores) (Hugall *et al.*, 2002; Buckley *et al.*, 2009; Bigg *et al.*, 2008). Unfortunately, there is not a general agreement about the best procedure to downscale climatic simulations; further, the uncertainties of GCMs may be propagated by such downscaling (Katz, 2002). The main weakness of these downscaled regional predictions is that sometimes they do not take in consideration the temporal variations of the local climatic patterns, and they simply reproduce current local climatic anomalies in the past scenarios. However, the extent of the Polar icecaps influences the global atmospheric circulation (e.g., the changes to global circulation caused by the large extensions of ice sheets last glacial maximum 21,000 years ago) (Bowen, 1995). Hence, if global circulation changes through time, it is likely that local circulation would have changed as well, thereby invalidating current local climatic anomalies as proxies for past anomalies.

Apart of the uncertainties related with GCM-based past climatic simulations, the almost exclusive use of climatic variables in while using PSDMs for palaeontological research implies to some extent the assumption that climate factors are the main drivers of species distributions. This supposition is supported by current correlations between climate and species ranges (see Field *et al.*, 2009 and references therein) but it is not exempt of controversy, since other environmental factors and historical and populational processes may also constraint species distributions (Araújo *et al.*, 2005; Lobo *et al.*, 2006; Beale *et al.*, 2008; Peterson *et al.*, 2009; Hortal *et al.*, 2010). Selecting predictors accounting for causal relationships with the basis of correlative analyses is a complex task (Shipley, 2000). This is also the case for SDMs (Bahn *et al.*, 2007). Both, species distributions and climatic variables are spatially structured; due to this, many climatic predictors would be able to describe a species' presence/absence data set simply because their spatial structures covary to some extent, regardless of the existence of a truly causal relationship. Any physiological or biological knowledge on the target species could simplify the selection of the causal variables (Kearney *et al.*, 2009). However, in the absence of such kind of supplementary information diverse statistical techniques can be used to select the most appropriate set of explanatory variables both for presence (Basille *et al.*, 2008; Calenge *et al.*, 2005) and presence-absence data (Murtaugh, 2009). Selecting the minimum number of reliable predictors is key when using SDMs, since the larger the number of variables, the narrower the model predictions will be (Beaumont *et al.*, 2005; Bulluck *et al.*, 2006; Soberón, 2010). A thoughtful selection of predictors, however, does not change the fact that SDMs are correlative or forecasting simulations (*sensu* Legendre *et al.*, 1998, p. 493), and therefore that the predictors that are finally selected to construct the model may not be causally related with the species distribution. Even when they apparently provide an accurate identification of the environmental conditions accounting for the distribution of a species, they may provide inaccurate predictions when transferred to other temporal scenarios (Varela *et al.*, 2009).

3.3.- The modelling technique

The SDM techniques used to model the geographic distribution of species include a diverse array of different statistical and mathematical procedures aiming to relate the observed distribution data of species to a set of spatially defined variables, usually environmental factors (Guisan *et al.*, 2000; Elith *et al.*, 2006; Franklin *et al.*, 2009). These techniques can be divided in: (i) those based in the statistical fitting of data to the theoretical relationships between the species' presence and the environment (GLMz, GAMs, PLS, CART; (Yee *et al.*, 1991, Vaz *et al.*, 2008, Carrascal *et al.*, 2009); (ii) those generated by machine-learning techniques that capture the complex spatial patterns in the observed data without assuming any underlying probability distribution (ANN, GARP, MaxEnt; (Stockwell *et al.*, 1999; Olden *et al.*, 2008; Phillips *et al.*, 2008; Phillips *et al*., 2009); (iii) and those based on methods derived from geometrical or set theory, that only use the information coming from the observed presences (BIOCLIM, DOMAIN, BIOMAPPER, Mahalanobis distance; Busby, 1986; Carpenter, *et al*., 1993; Hirzel *et al.*, 2002; Farber *et al.*, 2003).

The first two kinds of techniques require both presence and absence data as input, and are therefore considered *discrimination* procedures, for they aim to generate a function to discriminate among the different states of a variable. Obtaining absence information for the SDMs carried out with current data is problematic (Lobo *et al.*, 2010) because (i) it is difficult to distinguish true absences from the lack of information in the absence of survey effort measures (which are generally inexistent); and (ii) absence of an species may caused by the effects of non-environmental and contingent factors that are hard to include in any modelling procedure.

These drawbacks force SDM users to incorporate the so-called pseudo-absences and/or background data; absences selected at random from areas where the species has not been recorded or the environmentally conditions are *a priori* unsuitable (Ferrier *et al.*, 1997; Zaniewski *et al.*, 2002; Engler *et al.*, 2004; Lobo *et al.*, 2006), or absences selected at random from the entire study area (Stockwell *et al.*, 1999; Elith *et al.*, 2006). These pseudo-absences, however, should be used with caution (Lobo *et al.*, in press) because their selection may seriously influence the obtained geographic representation (Chefaoui *et al.*, 2008; Lobo *et al.*, 2010). Depending on the protocol used to select the pseudo-absences (or the decision of using only presences), the geographical response described by the SDM results can oscillate between the realized and the potential distribution of the species (Jiménez-Valverde *et al.*, 2008; Colwell *et al.*, 2009; Soberón *et al.*, 2009). In fact, using background absence data selected at random is appropriate to estimate the probability of use of a resource against their availability in order to identify environmental or habitat preferences (i.e., Resource Selection Functions; Boyce *et al.*, 1999), but not to identify realized or potential distributions (Manly *et al.*, 2002).

When SDMs are transferred between different temporal scenarios separated by many generations, absence data are even more problematic. As previously mentioned, spatial, collector and taphonomic biases are the norm in paleontological data, thus hampering their use for the validation of SDMs built from current data. Furthermore and importantly, the non-environmental and contingent effects that are behind the different realized distributions from each temporal scenario prevent the direct use of absence information to calibrate PSDMs; even in the case that such type of factors can be included in the modelling process for a given temporal scenario, there is no guarantee that their effect would be similar in a different period. Based on these conceptual and methodological drawbacks, we recommend not using discrimination or correlative techniques to model fossil data.

This leaves presence records from fossil remnants as the only reliable source of information on the past distribution of a species. These presence data provides valuable information on the environmental conditions in which the species may have had a positive net rate of demographic growth. Therefore, it can be used to estimate the location of the regions with similar conditions to those of the localities with observed data by means of the simple geometrical or set theory-derived methods mentioned above. That is, to offer a preliminary cartographic picture of the regions that could be inhabited by the species in the absence of significant dispersal limitations, local extinctions and/or survey biases (i.e., its potential distribution; Jiménez-Valverde *et al.*, 2008; Colwell *et al.*, 2009; Soberón *et al.*, 2009; Lobo *et al.*, 2010). Establishing a robust methodological framework for the use of past climatic simulations and PSDMs in the emerging field of Palaeobiogeography needs a careful selection of methodological choices. Rather than being fascinated by complex methods, which often provide too narrow responses to the environment (Jiménez-Valverde *et al.*, 2008), choices should be based on the capacity of SDM techniques to represent the species' responses to climatic and non-climatic factors for a given period, and to provide reliable projections of these responses to other moments of time. Given the concerns above, and the problems found when using presence/absence approaches to estimate the past distribution of species (Varela *et al.*, 2009), we argue that although presence/absence SDMs may be suitable for describing the distribution of a species in a single temporal scenario, they are certainly not adequate for predicting the species' response throughout several scenarios of changing climate. Thus, we stress that the abovementioned discrimination techniques and other similar procedures should be avoided for estimating the past distribution of species, because they will likely underestimate their potential distribution.

The different SDM techniques available to predict species distributions from presence-only data (Tsoar *et al.*, 2007; Calenge *et al.*, 2008) are based in the estimation of both the species tolerance range and the species optimum conditions according to the selected environmental predictors. Assuming that (i) a species may be able to survive outside the environmental conditions provided by the observed localities (Soberón *et al.*, 2005; Varela *et al.*, 2009; Soberón *et al.*, 2009), and (ii) that the species can only inhabit a portion of their fundamental niche depending on the available environmental space (Jackson *et al.*, 2000), the estimation of the potential distribution of species from observed occurrence can be carried out by a Multidimensional Enveloping procedure (MDE; see (Busby, 1986). MDE can be used to generate either binary or continuous suitability maps. Binary geographical projections (i.e., suitable *versus* unsuitable localities) can be obtained by estimating the extreme maximum and minimum environmental values in which the species may inhabit, followed by a generalized intersection procedure to delimit the suitable conditions in the multidimensional environmental space which will be finally transferred to the geographical space. Continuous suitability representations require the estimation of both tolerances and environmental optimum in order to draw the most distant and near favourability values. Tolerance estimations are highly dependent of the inclusion of extreme occurrences and, as long as they are reliable, we advocate that such information may be very important to estimate the whole potential distribution of the species. In the specific case of paleontological data we also recommend using as much as possible past and recent information on presences to train the PSDMs, thus maximizing the full spectrum of environmental conditions at which a species may inhabit (Varela *et al.*, 2009). In the same way, if we aim to provide information about the variability in the climatic suitability for the species, we suggest using a distance measure from the optimum, such as the scale-invariant Mahalanobis Distance

(Kadmon *et al.*, 2003; Calenge *et al.*, 2008b; Etherington *et al.*, 2009; Allouche *et al.*, 2008). Of course, the selection of the climatic optimum is a key point since it may also highly influence the provided results. MDE could introduce the distribution of the data within the variables while modelling climatic suitability (Ruegg *et al.*, 2006). However, it is important to note that this approach will only produce accurate results when using complete and non biased presence data sets. Mean, median or any other central tendency measure can only provide good estimations of the species optimum when the data set constitutes a reliable subsample of the species requirements (Nogués-Bravo *et al.*, 2008). In the case of paleontological data we need to emphasise the role of environmental limits (Huston, 2002) as well as to avoid the effect of bias in current and past fossil distribution data. Thus, we recommend the use of amplitude ([maximum - minimum]/2 +minimum) to calculate the central point of the n-dimensional environmental explanatory values in order to promote that the optimum niche conditions are equidistant from the extremes values (Varela *et al.*, 2010).

4. Former species distribution modelling applications in Palaeontology

During our literature search for applications of SDM in Palaeontological research (September 2010) we found a total of forty papers (Tables 1,2 and 3; see also Nogués-Bravo, 2009). These works study not only an heterogeneous group of target species, including plants, vertebrates and insects (Jakob *et al.*, 2009; Jezkova *et al.*, 2009; Marske *et al.*, 2009), but also forests and even biomes (Bonaccorso *et al.*, 2006; Hilbert *et al.*, 2007; Carstens *et al.*, 2007). Their geographic extent is also heterogeneous, varying from regional (Iberian Peninsula (Benito Garzón *et al.*, 2007)), to continental (Europe, North America (Banks *et al.*, 2006)) or even global (Yesson *et al.*, 2006). In this section we review these manuscripts in light of the occurrence data, predictors and SDM techniques they used; further, we provide a synthesis on the basic characteristics of the PSDM applications conducted so far. This complements the former review by Nogués-Bravo (2009) by discussing in detail the limitations of former PSDM works based on the theoretical and practical needs of this kind of studies discussed above.

4.1.- The occurrence data

The training datasets include current georeferenced species occurrences in 29 out of the 40 papers, and current species distribution maps (in eight papers); only three papers are based just on georeferenced fossil records and another eight use both current and past georeferenced

TRAINING DATA			**REFERENCES**
Current data	**Fossil data**	**Target species**	
species distribution maps	-	*Abies* spp.	Alba-Sanchez *et al., 2010*
georeferenced occurrences	georeferenced fossil sites	*Rangifer tarandus*, *Cervus elaphus*	Banks *et al., 2008a*
-	georeferenced archaeological sites	*Homo sapiens*	Banks *et al., 2008b*
-	georeferenced archaeological sites	*Homo sapiens*	Banks *et al., 2006*
georeferenced occurrences	georeferenced archaeological sites	*Rupicapra rupicapra*	Baumann *et al., 2005*
species distribution maps	-	19 tree species	Benito Garzón et al, 2007
georeferenced occurrences	-	*Gadus* spp.	Bigg *et al., 2008*
georeferenced occurrences	-	6 trees, 11 birds	Bonaccorso et al., 2006
georeferenced occurrences	-	*Argosarchus horridus*	Buckley *et al., 2009*
georeferenced occurrences	-	*Prunus lusitanica*	Calleja *et al., 2009*
georeferenced occurrences	-	forest spp.	Carnaval et al., 2008
georeferenced occurrences	-	*Hypsiboas* spp.	Carnaval *et al., 2009*
georeferenced occurrences	-	Frogs, trees and mamals	Carstens et al., 2007
georeferenced occurrences	-	*Trochulus villosus*	Depraz *et al., 2008*
species distribution maps	-	Indigenous forests	Eeley *et al.*, 1999
species distribution maps	-	rodents	Flojgaard *et al*., 2009
georeferenced occurrences	-	*Ochotona princeps*	Galbreath *et al., 2009*
species distribution maps	-	100 plant spp.	Hijmans *et al*., 2006
georeferenced occurrences	-	*Gnarosophia bellendenkerensis*	Hugall *et al., 2002*
species distribution maps		forest classes	Hilbert *et al*., 2007
georeferenced occurrences	-	*Chaetodipus penicillatus*	Jezkova *et al., 2009*
georeferenced occurrences	-	*Hordeum* Species (Poaceae)	Jakob *et al., 2009*
georeferenced occurrences	-	*Melanoplus marshalli*	Knowles *et al., 2007*
georeferenced occurrences	-	*Agyrtodes labralis*	Marske *et al., 2009*
georeferenced occurrences	georeferenced fossil sites	8 tree species	Martinez-Meyer*et al.*, 2006
georeferenced occurrences	georeferenced fossil sites	23 mammal species	Martinez-Meyer*et al.*, 2004
georeferenced occurrences	-	*Saproscincus* spp.	Moussalli *et al., 2009*
-	georeferenced fossil sites	*Mammuthus primigenius*	Nogues-Bravo*et al., 2008*
species distribution maps	georeferenced fossil sites	tree spp.	Pearman *et al.*, 2008
georeferenced occurrences	-	*Aphelocoma* jays	Peterson *et al., 2004*
georeferenced occurrences	-	*Schiffornis* sp.	Peterson *et al., 2008*
georeferenced occurrences	georeferenced fossil sites	*Laurus sp.*	Rodriguez-Sanchez*et al., 2008*
georeferenced occurrences	-	*Catharus ustulatus*	Ruegg *et al., 2006*
georeferenced occurrences	-	Atta spp.	Solomon *et al.*, 2008
species distribution maps	-	22 tree spp.	Svenning *et al.*, 2008
georeferenced occurrences	-	*Crocuta crocuta*	Varela *et al., 2009*
georeferenced occurrences	georeferenced fossil sites	*Crocuta crocuta*	Varela *et al., 2010*
georeferenced occurrences	-	20 terrestrial vertebrates	Waltari *et al.*, 2007
georeferenced occurrences	-	13 mammal species	Waltari *et al.*, 2009
georeferenced occurrences	georeferenced fossil sites	*Drossera* sp.	Yesson *et al., 2006*

Table 1. Summary of the data used in the 40 papers analyzed.

occurrences (see Table 1). However, the geographic and temporal extent of the data are rarely commented, and the same occurs with the completeness of the presence data samples or the selection of the absence data (but see Varela *et al.*, 2010 and Nogués-Bravo *et al.*, 2008). The geographic extent of the training data is usually the area where the model will be projected, sometimes covering the total extent of the species' distribution, but others not (Banks *et al.*, 2008). This latter practice can be a major issue for the reliability of PSDM, because failing to

GEOGRAPHIC EXTENT	CLIMATIC VARIABLES				REFERENCES
	GCM past	Downscaling/variables	Resolution	MODEL	
Iberian Peninsula	CCSM and MIROC	current local climate to estimate past local climate	200 m	maxent	Alba-Sanchez *et al., 2010*
Western Europe	PMIP2 protocol	Refined grid over Europe	60 km	GARP	Banks *et al., 2008a*
Western Europe	PMIP1 protocol	Refined grid over Europe	60 km	GARP	Banks *et al., 2008b*
Western Europe and North America	HadCM3	-	100-200 km	GARP	Banks *et al., 2006*
Switzerland	-	use current climate to estimate past climate	1 km	LGMz	Baumann *et al., 2005*
Iberian Peninsula	ECHAM3 and UGAMP	current local climate to estimate past local climate	-	Random Forest	Benito Garzón et al, 2007
North Atlantic	Ocean GCM	interpolation	5'	maxent and "ecophysiologic ranges"	Bigg *et al., 2008*
Amazon Basin	HadCM3	-	0.1°	GARP	Bonaccorso et al., 2006
New Zeland	-	based on current climate and indirect data	100 m	maxent	Buckley *et al., 2009*
Iberian Peninsula	ECHAM3	anomaly data and interpolating by thin-plane splines	1 km	random forest	Calleja *et al., 2009*
South America	ECHAM3	bilinear interpolation	30"	maxent and bioclim	Carnaval et al., 2008
Brazilian Atlantic Rainforest	-	-	-	maxent	Carnaval *et al., 2009*
Western North America	CCSM3	interpolation	-	maxent	Carstens et al., 2007
Central Europe	CCSM	current local climate to estimate past local climate	10'	bioclim	Depraz *et al., 2008*
South Africa	-	use current climate to estimate past climate	15"	bioclim	Eeley *et al.*, 1999
Eurasia	S3P and LMDZHR	current local climate to estimate past local climate	30"	maxent and bioclim	Flojgaard *et al*., 2009
North America	CCSM3 and MIROC	current local climate to estimate past local climate	2.5'	maxent	Galbreath *et al., 2009*
America	ECHAM3	current local climate to estimate past local climate	1km	maxent, bioclim, Domain and GAM	Hijmans *et al*., 2006
North Queensland, Australia	-	use current climate to estimate past climate	80 m	bioclim	Hugall *et al., 2002*
North Queensland, Australia	-	use current climate to estimate past climate	1 ha	Artificial neural network	Hilbert *et al*., 2007
Eastern North America	MIROC	interpolation	2.5'	maxent	Jezkova *et al., 2009*
South America	CCSM and MIROC	interpolation	0,01°-0,04°	GARP	Jakob *et al., 2009*
North America	CCSM3	interpolation	1'	maxent	Knowles *et al., 2007*
New Zeland	-	use current climate to estimate past climate	100 m	maxent	Marske *et al., 2009*
North America	HadCM2	resampled	0.1°	GARP	Martinez-Meyer *et al.*, 2006
North America	-	use current climate to estimate past climate	-	GARP	Martinez-Meyer *et al.*, 2004
Australian Wet Tropics	-	estimated from pollen	-	GLMz averaged	Moussalli *et al., 2009*
Eurasia	GENESIS	-	2°	Mahalanobis distances, maxent and bioclim	Nogues-Bravo *et al., 2008*
Europe	UBRIS-HadCM3	current local climate to estimate past local climate	1 km	boosted regression tree	Pearman *et al.*, 2008
North America	HadCM	current local climate to estimate past local climate	0.1°	GARP	Peterson *et al., 2004*
Central and South America	MIROC and CCSM	current local climate to estimate past local climate	0.04°	GARP and maxent	Peterson *et al., 2008*
Europe and the Mediterranean	ECHAM3 and UGAMP	current local climate to estimate past local climate	100 km	maxent	Rodriguez-Sanchez *et al., 2008*
America	ECHAM	current local climate to estimate past local climate	10 km	bioclim	Ruegg *et al., 2006*
Central and South America	ECHAM	current local climate to estimate past local climate	100 km	maxent	Solomon *et al.*, 2008
Europe	S3P and LMDZHR	Refined grid over Europe	60 km	maxent and bioclim	Svenning *et al.*, 2008
Eurasia and Africa	GENESIS	-	4.5° x 7.5°	LGMz and Bioclim	Varela *et al., 2009*
Eurasia and Africa	GENESIS	-	2°	Mahalanobis distances and Bioclim	Varela *et al., 2010*
North America	CCSM and MIROC	current local climate to estimate past local climate	2.5'	maxent and GARP	Waltari *et al.*, 2007
North America	CCSM and MIROC	current local climate to estimate past local climate	2.5'	maxent and GARP	Waltari *et al.*, 2009
Global and Australia	BRIDGE	-	2°	Bioclim	Yesson *et al., 2006*

Table 2. Geographic extent, General Circulation Models for the past, downscaling methodologies used for constructing the variables and models used in the 40 papers analyzed.

include data from the entire geographic extent of a species could spuriously narrow down the sampled tolerance range for a species and therefore result in an underestimation of its potential distribution (Thuiller *et al.*, 2004).

Importantly, the majority of PSDM applications were trained using only a single temporal scenario (Table 1). In almost three quarters of the works (29 cases) the SDM was calibrated using only the current species' distribution (see Table 1), a procedure in which the obtained models may fail to represent the distributions when transferred to past periods (Varela *et al.*, 2009). In fact, the assumption that the projections from a PSDM calibrated in a given period are able to predict the presence of the species in a different moment of time was only evaluated in certain papers (see Nogués-Bravo *et al.*, 2008 and Varela *et al.*, 2009), giving positive results for the former, but not for the latter. Further, 34 out of 40 papers use absence data to train the models (see Table 1) and 25 cases use MaxEnt or GARP techniques for estimating the species geographic range using background absences in the training procedure. As we discuss above, the use of presence-absence techniques and the effect of including absence data in the training data set are likely to provide erroneous estimations.

4.2.- Predictor variables

Twenty-two out of the 40 papers use diverse downscaling methodologies to build their climatic explanatory variables (see Table 2). In 15 of these studies it is assumed that the spatial patterns, amplitude and sign of current climatic anomalies at the local scale should be identical across time, and they use them to construct fine-scale climatic layers. Seven papers adopt an even simpler strategy and construct the variables describing past climate simply by adding or subtracting certain values to the current climatic layers. As discussed above, both methods are likely to include significant errors in the climatic predictors. Further, the lack of a standard for downscaling past climate scenarios includes a source of variability in the predictors used for analyses on the same geographic area and temporal scenario, thus hampering the direct comparability between their results.

Although it is well known that the number and identitiy of the predictors deeply influence the SDM results, few papers use any methodological approach to choose the independent variables. In fact, the predictors used in the analysis are generally chosen on the basis of their easy availability. As a result, the 19 WorldClim variables (available at http://www.worldclim.org/) are the most used for current time; the more difficult accessibility to GCM-derived climatic layers for past scenarios results in that a diverse array of GCMs have been used for this task.

Given the difficulty of extrapolating GCMs to the past and thus the limitations in projecting complex aspects of climate, Annual Mean Temperature and Annual Precipitation are the two predictors most commonly included in the PSDM.

4.3.- Modelling techniques

Most of the analyzed studies use presence/absence-based SDM techniques to estimate the past distribution of species, including MaxEnt, GLMz, GAM, GARP, RF, BRT and ANN (see Table 2). From these, MaxEnt is the most popular, being used in almost half of the works (19 cases), followed by GARP (11 cases). Presence-only SDM techniques are however used in 12 papers; all these papers use Bioclim, together with Mahalanobis Distances in two occasions (Nogués-Bravo *et al.*, 2008; Varela *et al.*, 2009). It is also necessary to outline that PSDM results are presented as climatic suitability maps in nine cases. This practice should be disencouraged, because SDMs do not estimate the climatic suitability of the species, but rather model the species presence based on the local conditions; due to this, the continuous SDM results should be always transformed to binomial maps by applying an appropriate threshold (Jimenez-Valverde *et al.*, 2007).

4.4.- Problems and limitations of former PSDM approaches

Our review shows that diverse methods have been used for estimating the past distribution of species. According to the conceptual and methodological recommendations provided above, we believe that most of these studies follow unreliable PSDM approaches that could be overestimating the role that climatic changes had on past species range shifts and/or extinction events. In general, the choice of the distributional data used in the model training process is based only on the type of information available for the species (either current, fossil, or both), and not on the adequacy for the question at hand. This strategy implicitly assumes that the available information of the species is sufficient to estimate their climatic requirements, and therefore, to calibrate a model that can be safely projected to the past. Unfortunately, given the abovementioned reliance of SDM results on the distributional data used we believe that this assumption may prove to be false in most of the cases, and could be leading to underestimations of the geographic ranges of the species in different periods of time. The probability of underestimating the species potential requirements will however diminish if the training dataset on species occurrences covers the entire geographic and temporal extent where the species has lived, and also by avoiding the inclusion of any kind of absence data, including pseudo-absences (see above, and also Jiménez-Valverde *et al.*, 2008).

We also advocate that PSDM are constructed using a careful selection of climatic predictors, a step that is commonly overlooked in the reviewed literature. To do this, we recommend using multivariate niche description techniques such as Ecological-Niche Factor Analysis (ENFA; (Hirzel *et al*., 2002; Basille *et al*., 2008) to select those variables with higher probabilities of being causally related with the species' presences. Whenever possible, the projections of PSDM at different moments of time should be cross-examined to ensure that models calibrated with data from a certain period are able to describe the range of the species in other moments of time.

Finally, we want to stress that the SDM techniques used should be those appropriate to the posed questions. Different SDM procedures produce wider or narrower geographic predictions and consequently they can have a profound impact in the biological interpretation of the results. We believe that in absence of any supplementary information about the species' climatic requirements, the methodological approach used for PSDMs needs to be conservative. While data for these analyses is typically composed of samples of the species' geographic range at different moments of time, these ranges are dynamic entities that vary as a consequence of the interactions between the potential distribution of the species and both climatic and non-climatic factors. Given the importance of non-climatic factors in preventing the species to be present in climatically suitable areas, discrimination techniques based on absence information should be discarded when estimating the climatic niche and the past distribution of species, because they would underestimate its potential distribution. In this context, we think the most adequate option to predict the species' potential distribution through time is using the conservative multidimensional climatic envelope. Similarly, Mahalanobis Distance would be a proper solution when the aim is to estimate the climatic suitability for the species based on an hypothetical climatic optimum.

5.- Future prospects for Palaeobiogeography

The generalization of Palaeo-Species Distribution Modelling approaches has the potential of generating fresh palaeontological information ans hypotheses in the forthcoming years. To take full profit of such potential it would however be fundamental: (i) to create a global database to compile all the distributional information available for the Pleistocene; (ii) to develop high resolution climatic layers for different past scenarios by means of a widely-agreed standardized protocol; and (iii) the in-depth investigation of the nature and temporal variation of species–climate relationships, as well as of which SDM methodologies provide the most adequate simulations of these changing relationships.

The analysis of the Pleistocene distribution of any species implies using data from different fossil sites. Therefore, one of the first goals for the development of modern Palaeobiogeography should be establishing a global open-access database, similar to the ones available for current species, such as GBIF (http://www.gbif.org/). As we have mentioned, some initiatives are already aiming to provide similar databases on the Internet, including the Paleobiology Database (http://www.paleodb.org/cgi-bin/bridge.pl), Faunmap (http://www.museum.state.il.us/research/faunmap) or Stage Three Project (http://www.esc.cam.ac.uk/research/research-groups/oistage3). However, there are several points that need to be improved. First, the available information about fossil dating is extremely broad. As an example, *Homo antecessor* is roughly assigned to the Pleistocene (1.810 to 0.011 Ma) (query on The Paleobiology Database) when it has been dated by paleomagnetism as being not older than 780 ma, and assigned to the end of the Earlier Pleistocene using ESR and U-series (Falgueres *et al.*, 1999). Second, the temporal and spatial scopes of these databases are limited. For example, The Stage 3 Project compiles European fossil sites previous to the Last Glacial Maximum, and FAUNMAP is geographically restricted to North America. Third, all these databases have rigid taxonomic classifications. Pleistocene mammal taxonomy have been changed in the light of new evidences (Alroy, 2003) and fossil records could be reclassified in the future due to the appearance a new evidences based on ancient DNA studies or any new technology. Therefore, any durable database should allow using as many taxonomic classifications as it would be necessary, providing taxonomic fields that allow eventual changes in the systematic of the group or the reassignment of specific fossil remnants to different taxa in the light of future revisions. The experience of neosystematicians in building standards for biodiversity information (see the most updated information on the Taxonomic Database Working Group at http://www.tdwg.org/) will make the design of such Palaeodistributional database relatively easy.

Most difficulties in gathering information about the Pleistocene fossil record may be trivial. Estimating the past geographic location of the fossil remnants should not be a significant problem, for Pleistocene landmass distribution is similar to the current one except for the coastline variations in relation to the glacial cycles (Peltier, 2007). Therefore, in the absence of traslocations the original location of the remnants can be safely assigned to the current location of the deposit. Finally, to guarantee the success of the database on Paleodistributional data we suggest to follow the philosophy of the community of molecular biologists, where many journals require the submission of any sequence information used in the manuscript to a unified database, the GenBank of GenBank (http://www.ncbi.nlm.nih.gov/genbank/) prior to publication. A similar strategy followed by Palaeontology, ecology and biogeography journals would help establishing a similar philosophy in Palaeontology, encouraging researchers to upload the faunal lists of their fossil sites into an open access database. The unified source of information that would be obtained with such a database will constitute a basic resource for the study of species ranges dynamics through time, the relationships between species distribution and climatic change, or any other spatio-temporal pattern, and hence should be the pillar of the development of modern palaeobiogeography and palaeoecology.

A unified database on the distribution of the diversity in the past is not the sole requisite for the advancement of Paleaobiogeography. Species relationships with climate are ultimately determining the long-term viability of local populations, and are therefore dependent on fine-scale climate patterns (Seo *et al.*, 2009), so understanding these relationships also needs the development of high-resolution climatic layers for past periods. Given the uncertainty inherent to GCMs, the development of different temporal simulations may also help assessing the robustness of PSDM results to differences in the parameterization of the climatic models (see also Araújo *et al.*, 2007). Also, the projection of GCMs to continuous temporal series of climatic projections rather than to key moments in time could permit to create temporally dynamic models, which would in turn help analysing hypotheses on the dispersal of species and their range dynamics. Finally, we argue that more theoretical research is needed to understand the species–climate relationships, following the line of research recently re-open by Soberón (2007, 2010) and Soberón *et al.* (2009) (see also (Kearney 2006; Jiménez-Valverde *et al.*, 2008 or Colwell *et al.*, 2009). Such research will allow identifying the factors that should be taken into account to simulate the impacts that climatic changes have on species distributions.

6.- CONCLUSIONS

Given current global concern about the consequences of climatic changes, the study of Pleistocene biogeography could provide new information about the biological consequences of climatic changes. The development of Palaeo-Species Distribution Models can be a central part of such research, taking profit of the information on the past occurrence of species available from the fossil record, the development of global climate models and their projection to past scenarios, and the current theoretical advances on the relationship between the fundamental niche of the species and their geographical distribution. Here we argue that the fossil data used to calibrate the PSDMs should include as much information as possible, covering the entire geographic extent of the species' range and its complete fossil record whenever feasible. Also, absence and pseudo-absence data should be avoided, for they could add misleading information that would difficult the descrition of species–climate relationships. Although the predictors used should preferably have adequate resolution to describe these relationships, we recommend not to downscale the geographical projections of GCMs using simplistic rules. Here it would be preferable to assume the limitations on the resolution of the study to coarse or to wait for the development of regional GCMs that allow projecting past climatic layers with increasingly higher spatial resolution. The selection of the adequate predictors is also a key point in the construction of PSDMs; here we suggest using ENFA analysis to selecting the most biologically meaningful variables. Based on the restriction to presence-only SDMs we suggest, the most adequate PSDM methodologies would be (a) climatic envelopes based on the climatic tolerance range of the species when the aim is to detect geographic range shifts in relation to climatic changes; or (b) distance-based techniques such as Mahalanobis Distances when some continuous information about the climatic suitability for the species is required, although in this case the selection of the species' optimum should be discussed and justified. By following all these recommendations we believe that we will be able to diminish the errors in the estimations on the potential distribution of the species, and therefore ensure that the future use of PSDMs will bring robust results and at the same time stimulating ideas to the fields of Palaeoecology and Palaeobiogeography.

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Capítulo 7:

Discusión general, conclusiones y futuras líneas de investigación:

El objetivo general inicial de esta tesis doctoral buscó analizar la extinción de las poblaciones europeas de hiena machada, un carnívoro de gran talla que desapareció de Europa a finales del Pleistoceno. Sin embargo, a medida que el proyecto se fue desarrollando, surgió la necesidad de profundizar en las bases teóricas y metodológicas que sustentan el uso de los modelos de distribución de especies (SDM). Por este motivo, esta tesis doctoral es la consecuencia del trabajó realizado en dos direcciones complementarias; por una parte hemos tratado de comprobar el impacto que pudieron haber ocasionado tanto los cambios climáticos del pasado como las variaciones en las presas potenciales disponibles para las hienas a lo largo del Pleistoceno Superior, y por otra hemos analizado las posibilidades e inconvenientes de aplicar los modelos de distribución de especies cuando se pretende predecir los cambios geográficos que pudieron sufrir las especies en el pasado.

La hiena manchada habitó durante casi un millón de años en un continente en el que tanto el clima como las poblaciones de herbívoros se modificaron en numerosas ocasiones de manera drástica (Svenning *et al.*, 2009; Wagner *et al.*, 2009; Scott, 2010). Antes de comenzar este proyecto se asumía que los cambios climáticos del pasado habían sido la principal causa de la extinción de la megafauna, y por extensión, de las poblaciones euroasiáticas de hiena manchada (Lyons, 2003; DeMenocal, 2004; Prado *et al.*, 2001). Sin embargo, nuestros resultados indican que, si bien el clima europeo fue extremo para la supervivencia de la hiena, en ningún momento el continente dejó de ser habitable para la especie. Además, al igual que las poblaciones europeas, nuestros modelos predicen que las poblaciones africanas de hiena manchada sufrieron una retracción considerable de su área favorable para la supervivencia como consecuencia del enfriamiento del clima durante el máximo glaciar (hace 21.000 años). De modo que nuestros resultados indican que el clima, de manera aislada, solo puede explicar la extinción diferencial de las poblaciones más septentrionales de *Crocuta crocuta*, ya que el Sur del continente Euroasiático habría mantenido condiciones climáticas favorables durante todo el Pleistoceno.

Como los cambios climáticos del pasado no resultaron suficientes para explicar la extinción de las poblaciones ibéricas de hiena manchada, realizamos una segunda aproximación, analizando los cambios faunísticos sucedidos a finales del Pleistoceno Superior como posible factor desencadenante de la desaparición de esta especie. El análisis sobre la capacidad de carga de un ecosistema Mediterráneo dio como resultado que la densidad de herbívoros de un ecosistema de finales del Pleistoceno podría mantener una población viable de hiena manchada, incluso después de considerar la posible interferencia competetitiva con otro gran carnívoro como *Canis lupus*. De este modo, ni los cambios climáticos ni los faunísticos pueden ser argumentados como condición suficiente para explicar la extinción de las poblaciones europeas de hiena manchada, al menos, de una manera aislada.

Estos resultados apuntan la necesidad de dar un paso más y crear modelos más complejos, que tengan en cuenta las relaciones y sinergias que se establecen entre los diferentes factores que afectan a los ecosistemas y por ende, a la supervivencia de las especies. En el caso de la hiena manchada creemos que es necesario investigar dos factores que aun no han sido considerados: la presión que podría haber ejercido *Homo sapiens* sobre las poblaciones de hienas y la distribución geográfica de los sistemas kársticos que utilizan las hienas como refugio. En este sentido, los resultado obtenidos abren nuevas líneas de investigación, que vuelven a tener dos vertientes, una práctica, en la cual se deberá testar el papel de factores como la competencia con *Homo sapiens* o la distribución espacial de los sistemas kársticos, y otra teórica, que apunta a la necesidad de profundizar en nuestro conocimiento sobre los sistemas de interacciones ecológicas, para poder predecir las consecuencias de las modificaciones en alguno de sus parámetros (ya sea el clima, la abundancia relativa de las especies o la presencia/ausencia de un recurso limitante).

Por otra parte, al tiempo que construíamos nuestros modelos para testar las hipótesis biológicas, también trabajamos en paralelo analizando las asunciones teóricas de la metodología comúnmente utilizada por los modelos de distribución de especies. El interés por estas técnicas se ha incrementado exponencialmente en los últimos años (Guisan *et al.*, 2005; Austin, 2007), con el propósito de predecir la distribución geográfica de una especie utilizando la información biológica existente En nuestro caso nos encontramos con un problema de fondo cuando tratamos de predecir la distribución de la hiena manchada basándonos en datos actuales (Capítulo 5). Nuestro modelo, a pesar de contar con validaciones muy favorables, erraba al predecir la distribución de la especie en el pasado. Este resultado indica que, a pesar de contar con valores de validación aparentemente altos, los modelos pueden fallar cuando se extrapolan en el tiempo. Nuestra hipótesis para explicar este fenómeno ha sido que los datos de presencia de una especie (su distribución realizada) pueden no representar el total de condiciones ambientales favorables para esa especie. Por ello, los modelos calibrados con una única muestra de un escenario, pueden dar errores al ser extrapolados. Después de obtener este resultado decidimos hacer una revisión de las herramientas metodológicas y los tipos de datos utilizados para predecir la distribución de las especies en el pasado. Los resultados de ese trabajo indican que los métodos empleados son muy heterogéneos. Nuestras recomendaciones a la hora de construir modelos para predecir el rango geográfico ocupado por las especies en el pasado son, por una parte, conocer los sesgos espaciales, temporales, tafonómicos y el esfuerzo de muestreo de la especie de interés, a fin de interpretar adecuadamente los datos procedentes del registro fósil. Después, consideramos que la elección de las variables climáticas que se incluirán en el modelo es fundamental, y para ello recomendamos métodos como ENFA. Y por último, consideramos que los únicos modelos que intrínsecamente no subestiman la capacidad potencial de una especie, son los modelos “geométricos”, basados en rangos (e. g. “climate envelope”, Bioclim) o en distancias desde un centroide (e. g. Distancias de Mahalanobis), y por este motivo, recomendamos su uso para predecir los cambios potenciales en el área ocupada por las especies en el pasado. Estos resultados apuntan de nuevo a la necesidad de continuar ahondando en el estudio teórico de la relación entre las especies, el clima, y la distribución geográfica.

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Crocuta crocuta.
Fotografía: Sara Varela

CONCLUSIONES Y FUTURAS LÍNEAS DE INVESTIGACIÓN:

1. Las poblaciones europeas de hiena manchada no parecen haberse extinguido por un único motivo, como pudieron haber sido los cambios climáticos ocurridos durante el Pleistoceno o los cambios en las faunas de herbívoros. *Por ello, en el futuro será necesario considerar modelos predictivos de mayor complejidad que combinen los efectos generados por diferentes factores para conocer si en este caso es posible explicar más adecuadamente la desaparición de las poblaciones europeas de* Crocuta crocuta *a finales del Pleistoceno.*

2. Nuestros resultados apuntan a que, durante los periodos interglaciares, las áreas más septentrionales de Europa poseían un clima favorable para la presencia de hiena manchada. *Como el registro fósil indica que la especie nunca ha habitado por encima del paralelo 55 N, será necesario investigar cual pudo haber sido la barrera que impidió la colonización del norte de Europa durante estos periodos o cual es la causa de la inexistencia de estos datos.*

3. Nuestros modelos indican que al igual que en Europa, en África las poblaciones de hiena manchada pudieron haber sido afectadas drásticamente por los cambios climáticos del Pleistoceno, ya que durante el máximo glaciar existiría una única área favorable para la especie situada en el Sur de este continente. *Por este motivo, será necesario investigar los factores que pudieron favorecer la supervivencia de las poblaciones africanas después de la crisis climática del último máximo glaciar.*

4. Los modelos de distribución de especies en Paleontología deben utilizar todos los datos disponibles sobre la distribución de las especies, tanto fósiles como actuales, para de esta manera poder ofrecer una imagen más cercana al conjunto de condiciones ambientales que potencialmente puede habitar cada especie. Usando partes de la distribución realizada de una especie (ya sea temporal o espacialmente), el modelo puede producir predicciones potenciales erróneas cuando se extrapola fuera de las condiciones donde fue calibrado.

5. Para predecir la distribución espacial de una especie en el pasado, debemos interpretar adecuadamente los datos fósiles, seleccionar las variables que tengan un significado biológico para la especie, y utilizar modelos que no subestimen los requerimientos potenciales de las especies. *En este sentido, el primer paso imprescindible que se deberá dar para avanzar en el estudio de la paleobiogeografía será construir una base de datos que compile los registros fósiles de las especies que habitaron en el pasado. Esta base de datos debe ser libre y accesible desde internet, de modo que a partir de la información generada, se puedan generar modelos para comprobar hipótesis biogeográficas cada vez más ambiciosas e innovadoras.*

CONCLUSIONS AND FUTURE RESEARCH LINES:

1.-European spotted hyena populations did not disappear as consequence of a unique and single factor. Climatic changes or prey diversity changes, acting separately, were not able to explain this extinction event. *Therefore, we suggest building more complex models able to incorporate the joint role played by different factors in order to increase the reliability of our predictions.*

2.- During the interglacial periods North Europe was predicted to have conditions suitable to the survival of hyenas. However, there are no fossil records of the species further north than 55ºN. *Therefore, in the future it will be important to investigate which barriers could have prevented* Crocuta crocuta *to colonize Northern Europe during the Pleistocene.*

3.- Our models predict African spotted hyenas population reduced survival as a consequence of past climatic changes. *As consequence, in our next studies we will analyze which factors, present in the African ecosystems, could have helped* Crocuta crocuta *to recover after the climatic crisis.*

4.- Species distribution models should be built using as much information about the species as possible. Using one single temporal scenario data set could produce misleading results when transferred to a new time.

5.- Carrying out accurate models to hindcast the species geographic ranges to past scenarios requires to consider spatial and temporal biases of the fossil record. Also, the selection of the variables should follow a theoretical biological framework (i.e. it should not be based only on a mathematical correlation) and we should use models that do not underestimate the species' potential response to the climatic changes. *In order to advance in the field of Palaeobiogeography we need to establish high-quality open access databases. After doing so, we would be ready to test new and more ambitious biogeographical questions about both, past and future ecosystem functioning.*

Crocuta crocuta. Fotografía: Sara Varela