UNIVERSIDAD DE GRANADA DEPARTAMENTO DE ZOOLOGÍA



CRÍA COOPERATIVA Y PARASITISMO DE CRIA

EN LA CORNEJA NEGRA

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CRÍA COOPERATIVA Y PARASITISMO DE

CRÍA EN LA CORNEJA NEGRA

Memoria que la Licenciada María Roldán González presenta para aspirar al Grado de Doctor por la Universidad de Granada

Esta memoria ha sido realizada bajo la dirección de: Dr. Manuel Soler Cruz

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A mi madre

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RESUMEN

Los cuidados parentales implican cualquier tipo de comportamiento de los padres que incremente el éxito reproductor de su descendencia. Dado que el cuidado parental es una de las actividades relacionadas con el éxito reproductor del individuo que mayor cantidad de energía consume, no debe sorprender que comportamientos como la cría cooperativa o el parasitismo de cría hayan evolucionado para reducir los costes de los eventos reproductores. Aquí estudiamos ambos comportamientos, así como la interacción entre ellos, en una población de corneja negra localizada en el Sur de España.

En la presente tesis describimos la segunda población de corneja negra encontrada en toda el área de distribución de la especie y la comparamos con la ya conocida. Ambas poblaciones presentan características muy similares. La principal diferencia estriba en la tasa de puestas de reposición, siendo casi nula en nuestra población de estudio mientras que en la del norte de España es bastante frecuente. Por otra parte, no hemos encontrado los efectos positivos del tamaño de grupo sobre el éxito reproductor descritos en otras poblaciones de aves cooperativas. Por el contrario, hemos encontrado algunos efectos negativos como la relación del tamaño de grupo y el incremento en el número de pollos muertos por inanición.

Resumen

El parasitismo de cría es otro de los comportamientos que los individuos pueden desarrollar con el fin de reducir los costes de los cuidados parentales, pero éste no es el único tipo de parasitismo que reduce tales costes. En la presente tesis, en primer lugar, hacemos una revisión de todos los comportamientos animales que reducen la inversión parental del parásito, englobándolos todos bajo el término "parasitismo de cuidados parentales". Al contrario que las clasificaciones existentes, nosotros proponemos una basada en los costes que el parasitismo implica para el hospedador. Además, discutimos bajo el prisma de las teorías de la inversión parental y la carrera de armamentos coevolutiva, las contra-adaptaciones que los hospedadores han desarrollado frente al parasitismo de cuidados parentales.

La interacción de la cría cooperativa y el parasitismo de cría han sido muy poco estudiados. En este estudio comparamos el parasitismo de cría del críalo europeo en dos poblaciones cooperativas de corneja y encontramos que, en una de ellas (Guadix), la corneja negra es el hospedador secundario, siendo el hospedador primario la corneja, mientras que en la otra población (La Sobarriba) es al contrario, es decir, la corneja es el hospedador preferido (más parasitado) mientras que las tasas de parasitismo en la urraca son bajas, a pesar de que el éxito reproductor del críalo en urraca es mayor en ambas poblaciones. El motivo de este cambio de hospedador no está claro, pero analizamos varias posibilidades como

Resumen

son: la fecha de puesta, la disponibilidad y accesibilidad de los nidos y la existencia de razas dentro de la especie.

Otro importante aspecto en relación con el parasitismo de cría es conocer los mecanismos mediante los cuales la descendencia parásita consigue engañar a los padres hospedadores para conseguir que le den los mejores cuidados. Hemos estudiado el comportamiento de petición de alimento de los pollos en nidos parasitados y no parasitados de corneja y comparamos los comportamientos de los pollos y los adultos. Nuestros resultados muestran que, aunque los pollos de críalo presentan un comportamiento petitorio de mayor intensidad, no son capaces de competir con el mayor tamaño de los pollos hospedadores. Probablemente debido a esta preferencia de los adultos de corneja por alimentar a los pollos de mayor tamaño, sus propios pollos resultan favorecidos respecto a los parásitos.

También pusimos a prueba la hipótesis del mimetismo de la llamada de petición de alimento del pollo de críalo comparando las llamadas emitidas por los pollos en los nidos de sus dos hospedadores principales en Europa: la urraca y la corneja. Nuestros resultados muestran que las llamadas de petición de alimento del críalo en ambos hospedadores se diferencian en su estructura (número de notas por llamada), pero no son miméticas con las del hospedador. Además, llevamos a cabo un experimento de intercambio de pollos para determinar si estas diferencias

eran debidas a factores genéticos o ambientales. Los resultados nos permiten descartar los factores genéticos y sugieren que las modificaciones de las llamadas de petición de alimento descritas puedan ser debidas a un proceso de aprendizaje que se produce cuando los pollos eclosionan.

SUMMARY

Parental care involves any sort of parental behaviour that increases the fitness of assisted offspring. As parental care is one of the most energy-consuming activities that affect an individual's fitness, it is not surprising that behaviours like cooperative breeding or brood parasitism had been evolved to reduce such costs of reproductive events. Herein we studied both behaviours in a population of carrion crow located in South Spain, as well as the interaction of both.

In this thesis we describe the second found cooperative population of carrion crow and compare it with the other one already studied. Both populations are quite similar but differ in the re-nesting rate that is almost absent in our study area. On the other hand, we do not find the expected positive effect of group size on breeding success and that had been described in other cooperative populations. On the contrary, we found some negative effects related to group size like the increase of starved nestlings.

Brood parasitism is another behaviour that individuals could develop in order to benefit from the reduction of parental care costs, but it is not the only kind of parasitism that reduces such costs. In the present thesis we review all the behaviours that reduce parental care investment of the parasite individual and encompass them under the heading of "parental-care parasitism. As opposed to the already existing classifications, we categorise Summary

those parasitic behaviours according to the costs produced to the host. Furthermore, we discuss them under the view of the parental investment and coevolutionary arms race theories, the counter-adaptations that hosts have developed against parental care parasitism.

The interaction of cooperative breeding and brood parasitism have been faintly studied. Herein we compared brood parasitism by great spotted cuckoos in two cooperative populations of carrion crow, and found that in one of them carrion crow is the secondary host, being the magpie the main one, but in the other population it is the inverse, that is, carrion crow is the preferred (more parasitized) host, while magpies presented small parasitism rates, even when cuckoo reproductive success in crows is lower in both populations. The cause of this change in host preference is still unclear to us, but some possibilities such as laying date, availability and accessibility of nests, and the existence of gentes are discussed.

Another interesting point related to brood parasitism is to know the mechanisms by which the parasitic offspring cheat their foster parents to achieve the best care from them. Thus, we studied the begging behaviour of nestlings in both parasitized and non-parasitized carrion crow nests, and compared nestling's and adult's behaviours. Our results show that although great spotted cuckoo nestlings begged more intensively, they were not able to outcompete the larger host nestlings, probably because crow adults fed preferably their own chicks.

Summary

Finally, we tested the hypothesis of mimicry of the begging call of great spotted cuckoo nestlings by comparing them in its two main hosts in Europe: the magpie and the carrion crow. Our results show that cuckoo begging calls in both hosts differed in call structure (number of notes per call), but are not mimetic to host's ones. We performed a cross-fostering experiment to determine whether those differences were due to genetic or environmental factors. The results allowed us to discard genetic factors, and suggest that modifications described in cuckoo begging calls could be due to a learning process of the hatchling.

INTRODUCCIÓN

La reproducción es el fin último que persiguen los seres vivos. El hecho de dejar descendientes en las mejores condiciones posibles para su reproducción es la clave para pasar exitosamente los genes propios a la siguiente generación y es la forma en la que medimos la eficacia biológica de los individuos. Para que la descendencia crezca en condiciones óptimas y sea capaz de reproducirse, muchos animales cuidan, protegen y alimentan a sus descendientes, estos cuidados se conocen como cuidados parentales. Los cuidados parentales incluyen cualquier tipo de comportamiento por parte de los adultos que incremente la eficacia biológica de la descendencia que se cuida (Clutton-Brock 1991). Se han descrito cuidados parentales en la mayoría de los grupos animales, pero están especialmente bien desarrollados en numerosas especies de insectos, crustáceos y vertebrados (Glazier 2002), sobre todo, aves y mamíferos. Puesto que en muchas especies el cuidado parental es una de las actividades que más energía consume, afecta muy directamente la eficacia biológica de los padres (Trivers 1972; Clutton-Brock 1991). Por una parte reporta beneficios que, en la mayoría de los casos, se basan en la supervivencia, crecimiento y reproducción futura de la descendencia. Por otra parte, genera costes disminuyendo su supervivencia y, principalmente en el caso de la hembra, su reproducción futura, e incluso, la supervivencia de su descendencia

futura. Estos costes varían ampliamente en función de las condiciones ambientales y la calidad de los padres (Clutton-Brock 1991). Dado que la mayoría de las especies desarrollan algún tipo de cuidado parental, es lógico pensar que el balance entre costes y beneficios es positivo para los padres. A este respecto, la teoría de la inversión parental (Trivers 1972) asume que el cuidado parental es el resultado evolutivo de la relación entre costes y beneficios en la eficacia biológica del individuo; así los padres incrementarían su eficacia biológica haciendo balance entre la inversión parental presente y futura (Trivers 1972; Carlisle 1982; Winkler 1987; Montgomerie & Weatherhead 1988; Clutton-Brock & Vincent 1991).

Puesto que el cuidado parental es costoso y es importante para los padres ahorrar energía para futuros eventos reproductores, no es de extrañar que interacciones entre individuos de la misma o de diferentes especies como la cría cooperativa o el parasitismo de cría estén representadas en muchas especies.

Cría cooperativa

La reducción de la reproducción individual para favorecer la reproducción de otros individuos está ampliamente distribuida entre organismos y ofrece algunas de las evidencias indirectas más fuertes de selección de parentesco. Los insectos sociales son un caso claro a este respecto; la "eusocialidad" en

termitas, hormigas, abejas y avispas conlleva la existencia de castas estériles cuya función básica es incrementar la tasa reproductora de la reina (generalmente su madre) colaborando en la cría de la descendencia de la reina (generalmente hermanos y hermanas de los individuos de las castas estériles) (Hamilton 1964). Pero la eusocialidad no es exclusiva de insectos, dentro de los vertebrados, también encontramos una especie eusocial: la rata topo desnuda (*Heterocephalus glaber*, Faulkes & Abbott 1997). Sin embargo, no sólo las especies eusociales cooperan en la cría de la descendencia de otros individuos, hay muchas especies en las que, sin existir castas estériles, existen "ayudantes" (individuos que se dedican a criar a hijos de otros, Brown 1987). Estos casos de cría cooperativa son relativamente frecuentes en aves (Skutch 1961; Lack 1968; Woolfenden 1975).

Existen muchas definiciones para la cría cooperativa, entre ellas la que aporta Pruett-Jones (2004) parece ser la que mejor refleja el proceso de formación de los grupos: "el retraso en la dispersión de los juveniles y el cuidado aloparental por esos individuos filopátricos". En la mayoría de las especies de vertebrados, y especialmente en las aves, la cría cooperativa se produce en las sociedades familiares (ej. carricero de las Seychelles, *Acrocephalus sechellensis*, Brown 1987; suricatas, *Suricata suricatta*, Clutton-Brock et al. 1998). Sin embargo, la cría cooperativa también puede darse entre individuos no emparentados inmigrantes; calamón común,

Porphyrio porphirio, Craig & Jamieson 1985) o, en grupos mixtos con ayudantes emparentados e individuos inmigrantes (ej. charlatán moro, *Turdoides squamiceps*, Zahavi 1990).

Cría cooperativa en aves

La cría cooperativa en aves es conocida desde hace más de un siglo (Boland & Cockburn 2002). Desde entonces han sido descritas varias características ecológicas que son comunes en la mayoría de las especies cooperativas. Por ejemplo, la dependencia prolongada de la descendencia (Langen 2000), los tamaños de puesta reducidos (Brown 1987; Arnold & Owens 1998; Arnold & Owens 1999), la sensibilidad a la calidad del hábitat y patrones de uso del hábitat especializados (Walters et al. 2004), o ser más comunes en hábitats abiertos, con una cobertura arbórea poco densa (Cockburn 1996).

Pero aún con los conocimientos adquiridos durante este siglo de estudio, la cría cooperativa en aves sigue generando incógnitas, ya que estas características ecológicas y de estrategia vital no son predictivas, puesto que algunas son también compartidas por especies no cooperativas. Por otra parte, tampoco los análisis filogenéticos parecen aportar una respuesta convincente (Ligon & Burt 2004) pues las especies cooperativas existen en una diversidad de taxones sin aparente relación entre ellas. El hecho de que aún no esté descrita la "pieza clave" que propicie la cooperatividad en aves

hace que sea un tema que sigue ocupando un puesto importante en las líneas de investigación de la biología evolutiva actual.

A pesar de los interrogantes, lo que sí parece demostrado es que la cría cooperativa reporta ventajas a las especies que siguen esta estrategia. Entre las más importantes se pueden citar: elevada supervivencia (Black & Owen 1987; Ekman et al. 2000; Kraaijeveld & Dickinson 2001; Green & Cockburn 2001), protección frente a depredadores (Griesser 2003), aumento en la eficacia de la obtención de alimento (Scott 1980; Barkan et al. 1986; Ekman et al. 1994), facilidades en el mantenimiento de la termorregulación (du Plessis 2004), posibilidades de heredar parte del territorio y el estatus de dominancia dentro del grupo por parte de los hijos (Woolfenden & Fitzpatrick 1984; Wiley & Rabenhold 1984), y acceso potencial a oportunidades reproductoras (Wiley & Rabenhold 1984; Stacey & Ligon 1987; Zack 1990; Stacey & Ligon 1991; Komedeur 1996; Ragsdale 1999), entre otras. Pero también presenta costes derivados, como la competencia por los territorios vacantes (Koenig et al. 1995; Cockburn 1998), baja disponibilidad de emparejamientos entre no parientes (Walters et al. 1992; Brown & Brown 1998; Ekman et al. 1999) y un mayor riesgo de morir antes de llegar a reproducirse (Rabenold 1990; Russell & Rowley 1993).

Parasitismo de cuidados parentales

En la presente tesis doctoral proponemos un nuevo término, "parasitismo del cuidado parental", que definimos como la interacción en la cual un individuo (el parásito) obtiene beneficios reproductivos reduciendo o eliminando los costes mediante la explotación de cualquier tipo de cuidado proporcionado por otros individuos (los hospedadores). El parasitismo del cuidado parental existe tanto a nivel intraespecífico como a nivel interespecífico en una gran mayoría de grupos animales (ver Capítulo 2).

Parasitismo de cría en aves

El parasitismo de cría es un tipo de parasitismo del cuidado parental en el cual una hembra pone sus huevos en un nido ajeno donde su descendencia será cuidada por el/los hospedador/es. En aves, donde esta estrategia reproductiva ha sido ampliamente estudiada (ej. Rothstein 1990; Johnsgard 1997; Davies 2000), el parasitismo de cría puede ser facultativo, cuando el individuo parásito, además de parasitar a otros individuos, es capaz de criar a parte de su propia descendencia (*Coccyzus* sp.; Payne 1977), u obligado, cuando toda la descendencia del individuo parásito es criada por otros individuos de distinta especie (cuco común, *Cuculus canorus*; Wyllie 1981). Por otra parte, el parasitismo de cría puede ser intraespecífico,

cuando un individuo parasita a otro de su misma especie (más de 200 especies de aves, Yom-Tov 2001), o interespecífico, cuando parasita a individuos de especies diferentes (unas 100 especies de aves; Davies 2000). Por último, los parásitos de cría también se pueden considerar específicos, si tan solo parasitan a una o unas pocas especies hospedadoras (ej. *Vidua* sp.; Davies 2000), o generalistas, cuando parasitan a un amplio número de especies (ej. tordo cabecicafé, *Molothrus ater*; Friedman 1971).

Puesto que el parasitismo de cría es costoso para el hospedador, las especies que son (o han sido en el pasado) parasitadas a una elevada tasa desarrollan mecanismos de defensa frente a los parásitos. Uno de los más importantes es la habilidad de reconocer y expulsar huevos extraños del nido. Como respuesta a esta defensa contra el parasitismo de cría de los hospedadores, el parásito puede bien cambiar de especie hospedadora, o bien continuar parasitando a la misma especie (Davies 2000). En este segundo caso, la selección natural favorecerá la aparición de contraadaptaciones, como un aumento del mimetismo de sus huevos con los del hospedador, la producción de huevos crípticos o con características supernormales (Davies 2011). Una vez que el parásito consigue la aceptación de sus huevos por parte del hospedador, los costes para el hospedador derivados de la expulsión de un huevo parásito pueden superar a los costes de aceptarlo (Davies 2000). Si el parásito consigue evadir completamente el rechazo de sus huevos en nidos hospedadores, el

hospedador puede desarrollar la capacidad de reconocer y rechazar a los pollos parásitos (Langmore et al. 2003; Anderson & Hauber 2007). Como respuesta, y conforme a las predicciones de la teoría evolutiva, es esperable que los pollos parásitos desarrollen características miméticas con los pollos hospedadores (Langmore et al. 2011). Los padres hospedadores pueden utilizar el comportamiento de petición de alimento, principalmente el sonido, para diferenciar entre pollos parásitos y propios, lo que les permite expulsar o dejar de alimentar al pollo parásito (Langmore et al. 2003; ver Anderson & Hauber 2007 para una revisión de todas las hipótesis propuestas).

El mimetismo de los pollos parásitos con los hospedadores puede implicar características morfológicas diversas como el color de piel del pollo (ej. cuclillo broncíneo, *Chrysococcyx lucidus*; Davies 2000), las características del plumaje (ej. tordo pico corto, *Molothrus rufoaxillaris*; Davies 2000), y/o el patrón de color y manchas bucales (ej. *Vidua* sp.; Davies 2000; Payne & Payne 2002). Este mecanismo de reconocimiento de pollos por parte del hospedador podría desarrollar mecanismos de mimetismo del comportamiento petitorio en los pollos parásitos, que serían favorecidos por la selección natural (Soler 2009), ya que difícilmente serían reconocidos (Payne & Payne 2002) como ocurre en el tordo pico corto (Dearborn & Lichtenstein 2002).

Petición de alimento de los pollos parásitos

Diferentes especies de aves utilizan distintas estrategias para optimizar el número de pollos que pueden criar (Lack 1947). Una de estas estrategias es ajustar el tamaño de puesta, en cuyo caso todos los pollos sobrevivirían hasta abandonar el nido (Lack 1947). El reparto de alimento de los padres a los pollos en este caso sería equitativo, alimentando preferentemente aquellos que más lo necesiten (Soler 2001). Otras especies utilizan la estrategia de reducir el número de pollos (Lack 1947). En estas especies el tamaño de puesta es superior al número de pollos que pueden criar en condiciones normales, la hembra comienza a incubar antes de finalizar la puesta, lo que crea un orden jerárquico de tamaño (eclosión asincrónica) que provoca que los pollos más pequeños mueran de hambre (ver las revisiones publicadas por Magrath 1990; Slagsvold et al. 1995; Stoleson & Beissinger 1995; Stenning 1996). En este caso los padres alimentan preferentemente a los pollos de mayor tamaño por lo que los pollos más pequeños, en caso de escasez de alimento, morirían de hambre (Bengtsson & Ryden 1983; Cotton et al., 1999; Teather 1992; Price & Ydenberg 1995; Smiseth et al 2003). El hecho de alimentar preferentemente a los pollos de mayor tamaño es, junto con la eclosión asincrónica una de las claves de esta estrategia (Soler 2001).

Las especies parásitas que no expulsan los huevos o pollos del hospedador deben competir por la comida con los pollos hospedadores. Por lo explicado anteriormente, una de las más eficaces formas de competir es teniendo una ventaja en tamaño (Soler 2002). Esta ventaja pueden adquirirla de dos formas diferentes: parasitando especies de menor tamaño o eclosionando varios días antes que los pollos hospedadores.

Los pollos parásitos también pueden competir por la comida con los pollos hospedadores emitiendo llamadas de petición de alimento estructuralmente similares (miméticas) a las de los pollos de la especie hospedadora (Mundy 1973; McLean & Waas 1987; Payne & Payne 1998; Langmore et al. 2008; Anderson et al. 2009). Estas llamadas de petición pueden estar determinadas genéticamente en los parásitos de cría que rechazan huevos y/o pollos del hospedador (Langmore et al 2008). Pero, curiosamente, no sería necesario que los pollos parásitos mimetizasen por completo la llamada de petición del hospedador, sino sólo aquellas características vocales que atrajesen la atención de los padres adoptivos; esto es, sintonizar su llamada de petición de alimento con aquellas preferidas por los padres hospedadores (Davies et al. 1998; Madden & Davies 2006). Este sería el caso del cuco común que produce una llamada de petición de alimento que mimetiza a la pollada completa del hospedador, compensando así el bajo efecto que ocasiona la presencia de un solo pollo en el nido (Davies et al. 1998). Por otra parte, diferentes hospedadores

podrían tener distintas preferencias en cuanto a las características de la llamada de petición de alimento, por lo que los parásitos tendrían que cambiarla en función de la especie hospedadora (McLean & Waas 1987; Butchart et al. 2003). Pero no necesariamente, puesto que también pueden emitir llamadas que contengan elementos comunes que sintonicen con los requerimientos básicos de varias de ellas (McLean & Waas 1987; Butchart et al. 2003; Madden & Davies 2006).

La corneja negra. Cría cooperativa y parasitismo de cría por el críalo europeo

La corneja negra (*Corvus corone*) se ha considerado siempre como una especie de reproducción en parejas. Tan solo se ha descrito una población de corneja negra que presente cría cooperativa en Europa (Baglione et al. 2002). Baglione et al. (2005) destacaron que el hecho de que los juveniles no se dispersen podría estar relacionado con que en esta población, al contrario que en el resto de las poblaciones estudiadas, el territorio es defendido durante todo el año. Podría ser que en las poblaciones no cooperativas no fuera rentable para los juveniles defender los territorios (Baglione et al. 2005).

La corneja negra es la segunda especie hospedadora del críalo europeo (*Clamator glandarius*) en la Península Ibérica (Soler 1990). El críalo

europeo es un parásito de cría obligado que no expulsa los huevos o pollos del hospedador. Se han realizado pocos estudios que relacionen la cría cooperativa y el parasitismo de cría (ej. Poiani & Elgar 1994). Uno de los últimos estudios publicados hace referencia al parasitismo de cría por parte del críalo europeo en la población cooperativa de corneja negra mencionada más arriba. En este estudio, Canestrari et al. (2009) encontraron que los territorios defendidos por parejas presentaban una mayor probabilidad de ser parasitados y, que en ellos, los pollos parásitos presentaban una mayor diferencia en edad con los pollos hospedadores que en los territorios cooperativos. El críalo europeo eclosiona varios días antes que los pollos de la especie hospedadora, con lo que consigue adquirir un mayor tamaño que le otorga una ventaja en la competencia por el alimento (Soler 1990; Soler et al. 1996). Canestrari et al. (2009) sugirieron que en los nidos cooperativos, puesto que la hembra hospedadora pasa más tiempo incubando los huevos que en los territorios no cooperativos, sería más difícil para la hembra de críalo poder ajustar la fecha de puesta con tanta eficacia como en los territorios defendidos por parejas, por lo que los pollos de críalo presentarían una desventaja en estos territorios frente a los de territorios defendidos por parejas. Esta desventaja de los pollos de críalo en los territorios cooperativos sería compensada por un incremento en su supervivencia en estos territorios cooperativos gracias a la presencia de ayudantes.

OBJETIVOS

1. Determinar si existe o no cría cooperativa en la población de corneja negra de la Hoya de Guadix.

2. Poner a prueba algunas de las hipótesis generales sobre beneficios de la cría cooperativa en aves en la población de corneja negra de Guadix.

3. Determinar la influencia de los factores ambientales sobre el éxito reproductor, en cada una de sus fases, de la población de corneja negra de Guadix.

4. Hacer una revisión de los comportamientos animales que impliquen algún tipo de parasitismo de cuidados parentales, presentando una nueva clasificación basada en los costes producidos al hospedador y no en la clasificación taxonómica.

5. Revisar las relaciones coevolutivas existentes en las interacciones de parasitismo de cuidados parentales.

6. Comparar los parámetros más relevantes del parasitismo del críalo europeo sobre la corneja negra en dos poblaciones con cría cooperativa en España, en las que en una actúa como hospedador principal y en la otra como secundario.

7. Determinar las preferencias en el reparto de alimento entre los pollos por parte de los adultos de corneja negra en nidos parasitados y no parasitados por el críalo europeo, así como el comportamiento petitorio de los pollos de críalo.
8. Determinar si los pollos parásitos consiguen ser alimentados preferentemente por los padres adoptivos en el sistema críalo-corneja.

9. Estudiar las llamadas de petición de alimento del pollo de críalo europeo en sus dos hospedadores principales en Europa (urraca y corneja) para testar la hipótesis del mimetismo con respecto a las de los pollos hospedadores.

METODOLOGÍA GENERAL

Especies de estudio:

Corneja negra (Corvus corone)

Perteneciente al orden de los paseriformes (familia Corvidae), la corneja negra es un ave de tamaño medio (48 - 53 cm de longitud). Muchos autores han defendido que junto con la corneja cenicienta (C. cornix), constituía una subespecie de la especie Corvus corone. La situación taxonómica es compleja puesto que existen estrechas bandas de hibridación entre C. corone y C. cornix en Escocia, a través del centro de Europa, en Siberia central y Asia central. Sin embargo, estudios recientes sugieren que ambas "cornejas negras" deberían ser tratadas como especies separadas. Debido a que los plumajes son claramente diferentes, a las sutiles diferencias en las vocalizaciones y a las estrechas bandas de hibridación, se cree que se ha alcanzado la especialización, al menos parcialmente (dos Anjos 2009). La presencia de cornejas negras en el este y oeste del continente Euroasíatico separadas por C. cornix es patente. Actualmente se considera que, dentro de la especie Corvus corone existen dos subespecies: C. c. corone y C. c. orientalis, ésta última con tres razas (dos Anjos 2009).

La subespecie *C. c. corone* presenta una amplia distribución latitudinal en el Paleártico, habitando desde las zonas de clima sub-ártico y boreal

hasta las de clima templado y mediterráneo. Con respecto a la longitud, habita el norte y este europeo (excepto Irlanda y el norte de Escocia) siendo su límite oeste de distribución Dinamarca, oeste de Alemania, República Checa, Eslovaquia, Austria, Suiza y norte de Italia; donde hibrida con *C. cornix* que se distribuye por el resto de Europa (incluyendo Irlanda y norte de Escocia). Bastantes de los individuos que habitan el centro de Europa se dispersan hacia el sur y el oeste en invierno llegando a ocupar Córcega, Cerdeña y el sureste europeo (Cramp & Perrins 1988; dos Anjos 2009).

La subespecie *C. c. corone* la encontramos tanto en el interior como en zonas costeras y estuarios, en hábitats que incluyen tierras de cultivo, prados, pequeños bosques, bosques de ribera, parques y jardines, y zonas cercanas a fuentes de agua o vertederos (Cramp & Perrins 1988; dos Anjos 2009). En la Península Ibérica habita preferentemente medios abiertos con árboles dispersos o la periferia de bosques con cultivos, pastizales, campiñas, huertos o sotos fluviales; evita las zonas forestales extensas y cerradas (Molina-Villarino & Baglione 2003). En la zona de estudio de la presente tesis doctoral (ver descripción más abajo) habita principalmente en manchas de encinas, alimentándose también en las estepas cerealistas (Zuñiga et al. 1982).

La dieta en general es omnívora pero principalmente carroñera. Se alimenta de invertebrados y granos de cereal, pequeños vertebrados, huevos, pollos, carroña y deshechos dependiendo de la disponibilidad en la

zona (Cramp & Perrins 1988; dos Anjos 2009). Generalmente se alimenta en pastos y praderas en primavera y verano, y en campos de cultivo en otoño e invierno. Es común verlas siguiendo los arados (Cramp & Perrins 1988).

Su periodo de cría va desde mediados de Marzo hasta finales de Mayo, aunque puede variar entre poblaciones, principalmente dependiendo de la latitud (Cramp & Perrins 1988; dos Anjos 2009). Anidan principalmente en árboles altos, aunque ocasionalmente, en algunas zonas, también pueden usar cornisas, cortados, torres de alta tensión y edificios abandonados (Cramp & Perrins 1988; Molina-Villarino & Baglione 2003; dos Anjos 2009). El nido es abierto y es construido sobre una base sólida de ramas. Está constituido por un fondo de ramas de menor tamaño y flexibles sobre el cual suele encontrarse una capa de césped, musgo y/o raíces que será cubierta por pelo, lana, plumas, etc. y material suave de fabricación humana como trozos de tela o restos de prendas de vestir (Cramp & Perrins 1988; dos Anjos 2009). Sólo hacen una puesta anual de 3 a 6 huevos ovalados, un poco brillantes de color de fondo azul claro a verde con un patrón y densidad de pequeñas manchas marrones/negras muy variable (Cramp & Perrins 1988). La hembra es la única que se encarga de incubar los huevos durante un período de 17 a 22 días (Cramp & Perrins 1988). Los pollos permanecen en el nido durante 28 - 38 días y, tras abandonarlo, siguen

recibiendo cuidados por parte de los padres durante cinco semanas aproximadamente (Cramp & Perrins 1988; dos Anjos 2009).

Se trata de una especie esencialmente sedentaria. Su sistema de cría ha sido descrito como no cooperativo (Yom-Tov 1975; Bossema & Benus 1985; Richner 1989; Richner et al. 1989; Richner 1990; Saino 1994) pero, al menos en una población del norte de España, se ha descrito una alta tasa de cría cooperativa (75%) (Baglione et al. 2002) donde grupos de hasta 9 individuos (media de 3,2) colaboran en un mismo territorio para criar a la descendencia (Baglione et al. 2002), lo que aumenta el éxito reproductor, ya que éste está positivamente correlacionado con el tamaño de grupo (Canestrari et al. 2008). Los ayudantes son individuos no dispersantes o inmigrantes con algún grado de parentesco (Baglione et al. 2003).

Críalo europeo (Clamator glandarius)

El críalo europeo pertenece al orden de los cuculiformes (familia Cuculidae) y es un ave de mediano tamaño, presentando una longitud de 35 a 40 cm. Se distribuye por la cuenca del mediterráneo incluyendo países del sur de Europa, norte de África y este de Asia menor, así como países del centro-sur de África. Es un ave migradora en los bordes norte y sur de su área de distribución, mientras que en las demás zonas puede realizar desplazamientos de corta distancia para evitar climas de extrema sequía o humedad (Cramp & Perrins 1988; Payne 2009). Aunque existen pocos datos, se cree que las poblaciones paleárticas invernan en África al sur del desierto del Sahara y que migran en grandes grupos por dos rutas diferentes: a través del noroeste de África y a través de Egipto y oeste de Arabia, lo que se refleja en dos áreas de cría separadas en Europa (la presencia en Italia y los Balcanes está descrita como rareza) (Cramp & Perrins 1988). Los adultos llegan a las zonas de cría paleárticas entre principios de Febrero y mediados de Abril y comienzan el regreso a la zona de invernada a mediados de Junio. Los juveniles abandonan la zona de cría entre principios de Julio y primeros días de Agosto independientemente de los adultos (Cramp & Perrins 1988; Payne 2009). Habita zonas semi-áridas, sub-tropicales y tropicales; generalmente zonas templadas, evitando montañas, bosques y humedales (Cramp & Perrins 1988; Payne 2009). En la Península Ibérica habita zonas más o menos abiertas, sotos, setos arbolados, bosquetes, parques, cultivos de frutales (especialmente almendros), vegas, encinares adehesados y otros bosques aclarados, pastizales y ambientes perimarismeños, coincidiendo con los hábitats donde se alimenta y anidan sus hospedadores (Soler et al. 2003a). Su dieta es exclusivamente insectívora, constituyendo la base de su alimentación orugas gregarias tóxicas (principalmente orugas de procesionaria del pino (Thaumetopoea pityocampa)). Otras presas como saltamontes, grillos,

libélulas, hormigas, escarabajos y lagartos también han sido descritas durante la época de cría (Cramp & Perrins 1988; Payne 2009).

El críalo europeo, al igual que el cuco común, es una especie parásita de cría obligada. Son las dos únicas especies europeas que presentan esta estrategia reproductora en la cual la hembra parásita pone sus huevos en los nidos de otras especies (especies hospedadoras) donde el pollo parásito será criado. En la Península Ibérica, al igual que en todo el Paleártico, su principal especie hospedadora es la urraca (Pica pica), pudiendo también parasitar a otros córvidos como la corneja negra y, de forma ocasional, la chova piquirroja (Pyrrhocorax pyrrhocorax) y la grajilla (Corvus monedula) (Cramp & Perrins 1988; Soler 1990). Presenta un mecanismo de parasitación bastante peculiar en el que, al contrario de lo que ocurre en otros cucúlidos parásitos, macho y hembra colaboran con frecuencia. Según describieron Álvarez & Arias de Reyna (1974), cuando van a parasitar a una pareja de urracas, una vez elegido el nido donde depositar su huevo, la hembra de críalo se acerca poco a poco y, cuando está bastante cerca se esconde y, poco después, el macho se aproxima gritando y llamando mucho la atención hasta conseguir que las urracas salgan a perseguirlo. Cuando el macho ha conseguido que ambos adultos hospedadores se alejen del nido, la hembra aprovecha para depositar su huevo (Álvarez & Arias de Reyna 1974). Las hembras de críalo ponen los huevos desde el borde del nido (Arias de Reyna et al. 1982), con lo que provocan la ruptura de alguno de los huevos de la urraca, pero además, con frecuencia rompen otros huevos de los hospedadores picándolos, o haciéndolos chocar entre sí, pero, a diferencia de lo que hace el cuco, nunca retiran o comen ningún huevo (Soler 1990; Soler et al. 1997).

La hembra de críalo pone entre 15 y 25 huevos (Arias de Reyna et al. 1982) elípticos con terminaciones romas suaves y con un color de fondo bastante brillante verde-azulado pálido, con pequeñas manchas de color marrón claro-rojizo que mimetiza los de la especie hospedadora principal, la urraca (Soler et al. 2003b). Los huevos son incubados durante un período de 12-15 días por la hembra hospedadora (Cramp & Perrins 1988; Payne 2009). El período de incubación de las principales especies hospedadoras es mayor (en urraca de 17-18 días; en corneja de 17-20; Cramp & Perrins 1988; Payne 2009) que el del críalo. Los pollos de críalo, al contrario que los pollos de cuco, al nacer no expulsan los huevos ni los pollos hospedadores, sino que comparten el nido con ellos, por lo que mantienen una competencia con los pollos de la especie hospedadora por el alimento que llevan los padres (Soler 1990). Por esto, el hecho de eclosionar antes le proporciona al pollo de críalo una ventaja importante con respecto a los pollos de la especie hospedadora, ya que para cuando nacen éstos el pollo de críalo ya ha crecido y los padres ceban preferentemente al pollo de mayor tamaño (Soler 1990; Soler et al. 1996; Soler et al. 2002). El pollo de críalo permanece en el nido de la especie hospedadora entre 16 y 26 días

después de haber eclosionado y es alimentado por los padres hospedadores durante otros 25-59 días (Soler et al. 1994).

Zona de estudio:

El presente estudio ha sido realizado en un área de aproximadamente 40 Km² enclavada en la Hoya de Guadix (37°20' N, 3°04' W, 1100 m), la altiplanicie más elevada de Europa con una altitud media superior a los 1000 m y una extensión de unos 500 Km² situada al norte de la provincia de Granada (Sureste de España) y encajonada entre Sierra Nevada (al Sur), Sierra de Baza (al Este), Hoya de Baza (al Norte) y Sierra Harana (al Oeste) (Ver Figura 1).

La zona está formada por terrenos Neógeno Cuaternario postorogénico. A ambos lados del río Guadix predominan conglomerados, arenas y limos; al Noreste del río, hasta las proximidades de la Sierra de Baza y, al Sur, hasta Sierra Nevada, predominan conglomerados y costras. Normalmente los materiales son horizontales, por ello se permite la agricultura tanto en los llanos como en la vega, donde se vería favorecida por la gran fertilidad existente (Pérez Pujalte 1968; Julibert 1974; Mapas geológicos del Instituto Geológico y Minero de España).



Figura 1. Mapa de localización de la zona de estudio de la presente tesis. El polígono rojo de la ampliación muestra los límites de la zona de estudio.

Al tratarse de materiales blandos, los cursos de agua en determinadas zonas ejercen una fuerte erosión, dando lugar a cárcavas o ramblas con fuertes pendientes y poca vegetación donde no es posible la agricultura (Pérez Pujalte 1968; Julibert 1974; Mapas geológicos del Instituto Geológico y Minero de España).

Con respecto a la climatología, domina la variante Mesomediterránea con Ombroclima Semiárido (Rivas Martínez 1981). Se registra una temperatura media anual de 14°C y una precipitación media de 440 mm que se concentra principalmente en los meses de primavera y otoño.

Como consecuencia de la climatología desfavorable y del escaso desarrollo del suelo, la vegetación se encuentra muy degradada.

Teóricamente, la vegetación potencial correspondería a un coscojal con espino negro (*Rhamnus lycioides*), donde tanto la cobertura como la altura de la vegetación serían escasas. Las etapas seriales corresponderían a un retamal, donde la retama (*Retama* sp.), inhiesta (*Genista speciosa*) y bolinas (*Genista umbelata*) serían las especies dominantes, y a un espartal donde dominaría de forma casi exclusiva el esparto (*Stipa tenaccissima*) (Rivas Martínez et al. 1977; Valle & Díaz 1984 en Soler 1984).

Con respecto a los cultivos de la zona, se observa un claro predominio de los cultivos de secano (cereales y almendros) aunque también existen zonas de cultivo de regadío (cultivos de vega y frutales, principalmente melocotón). Además pueden observarse zonas de choperas utilizadas para la explotación maderera, así como dehesas de encinas.



Figura 2. Imágenes de los diferentes hábitats encontrados en la zona de estudio: (de izquierda a derecha) cultivo de cereales y almendros, cultivo de almendros con encinas dispersas, y cultivo de cereales con encinas dispersas y en pequeños grupos.

Procedimiento de trabajo:

A mediados de Marzo se comenzaba la búsqueda y localización de los nidos que se visitaban frecuentemente para determinar la fecha de puesta, el tamaño de puesta y si estaban o no parasitados. Posteriormente se visitaban en los días previamente calculados para concretar la fecha y éxito de eclosión. Durante la época en que los pollos permanecen en el nido, los nidos se visitaban con una frecuencia de 2 o 3 veces por semana para registrar el crecimiento de los pollos, así como detectar los eventos de depredación y, en su caso, realizar la búsqueda del posible nuevo nido de reposición. Varios días antes de que los pollos abandonen el nido (día 28 ± 1), llevábamos a cabo el último control en el que realizábamos medidas biométricas, extracción de sangre y marcaje de todos los pollos. En el caso de los nidos parasitados, se visitaban el día 17 ± 1 para realizar el mismo trabajo con los pollos de críalo antes de que dejaran el nido.

Durante el primer año de estudio, entre 1 y 3 pollos de corneja fueron marcados con radiotransmisores (Holohil RI-2B) en 17 territorios y se siguieron hasta el fin de la temporada de cría siguiente, con el objetivo de determinar la tasa de dispersión de juveniles de un año de la población estudiada.

Los procedimientos de trabajo concretos utilizados para el correcto desarrollo de cada uno de los objetivos están descritos con detalle en el apartado Material y Métodos de cada uno de los capítulos.

Capítulo 1

Breeding biology and fledging survival in Carrion Crow (*Corvus corone corone*, L. 1758) pair and group-breeding in a population at southern Spain

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SUMMARY

Cooperative breeding is not common among birds, although its frequency is higher within the Corvid Family. In this article, we study the effect of group size in the reproductive biology of the Carrion Crow (Corvus corone corone), a species usually described as noncooperative. Our population is located at the southern limit of the distribution of the species what could confer special characteristics to its breeding biology. Accordingly, although previous investigations have shown positive effects of non-breeding individuals on reproductive success, we found only a positive effect on laying date and, indirectly on fledgling production. But, surprisingly, we also found a higher starvation rate on nestlings in group-breeding territories than in pair-breeding ones. Furthermore, we explore the effect of brood parasitism by Great Spotted Cuckoos (Clamator glandarius) on the reproductive success of Carrion Crows according to group size. Nests in group-breeding territories are brood parasitized at the same rate than breeding pairs. Finally, we tried to determine the effect of meteorological variables (maximum and minimum temperatures and precipitation) on the breeding performance of this species, as well as its interaction with biotic factors. We found that meteorological factors represent an important role in each breeding stage (egg, nestling and fledgling).

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INTRODUCTION

Cooperative breeding birds are species in which individuals live in groups of three or more adults and care for the young at a single nest (Dickinson & Hatchwell 2004). Both parents and helpers should acquire benefits equal or greater than the costs involved in this intraspecific relationship to explain the maintenance of the system by natural selection (Verbeek & Butler 1980). On the one hand, Hamilton (1971) suggested some benefits of cooperative breeding for the breeding pair as shared vigilance and the selfish-herd effect (when individuals seek cover behind other group members). Afterwards, Brown (1988) added the sharing of information to the list of benefits and, lately, Dickinson & Hatchwell (2004) proposed the cooperative defence of the territory as an additional benefit. On the other hand, helpers can benefit from helping (i) by staying in a high quality territory ("marginal-habitat" hypothesis; Koenig & Pitelka 1981), (ii) through the inheritance of the territory (Wiley & Rabenhold 1984; Lindström 1986; Blackwell & Bacon 1993), (iii) through the acquisition of breeding skills (Emlen 1991; Cockburn 1998), (iv) by increasing their indirect fitness by feeding siblings (Hamilton 1964; Brown 1987) or, even, (v) by increasing their direct fitness through extra-pair paternity (Brown 1987; Hatchwell et al. 2004; Canestrari et al. 2005).

Cooperative breeding species share some important life-history traits like year-round residency, high survivorship, small clutch sizes and, in

many cases, constraints on independent breeding (Brown 1987; Stacey & Koenig 1990; Arnold & Owens 1998; Arnold & Owens 1999). Also, in Carrion crow (*Corvus corone corone*), after nest failure reposition clutches are usually more frequent in cooperative territories than in non-cooperative ones (Canestrari et al. 2008). Furthermore, the offspring of cooperative breeding species receive more prolonged care (McGowan & Woolfenden 1990; Heinsohn 1991) than non-cooperative breeding ones.

Despite the reported benefits to both parts, only about 8.4% of avian species show cooperative breeding (Cockburn 2003). However, in the Family Corvidae there exists a particularly high frequency (23%) of cooperative breeding species (Dickinson & Hatchwell 2004). It has been reported in a few African genera (Verbeek & Butler 1980), in the New World Jays genera (Brown 1978), North-Western Crows (Corvus curinus, Verbeek & Butler 1980), Common Crows (Corvus brachyrhynchos, Jollie 1976), and Azure-winged Magpies (Cyanopica cyana, Komeda et al. 1987; Cruz et al. 1990). However, there is an important lack of information about the persistence of cooperative breeding in different populations of the same species and on the effect of the presence of helpers on reproductive performance.

Another relevant topic scarcely explored in relation to cooperativity is brood parasitism. Brood parasites may prefer cooperative breeding species as hosts because nestlings are provided with a higher feeding rate (Poiani &

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Elgar 1994). But also cooperative species may be more difficult to parasitize because of the presence of helpers that allow the female spent more time in the nest, as shown by Canestrari et al. (2009) in a population of Carrion Crows parasitized by Great Spotted Cuckoos (*Clamator glandarius*). Accordingly, the study of this host – parasitic interaction is important to fully understand the mechanisms driving both cooperative breeding and brood parasitism.

Finally, some studies have emphasized the potential importance of meteorological variables (mainly temperature) in the occurrence of cooperative breeding in phylogenetically related species (Arnold & Owens 1999). In addition, other studies have shown an effect of rainfall on breeding success of several bird species (Järvinen 1980; Becker et al. 1985; Donazar & Ceballos 1989). Thus, it is important to control for the potential effect of the meteorology in any study about cooperative breeding. On the other hand, our studied population is located at the southern limit of the species distribution (Cramp & Perrins 1988), and may present a reduced breeding success comparing with populations located at the centre of the distribution, such as reduced clutch size as has been shown in other species (Slagsvold 1981; Sanz 1997; Sanz 1998; Fargallo 2004).

Herein we study the breeding biology of the Carrion Crow to investigate the effect of cooperative breeding and meteorology on reproductive success. Carrion crow was for long treated as a subspecies

separated from Hooded crow (*Corvus conone cornix*, Cramp & Perrins 1988), mainly because of the extensive hybridization zones existent in Europe. But recent research has indicated that Hooded and Carrion crows may merit treatment as two different species (dos Anjos 2009). General information on the breeding biology of the carrion crow is scarce as most papers deal on specific subjects (Yom-Tov 1975; Bossema & Benus 1985; Richner 1989; Richner et al. 1989; Richner 1990; Saino 1994). Thus, in spite of that in Europe two species of crow could be distinguished, most of the information has been collected on the hooded crow and no fundamental differences in their reproductive biology between both have been found (Cramp & Perrins 1988); thus, herein we will refer to average population parameters of both species.

Carrion crow (as well as the Hooded Crow) is usually described as non-cooperative breeders (Cramp & Perrins 1988) but a recent research highlighted the existence of cooperative breeding in one population in Northern Spain (Baglione et al. 2002). Moreover, this subspecies in the South of its breeding range suffers from brood parasitism by the Great Spotted Cuckoo, which allow us to explore the interaction between cooperative breeding and brood parasitism.

The aim of this paper is to study the breeding biology of another Carrion Crow population that show cooperative breeding, located in South Spain. According to the benefits of cooperation described above, we

predicted to find earlier laying date, lower predation rate, higher re-nesting rates, lower brood parasitism rate by the Great Spotted Cuckoo, higher breeding success and higher fledgling survival in the cooperative territories than in the non-cooperative ones. Also a reduced clutch size could be expected due to its peripheral distribution.

MATERIAL AND METHODS

Study area and Population

We studied a population of Carrion Crows located in Guadix (Southeastern Spain; 37°20'20.00" N, 3°04'13.04" W; elevation about 1100 m a.s.l.), the southern limit of the distribution of the species (Cramp & Perrins 1988). Cereal crops with oak trees and almond tree plantations represent the main landscape. The average nest density in the studied area was 0.71 nest/Km² (total of 57 territories). A total of 57 different territories (42 in 2006; 38 in 2007, and 44 in 2008) were followed from nest construction until fledgling. Differences in number of territories were due to the inaccessibility of the nest or the absence of reproductive individuals in a territory. Moreover, the number of territories diminished throughout breeding seasons mainly due to predation and desertion events. Potential predators in the area were Stone Martens (*Martes foina*), Genets (*Genetta genetta*), Magpies (*Pica pica*), Jackdaws (*Corvus monedula*), Comon ravens (*Corvus corax*) and other Carrion Crows. Brood parasitism by the Great Spotted Cuckoo is very

common in magpie's nests within the studied area (43.5%, Soler 1990; 55.7%, Soler et al. 2002) and also some crow's nests use to be parasitized (8.5%, Soler 1990; 28.5%, Soler et al. 2002).

Crows maintain territory boundaries that are constant over years. Thus, although most adults were unbanded, individual territories are recognizable across years which allow us to follow individual pairs/groups among years.

Groups' Survey and Breeding Success

During each breeding season (March-June), we performed observations (an average of 4.95 hours per nest, range from 2 to 8 hours) at each nest territory at sunrise or sunset. To survey cooperation we provide some carrion within the territory next to the nest and we directly observed or monitored (hard disk camera JVC GZ-MG50E) the number of individuals that approached the carrion (both procedures provided similar results; Chi-Square = 11.47 df = 14 p = 0.65). As Carrion Crows strongly defend territories against conspecifics during breeding season (Baglione et al. 2005) we can assure that all the individuals around the carrion belong to the group although they were not banded. Group size was obtained from the maximum number of individuals observed near the carrion at the same time. Group size was also surveyed each time we approach the nest for routine checking. We set as cooperative breeding territories those in which

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more than two different adults were observed foraging in the carrion. Not all territories could be surveyed for cooperation what makes the sample size in the whole population larger than the sum of cooperative and noncooperative territories. We cannot be sure that all individuals of the group approach to the nest during direct observations or to the carrion in videotaped ones, thus we obtained the minimum group size at each nest. Non-cooperative territories were surveyed more times to assure that there were only two adults at nest. So, we are confident that our classification of each territory as pair or group-breeding is quite reliable.

Data collection at each territory began with the finding of the new nest at the beginning of each breeding season. Subsequent visits allowed us to determine laying date, clutch size, hatching success and number of fledged young in each territory. We also recorded the number of died nestlings what we assumed as starving nestlings because there not exist partial predations in the area. In case of failure at eggs or hatching stages, the territory was surveyed looking for a possible replacement clutch.

Just before fledgling (27-30 days after hatching) all nestlings were banded with an unique combination of colour rings and plastic patagial wing tags (6.5 cm length x 3.5 cm width) that do not provoke any damage to the individual (Canestrari et al. 2007). Complete information on nestling body measures (weight (g), tarsus and wing length (mm)) were collected for

164 chicks in 119 broods from 57 different territories between 2006 and 2008.

Fledgling survival

In the first study-year (2006), 36 fledglings were equipped with a radiotransmitter when banded, in a total of 17 territories (from 1 to 3, average 2.12 banded fledglings per nests). Radio-transmitters (Holohil RI-2B, battery maximum life 18 months) weighted 11 g, what corresponds to 2.7% of average body weight of banded fledglings. Radio-transmitter was attached with a leg harness made of 3 mm silicon tubing following the method described by Baglione et al. (2005). We equipped with a radiotransmitter the larger fledglings at each nest to avoid potential negative effects of the transmitter on low quality nestlings, namely those of lower mass (Magrath 1991). Individuals were radio-tracked from banded date to the end of the following breeding season in a total of 42 occasions. As juveniles are dependent on their parents during the first five weeks after leaving the nest (Cramp & Perrins 1988), we calculated fledgling survival rate as the percentage of radio-tagged individuals that were still alive after five weeks. We also calculated yearling survival rate at the next breeding season considering only those individuals found dead because it is not possible to differentiate between dispersed and dead individuals.

Meteorological data

We obtained minimal and maximum temperatures (Tmin and Tmax respectively; degree centigrade) and precipitation (l/m²) data from the Can-Ibice meteorological station (Meteorological State Agency; 7 Km far away from the studied area) during the three studied breeding seasons. For each meteorological variable we calculated three different average values for each territory: during the five days before laying date (5-days earlier), during the incubation period and during the nestling period to obtain data representing the laying, incubation and nestling stage respectively.

Statistical Analyses

We use linear mixed models analyses (LMM; Genstat 12th edition) where fixed terms fitted into the model will vary depending on the specific analysis, including all those interactions with a biological meaning. We run three different models: (i) a meteorological-factors model, (ii) a biologicalfactors model, and (iii) a combined meteorological-biological factors model. These two former models allow us to determine how both meteorological and biological factors independently can affect the specie's breeding success. The third model is developed including only those meteorological and biological variables that presented a statistically significant effect in both former models. As it is usually assumed that biological variables have a higher influence on breeding biology than metheorological ones, we ran this later model with the aim of include both meteorological and biological variables in the same model and test the relative importance of meteorological variables with respect to biological ones with the aim to denote its respective relevance in the breeding biology of the population. Sample size could vary between analyses because we do not have the same set of data for all territories.

Within each set of data (meteorological, biological, or mixed meteorological-biological) we ran an analysis for each dependent variable. Biological variables for all three models were laying date (day 1 corresponds to march 1st), clutch size, number of hatched eggs, number of starved nestlings (from those nests non-predated and non-brood parasitized), number of fledglings from nests with hatched eggs, and number of fledglings from each year overall nests.

In meteorological-factors model analyses we set each single biological variable as dependent and we set as fixed factors the average of 'five days before laying date', 'incubation period' and 'nestling period' (as appropriate) for minimal temperature, maximum temperature and precipitation for each territory in all three years. Because data across territories would not be independent, we fitted territory identity as random variable. We also fitted year as random term because no differences exist among all three breeding seasons studied (Minimal temperature, Kruskal-Wallis test H = 0.258, p = 0.88; Maximum temperature, Kruskal-Wallis test

H = 0.438, p = 0.80; and Precipitation, Kruskal-Wallis test H = 0.545, p = 0.76).

In biological-factors model analyses, we set a different analysis including biological variables described above as dependent and as factor those biological variables with biological meaningful interactions. As laying date and group size are highly related (Wald statistic=6.53, df =1, p=0.015; Appendix 1), we run different analyses to test the effect on each variable independently. Also, working with both factors independently allows us to increase the sample size of the models. Because biological variables could be different between territories, we fitted territory identity and year as random variables.

To test the effect of different variables on fledgling survival, we run a model including as fixed terms group size and several nestling morphological characteristics (such as weight, tarsus, wing and tail lengths) some days before leave the nest (see above). As radio-tracking were performed only during 2006, year were not included in the model. Territory identity was fitted as random variable.

We also run the combined biological-meteorological-factors model for each dependent variable by including only those significantly explanatory variables from both separate models described above. Thus, we are able to distinguish between those biological and meteorological influences, but we can also measure the relative importance of the interaction of both biotic and abiotic variables. Territory identity and year were fitted as random. (See Appendices 1 and 2 for more detailed results).

From fixed terms, those that were nonsignificant (p>0.05) were sequentially eliminated from the model until all the variables were significantly explanatory. Significant probability values were derived from having all significant terms fitted in the model together, whereas those of nonsignificant terms were obtained by individually reintroducing each nonsignificant term to the minimal model (Crawley 2002; Russell et al. 2003).

Cooperation, re-nesting, predation, brood parasitism, fledgling success (number of nestlings that fledged from nests where at least one egg hatched) and breeding success (overall number of nestlings that fledged) rates were calculated. We run Chi-square, Kruskal-Wallis and Mann-Whitney U tests in Statistica 8.0 to test the differences in these variables between cooperative and non-cooperative territories, as well as differences among years of all dependent variables due to the low sample size (See Table 2). All average values are given \pm SE value.

RESULTS

Cooperation

On average, 66.67% of territories in the study area were cooperative and did not statistically differ between years (Kruskal-Wallis test H (2, N=60) =2.35 p=0.31). The average group size was 1.50 ± 0.99 (range from 1 to 5), which did not vary among years either (Kruskal-Wallis test H (2, N=60) =4.26 p=0.12) (Fig. 1).

Re-nesting

Re-nesting events never occurred after a successful attempt, and after a failed attempt occurred only rarely (10.42%; n=48). No significant differences in re-nesting rate were found between group and pair breeding territories (Table 2; Chi-square=0.92 df =1 p=0.34), which may be the consequence of the low sample size for re-nesting clutches (n=5). All the recorded re-nesting events were unsuccessful.



Figure 1. Cooperation rate (bars) and average group size (line) in all three years of study. Numbers in the bars show the number of cooperative territories each year. No statistically significant differences were found.

Reproductive Biology

Average laying date during the three years was day 33 ± 0.76 (n=108), although it varies from day 11 to 62. Pair-breeding females layed eggs significantly earlier than group-breeding females (Table 2; Wald statistic=6.53, df =1, p=0.015; Fig. 2a). When testing only the meteorological factors, the average minimal temperature during the five days before laying date (5-days-earlier-Tmin) showed a positive effect on laying date (Wald statistic=32.06, df=1, p<0.001; Appendix 1). This effect of Tmin is not present when combining both meteorological and biological factors in the same model (Wald statistic=7.59, df=1, p=0.01), in which case only the effect of group size was still present (Table 2).

Average clutch size was 4.55 ± 1.20 eggs per clutch (range from 1 to 8). No differences in clutch size between pair and group-breeding territories were found (Table 1; Wald statistic=1.07, df =1, p=0.306; Appendix 2). Within the whole population territories, early breeders had a significantly larger clutch size (Wald statistic=30.85, df =1, p<0.001; Appendix 2). As occurs in the laying date's analysis, the 5-days-earlier-Tmin showed a negative effect on clutch size (Wald statistic=5.31, df =1, p=0.045; Appendix 1), and it disappear in the combined model (Wald statistic=0.15, df =1, p=0.706) persisting only the effect of the laying date commented above (Table 2).

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Table 1. Average values (mean±SD or %) of several reproductive variables in both cooperative and non-
cooperative territories, as well as in the whole population. Numbers in brackets show the sample size.
Variables in bold are those showing statistically significant differences between cooperative and non-
cooperative territories. In both cases, $p=0.001$.

Cooperative breeding		Non-cooperative breeding	Whole population	
Laying date	30.68±6.74 (38)	35.45±6.21 (20)	33.06±7.85 (108)	
Clutch size	4.84±1.12 (37)	4.65±1.27 (20)	4.55±1.20 (116)	
Renesting rate	20% (5)	0% (5)	10.42% (48)	
Hatching success	97.44% (39)	90.0% (20)	74.59% (122)	
No. Hatched eggs	3.72±1.47 (36)	3.15±1.77 (13)	2.67±1.93 (104)	
Fledgling success	88.24% (34)	80.0% (10)	75.32% (77)	
No. Fledglings (hatched)	2.38±1.33 (34)	2.40±1.71 (10)	2.08±1.56 (77)	
Breeding success	86.11% (36)	72.73% (11)	55.66% (106)	
No. Fledglings (overall)	2.31±1.35 (36)	2.18±1.78 (11)	1.53±1.62 (106)	
Starved nestlings (per nest)	1.54±1.14 (24)	0.83±0.75 (6)	1.40±0.98 (43)	
Nests with starved nestlings	75% (24)	66.67% (6)	79.07 (43)	
Nestling starving rate	33.58 (134)	14.63% (41)	29.14% (175)	
Predation rate	2.50% (40)	0% (20)	19.35% (124)	
Brood parasitism rate	25.0% (40)	15.0% (20)	23.58% (123)	
Abandonment rate	2.50% (40)	5.0% (20)	8.06% (124)	
Survival rate (1 st 5 weeks)	90.91% (11)	75.0% (20)	80.56% (36)	
Survival rate (next breeding season)	72.73% (11)	55.0% (20)	63.89% (36)	

Hatching success was 73.17%, and the average number of hatched eggs was 2.67 ± 1.93 (range from 0 to 6). No effect of group size appears on the number of hatched eggs (Table 1; Wald statistic=1.03, df =1, p=0.317; Appendix 2). The number of hatched eggs was significant and

negatively affected by laying date (Wald statistic=8.37, df =1, p = 0.005; Appendix 2), and significantly smaller in parasitized nests than in nonparasitized ones (Wald statistic=11.64, df =1, p<0.001; Appendix 2). The precipitation during incubation period showed a negative effect on the number of hatched eggs (Wald statistic=9.92, df =1, p=0.002; Appendix 1), which still persists in the combined model. The effect of biological variables were also maintained except the effect of laying date (Wald statistic=1.30, df=1, p=0.257; Table 2).



Figure 2. Average (\pm SE) laying date (a), number of nestling died of starvation (b), fledgling survival rate during the five first weeks after nest abandonment (c) in both cooperative and non-cooperative territories during the study period. Statistical significant differences were found only on laying date (Table 1; Appendix 2).

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The average number of starved nestlings per nest was 1.40 ± 0.96 (range from 0 to 3; Table 1). Surprisingly, nests in group-breeding territories presented higher nestling mortality rate than nests in pairbreeding ones (Table 1; Wald statistic=10.12, df =1, p=0.014; Fig 2b; Appendix 2). But, the percentage of nests with at least one starved nestling was not significantly higher in cooperative than in non-cooperative territories (Kruskal-Wallis test H (1, N=30) =0.16, p=0.68). On the other hand, nests with more hatched eggs presented a higher nestling mortality rate (Wald statistic=7.95, df =1, p=0.015; Appendix 2), and in late breeders starvation is also more frequent than in early breeders (Wald statistic=5.31, df=1, p=0.027; Appendix 2). The maximum temperature during the nestling period showed a positive effect on the number of starved nestlings (Wald statistic=12.64, df=1, p=0.002; Table 2) that is still present in the combined model together to the already described biological interactions, except laying date (Wald statistic=0.38, df=1, p=0.535; Table 2).

Average fledgling success was 52.14%. The average number of fledged young in nests in which at least one egg hatched was 2.08 ± 1.56 (range from 0 to 5). Group size did not show any effect on the number of fledglings produced (Table 1; Wald statistic=0.01, df=1, p=0.929; Appendix 2). Early breeders produce a higher number of nestlings than late breeders (Wald statistic=6.53, df=1, p=0.013; Appendix 2). Both brood parasitism and predation rates reduced the number of nestlings produced

(Wald statistic=6.81, df=1, p=0.013; Wald statistic=11.68, df=1, p=0.001; respectively; Appendix 2). The average precipitation during the nestling period showed a positive effect on the number of fledglings (Wald statistic=11.04, df =1, p=0.002; Appendix 1), and it is still present in the combined model as biological factors did, except laying date (Wald statistic=2.93, df=1, p=0.087; Table 2).

Breeding success was 31.52%. The average number of fledged young from all nests under study was 1.53 ± 1.62 (range from 0 to 5). Within all surveyed territories, group-breeding ones did not produce a significantly different number of fledglings than non-cooperative ones (Table 1; Wald statistic=0.10, df =1, p=0.759; Appendix 2). As in fledgling success, early breeders produced a higher number of fledglings (Wald statistic=11.66, df=1, p<0.001; Appendix 2). Furthermore, predation rate showed a significant negative effect on the overall number of fledglings produced (Wald statistic=33.95, df =1, p<0.001; Appendix 2) as brood parasitism rate did (Wald statistic=4.73, df =1, p=0.032; Appendix 2). As occurred in the number of fledgling produced in successful nests, the average precipitation during nestling period showed a positive effect on breeding success (Wald statistic=15.78, df=1, p<0.001; Appendix 1), which is also maintained in the combined model, as the effect of biological variables (Table 2) *Table 2.* LMM analyses results for the combined meteorological-biological models. (r) variables fixed as random.

Model terms	Ν	Wald Statistic	df	Р	Random term estimated variance component ± SE	Average effect ± SE
Laying date	58					
5 days earlier Tmin Group size Territory identity (r) Year (r)		6.90 6.53	1 1	0.168 0.015	25.48±8.73 0.79±2.65	
Minimal model						
Constant Group size						32.89±1.48 -1.60±0.63
Clutch size	105					
5 days earlier Tmin Laying date Territory identity (r) Year (r)		0.15 30.85	1 1	0.706 <0.001	0.11±0.14 0.08±0.12	
Minimal model						
Constant Laying date						4.59±0.17 -0.07±0.01
N hatched eggs	92					
Incubation period rain Laying date Parasitism Territory identity (r) Year (r)		10.84 1.30 10.07	1 1 1	0.001 0.257 0.002	0.13±0.34 1.21±1.39	
Minimal model						
Constant Laying date Parasitism						2.93±0.76 -0.08±0.02 -1.27±0.40
Starved nestlings	29					
Nestling period Tmax Group size N hatched eggs Territory identity (r) Year (r)		12.64 4.99 13.73	1 1 1	0.002 0.044 0.001	0.32±0.30 1.16±1.31	
Minimal model						
Constant Nestling period Tmax Group size N hatched eggs						1.16 ± 0.65 0.04 ± 0.01 0.24 ± 0.11 0.58 ± 0.16

Table 2. (Continuation)

Model terms	Ν	Wald Statistic	df	Р	Random term estimated variance component ± SE	Average effect ± SE
Starved nestlings	42					
Nestling period Tmax Laying date N hatched eggs Territory identity (r) Year (r)	4.69	6.71 0.38 1 0.4	1 1 039	0.014 0.535	0.23±0.26 0.35±0.65	
Minimal model						
Constant Nestling period Tmax N hatched eggs						1.21±0.44 0.02±0.01 0.24±0.11
N Fledged young (hatched)	71					
Nestling period rain		11.69	1	0.002		
Laying date Parasitism Predation Territory identity (r) Year (r)		2.93 4.93 10.19	1 1 1	0.087 0.031 0.002	0.17±0.32 -0.03±0.09	
Minimal model						
Constant Nestling period rain Parasitism N hatched eggs						2.12±0.21 0.12±0.04 -0.81±0.37 -1.90±0.60
N Fledged young (hatched)	89					
Nestling period rain Laying date Parasitism Predation Territory identity (r)		4.55 4.62 8.53 22.69	1 1 1 1	0.033 0.032 0.003 <0.001	0.01+0.20	
Year (r)					0.01 ± 0.08	
Minimal model						
Constant Nestling period rain Laying date Parasitism Predation						1.69±0.13 0.07±0.03 -0.04±0.02 -0.86±0.29 -1.62±0.34
Survival rate

The survival rate of radio-tracked fledglings during the first five weeks after leaving the nest was 81.08%. Survival rate in group-breeding territories (90.91%) was higher than in pair-breeding ones (84.21%), although difference did not reach statistical significance (Table 1; Mann-Whitney U test Z=0.30 p=0.76; Fig. 2c). The yearling survival rate at the next breeding season was 63.89%, and no differences were found between fledglings from group and pair-breeders (Table 1; Chi-square=0.59 df =1 p=0.44).

Brood Parasitism and Predation Rates

Average brood parasitism rate by Great Spotted Cuckoos along the study period was 22.94% (n=124) but it significantly varied among years (Table 1; Kruskal-Wallis test H (2, N=123) =27.82 p<0.001). Parasitism rate increased from 7.14% in 2006 and 10.53% in 2007 to a very high parasitism rate of 51.16% in 2008. Group and pair–breeding territories were parasitized at a similar rate (Table 1; Mann-Whitney U test Z=0.63 p=0.53).

The average of failed nests by predation was 19.35% what did significantly varied between years (Kruskal-Wallis test H (2, N=124) =9.14 p=0.01). Predation rate was higher at egg stage (13.71%) than at the nestling stage (5.65%) (Chi-square= 4.61, df =1, p=0.03). Only 8.06% of nests failed because parents abandoned them (no differences among years were found; Kruskal-Wallis test H (2, N=124) =1.09 p=0.58). Both abandonment and predation rate did not differ significantly between group and pair-breeding territories (Table 1; Mann-Whitney U test Z=-0.16 p=0.88; Mann-Whitney U test Z=0.16 p=0.88; respectively).

DISCUSSION

Cooperation

Most Carrion Crow populations have been considered as formed by solitary breeders (Cramp & Perrins 1988). Until now, only one carrion crow population located in León (Northern Spain) has been described as cooperative (Baglione et al. 2005; Canestrari et al. 2008), although another population located in a Swiss urban area was found to exhibit a low rate of cooperation (6%; Richner 1989; Richner 1990). Cooperative breeding is not always easily detectable. In fact, before start this study we did not detect cooperation in the population of Guadix (Soler 1990; Soler et al. 2002), but when we studied this subject making the observations specially designed to detect cooperative breeding (see methods) we found a very high cooperation rate (66,49%), similar to that found in the cooperative population of León (75%; Baglione et al. 2005). Thus, we recommend making specifically-designed studies to determine the cooperation rate of a given crow's population.

Re-nesting

After a nest failure, re-nesting rate in the cooperative territories from León, is higher (70.29%) than in non-cooperative territories (29.71%) (Canestrari et al. 2008). In the rest of non-cooperative european populations, re-nesting rates are highly variable ranging from 34% to 78% (Loman 1980). However, re-nesting is very scarce in our study area (10.42%), we only detected five re-nesting events, and we found that group-breeding individuals renest less frequently (1 case) than pairs (4 cases), though differences did not reach significance (Table 1). This information suggests that the normal pattern of the species is re-nesting after nest predation and that special ecological conditions that imply the south limit of the distribution of the species, could be affecting our studied population making replacement clutches very scarce. The main of these special conditions of our population probably is the high maximum temperatures that frequently are raised during late-spring (up to 36°C), which would decrease the availability of larvae and adult insects for nestling feeding. Probably, this is the reason why reposition clutches are not adaptive in our study population. In fact, none of the five reposition clutches produced any fledgling.

Reproductive biology

One of the main characteristics shared by cooperative species is a small clutch size (Arnold & Owens 1998; Dickinson & Hatchwell 2004). Clutch

size for Carrion Crows at the first nesting attempt ranges from 3.2 to 4.8 eggs (Loman 1980; Cramp & Perrins 1988). In the population from León the average clutch size is 4.4 eggs and it is not influenced by the presence of helpers at the nest (Canestrari et al. 2008). In our population, clutch size (4.5 eggs) is not influenced by group size either (Appendix 2). Clutch size of both Spanish populations is slightly larger than in other more septentrional populations (Cramp & Perrins 1988). Probably this is the consequence of the fact that both Spanish Carrion Crow's populations are located at lower latitude than the other studied populations, and in other corvid species it has been shown that clutch size increases as latitude decreases (Soler & Soler 1992).

Hatching success in our study area is similar to those of other cooperative and non-cooperative European populations (Loman 1980; Parker 1985; Loman 1985; Cramp & Perrins 1988; Canestrari et al. 2008) and the number of fledglings produced in our population (2.08) is within the range of non-cooperative ones (from 1.2 to 3.6) (Loman 1980; Parker 1985; Loman 1985; Cramp & Perrins 1988).

Carrion Crow, as most corvid species, is a brood reductionist breeder. The female start incubating before clutch completion and thus, the last laid egg hatches later. As a consequence these chicks are handicapped by a lower size and, when food is not too abundant they usually starve (see below). Hatchwell (1999), in a comparative study of 27 cooperative

breeding species, found that care of helpers is additive when nestling starvation is frequent. In all those species where the starvation rate was 20% or larger there exist a compensatory care by helpers. In our study we found a nestling starvation rate of 29.14% but, surprisingly, those group-breeding territories suffered more starvation (33.58%) than pair-breeding ones (14.63%) (Tables 1 and 2; Appendix 2). This unexpected result could imply that non-breeding individuals are not helpers in the territory or, in case of true helpers, helping provided by them is not effective providing food to the nestlings. Canestrari et al. (2004) reported a high proportion of false feedings ("arriving at the nest with no food, consuming part or all the food brought to the nest, or taking back from a chick's gape the food that had just been delivered"; Canestrari et al. 2004) by helpers, but mainly by adult females. Although our sample size is low, we can argued that if in our studied population females were performing false feeding and non-breeding individuals were not compensating, this could be the cause of a higher nestling starvation in the cooperative territories than in the non-cooperative ones.

A higher breeding success in nests of cooperative breeders than in non-cooperative ones have been described in some studies (e.g., Boland et al. 1997; Brown et al. 1982; Emlen and Wrege 1991; Komdeur 1994; Mumme 1992 in Hatchwell et al. 2004), but also, some others have described the lack of this positive relationship between group size and

productivity (e.g., Legge 2000; Leonard et al. 1989; Walters 1990 in Hatchwell et al. 2004). While Canestrari et al. (2008) found that the presence of two helpers at the nest increases breeding success, in our population we have not found a positive effect of group size, which could be to differences in sample sizes used in both studies. Our results show that early breeders produce a larger number of fledglings than late breeders.

On the other hand, an earlier laying date usually is correlated with breeder's quality (e.g., Møller 1994; Hipfner et al. 2010). As Baglione et al. (2006) experimentally demonstrated, territories of better quality (with experimentally increased food resources) increased the year-round residency of individuals. Then, this suggests that cooperative territories are of better quality than non-cooperative ones. Thus, maybe is not the grup size, but the territory quality what is influencing breeding success

Survival rate

It has been shown that cooperative breeding species provide a prolonged care to the offspring after leaving the nest than non-cooperative ones (McGowan & Woolfenden 1990; Heinsohn 1991). We have not found a significant effect of group size in fledgling survival during this period. A group size higher than 2 did not affect fledgling survival until the next breeding season either.

Brood parasitism and predation rates

Little is known of how cooperative breeding is related to brood parasitism. Poiani & Elgar (1994) and Monadjem (1996) made a comparative analysis on Australian and South African avifauna, respectively, and did not find that brood parasites preferentially parasitize cooperative species. Furthermore, Langmore & Kilner (2007) studied the effect of brood parasitism on Superb Fairy-wren (*Malurus cyaneus*), and did not find differences in brood parasitic rates when comparing cooperative groups and unassisted pairs. Canestrari et al. (2009) made a similar comparison on the cooperative population of Carrion Crow at León (Northern Spain) and found that group size was negatively related to brood parasitism rate. However, in our population, group breeders were brood parasitized at a similar rate than pairs (Table 1).

The number of hatched eggs as well as the breeding success in our population is mainly diminished by both brood parasitism and predation (Table 2; Appendix 2). The reduction on the number of hatched eggs provoked by brood parasitism surely is due to the fact that Great Spotted Cuckoo females use to destroy on average 16.4% of the crow's eggs (Soler & Martínez 2000). Furthermore, cuckoo eggs hatch several days before those of the host, which in magpie nests provides the parasitic chick an advantage in size, allowing it to outcompete host nestlings (Soler 1990; Soler et al. 1996; Soler et al. 2002). Crows are about double the size of

Magpies and Great Spotted Cuckoos (Cramp & Perrins 1988), this difference in size makes the cuckoo chick usually unable to outcompete crow chicks even when hatching several days earlier (Soler et al. 2002). Probably, as suggested by Soler et al. (2002), this is the reason why we have not detected any negative effect of brood parasitism on crow at nestling stage (Table 2; Appendix 2).

Moreover, in several cooperative breeding species helpers are effective defending nests, so predation rate in nests with helpers usually is lower than in nests without helpers (Brown 1987; Emlen 1991; Cockburn 1998; Dickinson & Hatchwell 2004). In our study area, we have not found statistically significant differences between both groups of territories (Tables 1 and 2; Appendix 2) probably because predation influence is very low.

Meteorology

Within meteorological factors, only precipitation has been described in the literature as affecting avian reproductive biology and its effect is widespread in many different species (Järvinen 1980; Becker et al. 1985; Donazar & Ceballos 1989), including the Hooded Crow (Rofstad 1988). As it arise from our meteorological model (see Appendix 1), the three meteorological variables studied (minimum and maximum temperatures, and precipitation) showed a significant effect on reproductive success.

Minimum temperature during the five days before the laying of the first egg produces a delay of laying date and a decrease of clutch size. In contrast, maximum temperature during nestling period increases the number of starved nestlings, probably due to particularly high maximum temperatures that can be reached in a Mediterranean climate at end-spring, which could made more difficult to find food for the nestlings. In addition, precipitation showed opposite effects: during the incubation period decreases the number of hatched eggs, but during the nestling period increases the number of fledglings produced. The positive effect found during the nestling period could be due to an increase of feeding resources related to precipitation as Rofstad (1988) suggested. Furthermore, the combined model suggests that the role of meteorological factors on Carrion Crows' reproductive biology is comparable to those played by biological factors, as is shown in the model related to number of hatched eggs where the effect of precipitation during incubation period is present together with biological factors. Also, the positive effect of maximum temperature during the nestling period on starved nestlings is maintained in the combined model. Consequently, the effects of the dryer breeding seasons at the begining and warmer at the end occurring in our studied population are mainly to reduce breeding success (by decreasing hatching success and increasing nestling's starvation in the population. On the other hand, precipitation at the end of the breeding season increases breeding success (Table 2; Appendix 1).

In conclusion, in this study in which we describe the breeding biology of a new cooperative population of Carrion Crow, we have found that group-breeding individuals lay earlier than pair-breeding, but their nestlings starve at a higher rate. In general, a relevant positive effect of non-breeding individuals in the success of attended pairs remains undetected. On the other hand, we found that meteorological factors play an important role on breeding success of Carrion Crow in the studied population.

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Breeding biology and fledging survival in Carrion Crow

Model terms	N	Wald Statistic	df	Р	Random term estimated variance component ± SE	Average effect ± SE
Laying date	108					
5 days earlier rain 5 days earlier T max 5 days earlier T min Territory identity (r) Year (r)		0.91 0.34 32.06	1 1 1	0.343 0.562 <0.001	5.84±6.21 49.71±55.05	
Minimal model						
Constant						
5 days earlier T min	33.22	2±3.44				0.26±0.05
Clutch size	105					
5 days earlier rain 5 days earlier T max 5 days earlier T min Territory identity (r) Year (r)		0.52 0.32 5.31	1 1 1	0.474 0.575 0.045	0.37±0.20 0.22±0.32	
Minimal model						
Constant 5 days earlier T min						4.58±0.23 -0.01±0.01
Hatched eggs	92					
Incubation period rain Incubation period T max Incubation period T min Territory identity (r) Year (r)		9.92 2.46 1.27	1 1 1	0.002 0.129 0.264	0.20±0.35 1.88±2.14	
Minimal model						
Constant Incubation period rain						2.94±0.93 -0.08±0.03
Starved nestlings	42					
Nestling period rain Nestling period T max Nestling period T min Territory identity (r) Year (r)		0.08 4.30 0.02	1 1 1	0.779 0.045 0.876	0.28±0.29 0.50±0.62	
Minimal model						
Constant Nestling period T max						1.19±0.43 0.02±0.01

Appendix 1

Appendix 1 (Continuation)

Model terms	Ν	Wald Statistic	df	Р	Random term estimated variance component ± SE	Average effect ± SE
No. Fledged young (hatched) Nestling period rain Nestling period T max Nestling period T min Territory identity (r) Year (r)) 71	11.04 0.00 0.35	1 1 1	0.002 0.945 0.554	-0.07±0.36 0.26±0.52	
Minimal model Constant Nestling period rain No. Fledged young (overall)	89					2.13±0.29 0.13±0.04
Nestling period rain Nestling period T max Nestling period T min Territory identity (r) Year (r)		15.78 1.01 0.00	1 1 1	<0.001 0.324 0.980	-0.02±0.28 0.53±0.73	
Minimal model Constant Nestling period rain						1.73±0.29 0.14±0.04

Breeding biology and fledging survival in Carrion Crow

Appendix 2

Model terms	Ν	Wald Statistic	df	Р	Random term estimated variance component ± SE	Average effect ± SE
Laying date	58					
Group size Territory identity (r) Year (r)		6.53	1	0.015	26.19±9.10 3.65±4.94	
Minimal model						
Constant						
Group size	32.8	9±1.48				-1.60±0.63
Clutch size	57					
Group size Territory identity (r) Year (r)		1.07	1	0.306	0.62±0.34 0.003±0.06	
Minimal model						
Constant						4.79±0.18
Clutch size	105					
Laying date Territory identity (r) Year (r)		30.85	1	<0.001	0.11±0.14 0.05±0.08	
Minimal model						
Constant Laying date						4.59±0.17 -0.07±0.01
N. hatched eggs	49					
Group size Parasitism Territory identity (r) Year (r)		1.03 6.55	1 1	0.317 0.012	-0.24±0.41 -0.13±0.25	
Minimal model						
Constant Parasitism						2.73±0.47 -1.07±0.42
N. hatched eggs	93					
Laying date Parasitism Territory identity (r) Year (r)		8.37 11.64	1 1	0.005 <0.001	0.18±0.35 0.44±0.52	
Minimal model						
Constant Laying date Parasitism						2.96±0.41 -0.06±0.02 -1.36±0.40

Appendix 2 (Continuation)

Model terms	N	Wald Statistic	df	Р	Random term estimated variance component ± SE	Average effect ± SE
Starved nestlings	30					
Group size N hatched eggs Territory identity (r) Year (r)		10.12 7.95	1 1	0.014 0.015	0.81±0.31 0.04±0.09	
Minimal model						
Constant Group size N hatched eggs						1.46±0.24 0.31±0.10 0.41±0.14
Starved nestlings	43					
Laying date N hatched eggs Territory identity (r) Year (r)		5.31 4.27	1 1	0.027 0.048	0.33±0.23 0.04±0.09	
Minimal model						
Constant Laying date N hatched eggs						1.38±0.20 0.04±0.02 0.23±0.11
No. Fledged young (hatched)	44					
Group size Parasitism Predation Territory identity (r) Year (r)		0.01 9.95 14.08	1 1 1	0.929 0.006 <0.001	0.38±0.44 0.05±0.17	
Minimal model						
Constant Parasitism Predation						2.06±0.16 -0.14±0.36 -2.17±0.58
No. Fledged young (hatched)	72					
Laying date Parasitism Predation Territory identity (r) Year (r)		6.53 6.81 11.68	1 1 1	0.013 0.013 0.001	0.22±0.32 0.02±0.10	
Minimal model						
Constant Laying date Parasitism Predation						2.11±0.18 -0.06±0.02 -2.98±0.37 -2.10±0.61

Model terms	N	Wald Statistic	df	Р	Random term estimated variance component ± SE	Average effect ± SE
No. Fledged young (overall)	47					
Group size Parasitism Predation Territory identity (r) Year (r)		0.10 4.73 33.95	1 1 1	0.759 0.032 <0.001	0.30±0.43 0.01±0.14	
Minimal model						
Constant Parasitism Predation						1.58±0.25 -0.69±0.32 -1.83±0.31
No. Fledged young (overall)	90					
Laying date Parasitism Predation Territory identity (r) Year (r)		11.66 9.25 25.45	1 1 1	<0.001 0.004 <0.001	0.14±0.22 0.03±0.09	
Minimal model						
Constant Laying date Parasitism Predation						1.73±0.17 -0.06±0.02 -0.94±0.31 -1.76±0.35

Appendix 2 (Continuation)

Parental-care parasitism: how do unrelated offspring attain acceptance by foster parents?

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SUMMARY

In this review we describe a new term, "parental-care parasitism", that we define as the interaction in which an individual (the parasite) obtains reproductive benefits while reducing or completely eliminating its own costs of parenting by exploiting any type of offspring care provided by other individuals (the hosts). Parental-care parasitism comprises parasitic behaviors ranging from interactions in which just the nest is taken over to those where various combinations of nest, food and offspring care are parasitised. We subdivide parental-care parasitism into three categories depending on the strategy used by the parasite to reach host nest: 1) the parasite approaches the nest during host absence, 2) parasite and host adults meet at the nest but no aggression is carried out, or 3) the host tries to evict the parasite at the nest. We also discuss the costs and benefits for both parents and offspring, as well as for hosts and parasites, placing different forms of parental-care parasitism in an evolutionary context within the frameworks of both parental investment theory and coevolutionary arms race theory. Herein we thoroughly discuss the lack of offspring discrimination found in some species, some populations of the same species and some individuals within the same population on the basis of the coevolutionary arms race theory, and the fact that unrelated offspring attain acceptance by foster parents, contrary to the general predictions of parental investment theory. This review offers a conceptual framework that seeks to link parental investment theory with coevolutionary arms race theory.

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INTRODUCTION

Parental care involves any sort of parental behavior that increases the fitness of assisted offspring (Clutton-Brock 1991). Parental care has been described in most animal phyla but is especially well developed in numerous species of insects, crustaceans and vertebrates (Glazier 2002). The amount of parental care provided to offspring by different species is determined mainly by ecological factors that increase mortality of eggs or young, such as harsh physical conditions, difficulty of access to resources and a high risk of predation of eggs or young (Clutton-Brock 1991; Glazier 2002).

Parental care is a highly variable behavioral trait between species. It ranges from nest construction to a combination of nest preparation, feeding, cleaning and defense of the offspring. Many different behavioral traits have evolved within the animal kingdom that help offspring to survive the initial stages of life, with the parents providing nutrients, warmth, protection from enemies and the elements, a favorable nest environment and/or opportunities for learning the skills needed for survival or reproduction (Glazier 2002). Parental investment theory suggests that such variation arises from interspecific differences in the trade-offs between the fitness benefits for offspring and the fitness costs to parents (Clutton-Brock 1991). In many species parental care is one of the most energy-consuming activities that affect an individual's fitness (Trivers 1972; Clutton-Brock 1991). Parental investment involves important costs, such as a greater predation risk and large expenditure of time and energy (Clutton-Brock and Vincent 1991; Smith and Wootton 1995). Parental investment theory assumes that parental care is the evolutionary product of fitness costs and benefits; thus parents should be able to increase their fitness by trading off present and future parental investment (Trivers 1972; Carlisle 1982; Winkler 1987; Montgomerie and Weatherhead 1988; Clutton-Brock and Vincent 1991). In agreement with this, it is well known that parents are able to favor offspring of higher reproductive value (Lyon et al. 1994; Rytkönen 2002; Bize et al. 2006; Smiseth et al. 2007; Griggio et al. 2009).

Because parental care is costly and it is important for parents to save energy for subsequent reproductive events, parental investment theory predicts that parents should not provide assistance to young animals that are not their own genetic offspring. That is, parents should reduce or avoid care for unrelated offspring to save energy or other resources for future reproductive events. This is usually the case with paternal care in response to a reduced certainty of paternity not only in birds (Westneat and Sherman 1993; Sheldon et al. 1997; Møller and Cuervo 2000) but also in fish (Neff 2003a) and arthropods (Zeh and Smith 1985).

However, the capacity to recognize and discriminate against unrelated offspring has been shown to be well developed in some species (Buckley and Buckley 1972; Balcombe 1990; Phillips and Tang-Martinez 1998; Insley 2000; Searby and Jouventin 2003; Searby et al. 2004; Jesseau et al. 2008; Li and Zhang 2010) but not in others (Davies and Brooke 1989; Rotshtein 1990; Moksnes et al. 1991; Davies 2000). Because parental care is beneficial only if directed towards genetic descendants (Trivers 1972), why then do parents sometimes care for unrelated offspring that parasitize parental care? This essential question is addressed in the General Discussion.

The term "parasitism" includes those interactions in which one or several individuals (parasites) obtain benefits from other individuals (hosts), thereby decreasing the hosts' fitness. Thus, parasitism always affects host fitness and so host species are usually under strong selection pressures to develop defensive strategies (defenses) against their parasites, which may cause the parasites to improve their parasitic strategies (counterdefenses). This process is known as an "arms race" (Dawkins and Krebs 1979) and it usually occurs within a coevolutionary process that implies reciprocal evolutionary change in both the parasite and the host species (Thompson 1994) – but not always (see Janzen 1980).

We define "parental-care parasitism" as an interaction in which an individual (the parasite) obtains reproductive benefits while reducing or completely eliminating the costs of parenting by exploiting any type of offspring care provided by other individuals (the hosts). Thus, cases that include the parasitism of a resource prepared for direct use by the offspring are also encompassed within this term. Parental-care parasitism exists both at intraspecific and interspecific levels. This distinction is sometimes important because the costs to hosts and the virulence of parasites in each case are clearly under different constraints and selective pressures.

Within the term "parental-care parasitism", we include such behaviors as nest usurpation and theft of stored food, leaving parasitic offspring to be defended and fed by other individuals, and exploitation of worker labor in eusocial animals. We also include those cases in which it is the offspring itself who seek parasitism. Most cases of parental-care parasitism have been previously labeled "brood parasitism", but in some cases, they have been referred to as "reproductive parasitism", "kleptoparasitism", "kleptobiosis" and "social parasitism"; basing the classification mainly on the type of resource parasitized. This imprecise terminology is problematic to the study of host-parasite relationships because there is confusion over what each particular term means and how each should be used. This problem with terminology, and the fact that the costs incurred by hosts are highly different across different host-parasite systems, as we will describe below, are the reasons why we propose a new classification, based on behavior of both parasite and host, which will be useful when comparing different

parasitic interactions involving parental care. The main objective of this review is to present a new classification of parental-care parasitism in an evolutionary context within the frameworks of both parental investment theory and coevolutionary arms race theory.

We resolve the terminological issues by discussing cases of parasitic interactions that involve parental care, and the different adaptations that they present, along a parasitic behavioral gradient that we have divided into three categories: 1) the parasite approaches the nest during host absence, 2) parasite and host adults meet at the nest but no aggression is carried out and 3) the host tries to evict the parasite at the nest (Table 1). In addition to the behavior of the parasite, we further subdivided according to defensive mechanisms evolved by the host against its enemies and the possible coevolutionary arms race that has driven the process. Our selection of examples is biased in favor of those that outline a general rule or those in which individuals incur higher than expected costs. The review is also biased toward insect taxa, which is unsurprising given that 95% of all described species are arthropods (Hawksworth and Kalin-Arroyo 1995). This review offers a conceptual framework that seeks to link parental investment theory with coevolutionary arms race theory.

PARENTAL-CARE PARASITISM AND BEHAVIORAL CLASSIFICATION

We classify parental-care parasitism depending on the parasite strategy that used to approach the nest, mainly whether the parasitic female avoids the host or not to perform parasitism. Then, we subdivided each section depending on whether the host has developed defenses to the parasitism or not (see Table 1). We discuss each example under both parental-care investment and coevolutionary arms race theories whenever possible.

Parasitism performed during host absence

In some occasions, parasites approach host nest to perform parasitism when host is away, either because the host is not at the nest when the parasite arrives or because the parasite wait until the host leaves. In these two situations, host can both present defenses or do not, surely depending on the cost that this parasitism means to it and the duration of coevolutionary relationships between the parasite and the host species.

Without defense or counteradaptation

In many species, as in most non-eusocial Hymenoptera, parental care consists on providing a proper place and food to ensure an optimal development of the offspring. Thus, parents will leave the nest while

foraging and/or permanently after oviposition. In these species, parasitism is usually performed while the host is away foraging as happens in some Megachilid bees and Eumenid and Ammophiline (Family: Sphecidae) wasps (Field 1992a). The parasite enters a conspecific's nest, discard host eggs or small larvae (when present) and lay its own eggs after provision the cell. If the cell was already partially provisioned the parasite's offspring will also eat this food. After parasitic females never met and had not been described any defense against parasitism, even when the parasitic pressure could reach high percentages (36% in the case of the eumenid wasp *Zethus miniatus*) (Field 1992a). In other Megachilids, as in *Cerceris intricata* or *Crabro monticola*, when parasitism has been performed, host adopts the parasitic strategy itself (Field 1992a).

Also, an unusual example has been reported recently in *Dendrobates variabilis*, an Amazonian poison frog. Adult males carry and deposit their tadpoles within pools containing the eggs of unrelated conspecifics, which serve as food for cannibalistic tadpoles (Brown et al. 2008). Although this parasitic interaction mainly occurs at an intraspecific level, interspecific interactions have also been described (*D. variabilis* tadpoles also kill and consume *D. imitator* ones; Brown et al. 2008).

Parasite performance	Host l respo	behavioural nse	Taxon
Parasitism during host	Without defen	ce or counter-adaptation	Hymenoptera Anura
absence	Defense	Adults could meet	Hymenoptera* Araneae
		Adults never meet	Hymenoptera
Parasite and host meet without aggression	Without defen	ce or counter-adaptation	Heteroptera Lepidoptera Siluriformes
	With defence		Hymenoptera* Coleoptera
	Possible aggre host and paras	ession between ite	Perciformes Rodentia*
	With counter-a	adaptation	Hymenoptera
Parasite and host meet with aggression	Without offspi	ring recognition	Apodiformes Falconiformes Stigiformes
	With offspring	g recognition	Hymenoptera* Coleoptera* Aves * ¹

Table 1. Behavioral classification of parental-care parasitism

Classification of parental-care parasitism based on parasite behavior while approaching the host nest and on the host response to parasite attack. Also included are the taxa corresponding to each interaction.

* Host recognition of parasite offspring

¹ Avian orders included are: Anseriformes, Charadriformes, Ciconiformes, Cuculiformes, Falconiformes,

Galliformes, Passeriformes, Piciformes, Spheniciformes, and Stigiformes.

With defense

In accordance to parental investment theory, parents should defend their nest and offspring (Clutton-Brock 1991). These defenses could be either active or passive. The most intuitive and common defense against parasites is to fight them off the nest, but in the examples discussed in this section the parasitism is performed while host is away, so the host can mainly develop passive defenses.

Adults could meet. Even if the parasitism is performed while host is away, both host and parasite could meet at the nest. In these cases the most common defense is to try to drive off the parasite. Field (1992a) reviewed intraspecific parasitism in nest-building wasps and bees. In some parasitic interactions, as in ground-nesting Sphecid wasps and two Megachilid bees (*Haplitis anthocopoides* and *Chalicodoma pyrenaica*), the author describes that if both host and parasitic females meet at the nest they fight for it.

Furthermore, all species within the genus *Sapyga* (Hymenoptera: Sapygidae) are known to be obligate interspecific nest parasites of solitary bees, in particular of the megachilid genera *Osmia, Megachile,* and *Chelostoma* (Müster-Swendsen and Calabuig 2000). *Sapyga* parasitic female wasps enter host nests to oviposit while the owner is away. When parasitism is successful, first instar parasitic larvae kill and consume the egg or larvae of the host as well as the nectar and pollen provisions in the cell (Torchio 1972), thereby reducing host fitness.

Both passive and active defensive traits have been described for this interaction. As a passive defense, host females spend more time at the nest entrance (e.g., in *Osmia pumila*) or nest communally (Goodell 2003). Also, when interspecific parasites are common, some solitary bee species oviposit

within several nests (e.g., in O. pumila), increasing the odds that at least some nests will escape parasitism (Goodell 2003). On the other hand, it is surprising that solitary bees rarely attack parasites approaching nests (Weislo and Cane 1996). But if hosts and parasites meet at the nest the host female can actively defend her nest and aggressively evicts the parasite (Megachile rotundata; Torchio 1972; Goodell 2003). Moreover, as happens in many avian host species of brood parasites (Davies 2000), a very effective host defense is the recognition and subsequent destruction of parasitic eggs (e.g., in Chelostoma florisomne, Müster-Swendsen and Calabuig 2000) where host females vigorously clean the nest removing parasitic eggs and even some stored pollen (Müster-Swendsen and Calabuig 2000). The female megachilid is apparently efficient in detecting parasite eggs. However, egg recognition has not been described in other bee species. Perhaps weaker selection pressures due to a lower cost of parasitism, or the existence of other defensive mechanisms that protect the host from the parasite, account for the rarity with which egg-recognition behavior arises (see section below). In any case, females of some parasitic species (e.g., Sapyga clavicornis) are capable of penetrating a recently finished cell cap with the pointed tip of the abdomen, after which they oviposit inside the cell (Müster-Swendsen and Calabuig 2000). The most surprising antiparasite defense may involve the construction of an empty cell in front of brood cells. Thus, a parasite will oviposit in an unprovisioned brood cell
and its offspring will die of starvation (*C. florisomne;* Münster-Swendsen and Calabuig 2000). This defensive strategy decreases the rate of parasitism from 28.9% to 5.4% (Müster-Swendsen and Calabuig 2000). The evolution of empty cell construction appears to be the direct consequence of selective pressures imposed by the brood parasites of *C. florisomne* because, as Parker (1988) has pointed out, in two other *Chelostoma* species populations without nest parasites the females do not build empty cells.

On the other hand, Boulton and Polis (2002) describe the only example of which we are aware of nest parasitism within the order Araneae. The spider *Diguetia mojavea* (Araneae: Diguetidae) is parasitized mainly (76%) by two salticid species (*Metaphidippus manni* and *Habronattus tranquillus*) whose spiderlings also prey on those of the host (Boulton and Polis 2002). Possible host defense have been reported for *D. mojavea*. Only 0.6% of the host nests were parasitized in the presence of the host mother but the rate jumped to 81% when the mother was absent. Although it is not described how this defensive mechanism is developed, we could assume that it is an active defense. Furthermore, the large number of eggs laid by the host (1000 against only a few parasite eggs) has also been interpreted as a passive defensive mechanism because a larger clutch increases the probability that some host offspring will survive (Jackson 1978; Boulton and Polis 1999).

Adults never meet. Sometimes host female returns to her nest from foraging and find it parasitized. In these occasions some species do not present defenses (as discussed above), but some others have developed defensive behaviors. These interactions have been thoroughly studied in groundnesting crabronid wasps (subfamilies Larrinae, Crabroninae, Nyssoninae and Philanthinae). In his review of the phenomenon, Field (1992a) described how the usurper usually secures the host's nest before provisioning it. Nest usurpation often occurs while the original occupant is away hunting for prey. When the parasite closes the nest, the returning host can dig through the closure and attempt to evict the parasite (e.g., in *Lindenius columbianus, C. monticola*).

Sometimes both host and parasite never meet but host presents behavioral defenses against parasitism even if it would be performed when the host is absent. In these cases we can expect that parasitic rate should be high or parasitism costly enough to drive the host to develop defensive strategies. A good example of these interactions is the case of superparasitism in hymenopteran parasitoids. In the parasitoids' breeding strategy, the main parental cost is to find a suitable prey to lay the eggs. In cases of superparasitism, a parasitoid female deposits her egg(s) on a prey item that has already been victimized by other female, avoiding the main cost of breeding (see the review by Dorn & Beckage (2007) for more

details). As Field (1992b) stated, superparasitism in ectoparasitoids competing sequentially for the same host is functionally equivalent to brood parasitism. In this context, conspecific superparasitism can be interpreted as a kind of parental-care parasitism, in which the second comer parasitizes parental efforts by the first one. In any event, the original parasitoid loses if the second comer can destroy the eggs of the former by stabbing them with her ovipositor within the host before laying her own eggs (e.g., in *Encarsia formosa*; Hymenoptera: Aphelinidae; Dorn and Beckage 2007), or if there is competition for food between the two groups of larvae. Thus, as commented above, being parasitized represents an extra cost to the host, whose reproductive effort will be reduced to zero.

The costs to the host of this type of parasitism are high and so it would be expected to develop some counter-adaptations. Dorn and Beckage (2007) describe some defensive adaptations against superparasitism. For example, the original female may lay many eggs on the prey (e.g., *Trichogramma evanesens*; Hymenoptera: Trichogrammatidae), making it inappropriate for subsequent females. Another defense under conditions of massive superparasitism is a reduction in clutch size, which could prevent host death and increase the odds of survival for a latecomer (e.g., *Cotesia sp.*; Hymenoptera: Braconidae; Dorn and Beckage 2007). The latter could be seen as a case of tolerance instead of resistance (see General Discussion).

Parasite and host meet without aggression

Sometimes parasite and host meet but do not fight even if parasitism is performed when host female is present. In other occasions it is the offspring itself that perform parasitism and the host is completely cheated (see *Maculinea* larvae example below).

Without defense or counter-adaptation

The most intriguing example has been described in golden egg bugs *Phyllomorpha laciniata* (Hemiptera: Coreidae) where individuals are parasitized without showing any resistance even when it rises the odds of being predated (Kaitala 1996; Kaitala 1998; García-González and Gomendio 2003).

Golden egg bugs *Phyllomorpha laciniata* (Hemiptera: Coreidae) carry their eggs on their backs, which is advantageous because eggs laid on vegetation suffer very high mortality (97%; García-González and Gomendio 2003). Golden egg bug females glue eggs on the backs of other individuals of both sexes (Kaitala 1996). Egg carrying behavior is a costly form of parental care because individuals with eggs on its backs become more conspicuous and are more frequently attacked by predators than are egg-free ones (Kaitala 1996; Kaitala 1998; García-González and Gomendio 2003). Some eggs are laid on the back of the male that fertilized them and, in this case, egg-carrying behavior can be considered potentially adaptive

parental care. However, according to Tay et al. (2003), 87% of the eggs carried by a mated male have been fertilized by another male or males. In this case, the hypothesis of parasitic behavior may apply.

It is surprising that individuals do not resist attempts by females to lay eggs on them (Kaitala 1996). Moreover, although egg-caring males are able to remove some of the eggs glued on their backs, they cannot distinguish their offspring from the rest (Kaitala 1998), which implies high costs for egg carriers if they remove their own eggs.

Another intriguing parasitic interaction in which no defensive mechanisms have been developed is described in one of the most advanced parental care behaviors known among fish, in mouthbrooding cichlids (Sato 1986). Eggs of the mouthbrooder are usually picked up by the female immediately after oviposition and are incubated in her buccal cavity. After yolk sac absorption, the fry frequently swim out to forage and return, using the mouth as a refuge until they become fully independent (Sato 1986). Sato (1986) found that a Lake Tanganyika endemic mochokid catfish species, *Synodontis multipunctatus*, is an interspecific parental-care parasite of at least six species of mouthbrooding cichlids. Presumably, the female catfish lays her eggs at the same time as her host, which picks them up together with her own eggs. Once inside the host female's buccal cavity, they develop together with host fry (Sato 1986). But catfish parasitic offspring hatch earlier than those of the host and feed on them (Sato 1986) which, as commented above, implies an extra cost of parasitism to the host dramatically reducing its reproductive effort.

No counterparasitic defense mechanisms have been described in mouthbrooding cichlid fish. Perhaps the low parasitic pressure (the parasitism rate in different species ranges between 1.4% and 15%; mean = 6.3%; Sato 1986) is not strong enough for a counteradaptive strategy to evolve or, more probably, expelling catfish eggs incurs greater losses than benefits, as happens in some hosts of avian brood parasites (Davies 2000) as we discuss below.

Also offspring can seek parasitism without aggressive host responses. The larvae of several species of *Maculinea* butterflies (Lepidoptera: Lycaenidae) seek to parasitize the parental care of a certain nests of *Myrmica* ants (Formicidae). Butterfly females lay their eggs on host plants where their brood successfully grows by feeding on flowers. Subsequently, the fourth instar larvae descend to the ground where they attract ant workers by producing a cocktail of hydrocarbons that mimic the larvae of *Myrmica* ants (Akaino et al. 1999). Workers carry caterpillars inside the nest, where the latter use a combination of tactile, acoustic and behavioral signals to get the ants to adopt them (Akaino et al. 1999). Inside the nest, caterpillars either get the worker ants to feed them (Elmes et al. 1991a, b) or themselves prey on the ant brood (Thomas and Wardlaw 1992). As a result, *Maculinea* larvae gain about 98% of their final weight in the ant nest during the 11 or

23 months (depending on species) that they spend within it (Steiner et al. 2003). This parasitism harms the ant host by monopolizing worker care and/or by inflicting losses on the ant brood. It is surprising that no defenses against this parasitism have been reported.

On the other hand, one of the most advanced parental care behaviors known among fish is described in mouthbrooding cichlids (Keenleyside 1979, in Sato 1986). Eggs of the mouthbrooder are usually picked up by the female immediately after oviposition and are incubated in her buccal cavity. After yolk sac absorption, the fry frequently swim out to forage and return, using the mouth as a refuge until they become fully independent (Baerends and Baerends-Van-Roon 1950; Fryer and Iles 1972; in Sato 1986). Sato (1986) found that a Lake Tanganyika endemic mochokid catfish species, Synodontis multipunctatus, is an interspecific parental-care parasite of at least six species of mouthbrooding cichlids. Presumably, the female catfish lays her eggs at the same time as her host, which picks them up together with her own eggs. Once inside the host female's buccal cavity, they develop together with host fry (Sato 1986). But catfish parasitic offspring hatch earlier than those of the host and feed on them (Sato 1986) which, as commented above, implies an extra cost of parasitism to the host dramatically reducing its reproductive effort.

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With behavioral defense

In some occasions, both host and parasite meet but hosts do not try to drive off the parasite; on the contrary, they present passive defense against parasitism. A clear example is the interspecific parasitism that takes place in Parastizopus armaticeps (Coleoptera: Tenebrionidae). Both host parents collaborate in digging a burrow, guarding the nest and collecting plant detritus to feed their offspring (Rasa 1999). Parasitic females of the tenebrionid *Eremostibes opacus* enter nests of *P. armaticeps*, where they feed, oviposit and then leave (Rasa 1996). The parasitic larvae live in the sand under the detritus store and feed on it (Rasa 1996), reducing the food resources for both host parents and offspring (Geiselhardt et al. 2006). Studies by Rasa and Heg (2004) showed that 90% of *P. armaticeps* burrows are parasitized. Parasitic females avoid being attacked by host parents because of their chemical mimicry (Rasa and Heg 2004). When researchers experimentally introduced parasites in host nests, only 7% of host individuals ejected the parental parasites, after detecting them via olfactory cues. Other potential defensive behaviors against parasitic females have

been described, such as when *P. armaticeps* parents (mainly males) guard the burrow entrance. This defensive strategy, although probably evolved to evict same-sex intruders, could also repel nest parasites (Rasa 1999).

Another typical parasitic interaction where no aggression against the parasite occurs has been reported in eusocial Hymenoptera (ants, wasps, and bees) that are vulnerable to parasitic laying by individual workers (Oldroyd 2002). This parasitic interaction has been thoroughly reviewed for eusocial bees by Beekman and Oldroyd (2008). They discuss different kinds of worker parasitism: intracolony intraspecific parasitism in queenright colonies (e.g., *Apis mellifera, Bombus terrestris*), intercolony parasitism performed by a subspecies (*Apis mellifera capensis*), and intercolony intraspecific parasitism in queenless colonies (e.g., *A. florea, Apis cerana*).

Different defensive mechanisms have been described for each interaction. With regard to intracolony worker reproduction, the host reproductive female as well as her brood produce pheromones that inhibit ovarian development in the worker caste (e.g., Ratnieks 1988; Barron et al. 2001).

Also, once the parasitic egg is laid (either intracolony or intercolony), the colony's worker force usually recognizes and destroys them (Ratnieks 1988), a response that is favored by kin selection (Ratnieks 1988; Barron et al. 2001). This behavior, termed "worker policing" usually involves

removal (commonly by eating) of worker-laid eggs, which smell different from those laid by the queen (Ratnieks and Visscher 1989). However, intracolony worker-laid eggs are not always destroyed; bumble bee workers are permissive about egg dumping due to their high genetic relatedness to one another (Beekman and Oldroyd 2008).

Another exception to worker policing is the case of Cape honey bees (*Apis mellifera capensis*), where eggs laid by host workers (*A. m. scutellata*) are effectively policed (Martin et al. 2002) but not those laid by the parasite probably because *capensis* females lay eggs that smell like those laid by the host queen (Ratnieks 1993; 1995).

Possible aggression between host and parasite

In some other species in which hosts do not reject parasite individuals, occasionally the host drives off the parasite. There have not been described any differences in the performance of parasitism between those cases in which the parasite is rejected and those in which it is not. Thus, these data could suggest either that though a few individuals show defensive mechanisms, the parasitism is not costly enough to expand among the host population, or that the parasitic rate is increasing within the population and parasitism costs are also rising making defensive mechanisms evolutionarily worthwhile.

One of the animal taxa in which some species show this behavior is teleost fish, where the male often stays at the nest defending the eggs. Guarding is a very costly trait, as shown by the reduction in body mass of those males that engage in intense territorial defense of their nests (e.g., van der Berghe 1988; Ota and Kohda 2006). Paternal males experience higher energy costs than non-paternal ones (van der Berghe 1992). Parasitic male fish may spawn within a territory defended by the host male in order to fertilize some eggs there. The eggs fertilized by a male parasite will be reared and defended by the territorial male until they hatch.

Different reproductive strategies related to morphological and physiological specializations have been described in teleost fishes (e.g., Mori 1995; Ota and Kohda 2006). Territorial males attempt to gain access to female gametes through courtship and by trying to monopolise as many females as possible (Taborsky 1998). These males are sometimes parasitized by other males in two different ways. Smaller, inferior rivals cheat the parental male via satellite behavior: involving younger males that also participate in spawning, or by sneaky behavior: in which males dart in when territorial males are spawning and release their own sperm (e.g., in *Telmatochromis vittatus*, Ota and Kohda 2006; *Lepomis macrochirus*, Gross and Charnov 1980; *Neolamprologus furcifer*, Taborsky 1998). Alternatively, larger males, known as pirates, invade the nest, spawn and leave (e.g., in *Symphodus tinca*, van der Berghe 1988). Territorial males

may also steal fertilizations from neighboring territorial males, although this has only been reported in the centrarchid *Lepomis marginatus*, in which other parasitic morphs are absent (Mackiewicz et al. 2002). As defensive behavior before the performance of the parasitism, the host could fight off the intruder (e.g., Taborsky et al. 1987; van der Berghe 1988; Baba and Karino 1998; Taborsky 1998; Ota and Kohda 2006). Furthermore, when the parasitism has already been performed, males could stop care by completely cannibalizing clutches that contain a mix of self-sired and foreign-fertilized eggs (Frommen et al. 2007; Neff 2003b; Rios-Cardenas; Webster 2005). Although these strategies in fish have historically been described as alternative reproductive strategies (Krebs and Davies 1993) we should not ignore their intraspecific parasitic component (e.g., Taborsky 1997). In these cases, parasitic males obtain a reproductive benefit without suffering the costs associated with guarding.

Contrarily to fish, in some species the offspring need to be fed by their parents after birth or hatching. Almost all endothermic parents face the energy-costly behavior of both feeding their offspring and keeping them warm, which constrains their reproductive success (Clutton-Brock 1991). In some cases, parasitic offspring have developed a "food stealing strategy" that requires host parents to do more work to help their own young develop fully or else find that their genetic offspring suffer underdevelopment. Parasitic interactions of this sort can occur intraspecifically. For instance, in more than 100 mammalian species, neonates have been reported to suckle milk from females that are not their genetic mothers (Riedman 1982). However, alloparental care usually benefits close kin and has been reported mainly in communal breeding species, where it may generate inclusive fitness benefits for the "parasitized" female (Roulin 2002). But alloparental care has also been reported from noncommunal breeding species and in these cases, the behavior has been associated with mothers who have lost their own offspring or it may reflect the parasitic behavior of some young (Packer et al. 1992). Obviously, foster offspring will always benefit from receiving milk from foster mothers, so natural selection for juveniles that try to steal milk from nonmothers is easily explicable when juveniles are rarely punished for allosuckling (e.g., Roulin 2002; Zapata et al. 2009). In fact, high levels of milk theft by parasitic infants have been reported in several species (Murphey et al. 1995; Zapata et al. 2009). The milk theft by the allosuckler (parasitic offspring; Packer et al. 1992) costs the host female a reduction of available nutrients for her own offspring as well as reducing her future reproductive success (Roulin 2002). Allosuckling is less costly when the host female has lost all her offspring because she needs to evacuate the nonconsumed milk (Wilkinson 1992). Important benefits to the allosuckler have been described in the forms of an extra milk intake (Packer et al. 1992) and the acquisition of immunological compounds (Roulin and Heeb 1999). Exploited females frequently behave aggressively

against unrelated offspring that are trying to allosuck them, which can be considered a defensive strategy (Roulin and Heeb 1999).

With counteradaptation

In other cases, the host has developed efficient defensive mechanisms. Thus, the parasite can either change host or react against these defensive mechanisms beginning a process of coevolutionary arms race (Dawkins and Krebs, 1979). We can find an example of arms race interaction in those cases of parasitism where the parasite has developed a camouflage that avoids to be recognized by the host while performing parasitism. According to the arms race theory, we would expect the development of an adaptive counterdefense by hosts which have been reported in most occasions. For instance, in some social Hymenoptera, females can usurp other females' nests. These parasitic females may be either those unable to find their own colony or females that have lost their colony, as observed in the genus Polistes (Cervo 2006). During usurpation, a parasitic female enters a host colony of either the same or different species (interspecific parasitism, see below) and kills the host reproductive female (e.g., Hölldobler and Wilson 1990; Cervo 2006). In consequence, no more host workers are produced and the colony gradually becomes a mixed colony until finally only the brood of the usurper is present (Hölldobler and Wilson 1990). Although the parasite obtains benefits from the host only relatively briefly, during the first stages of colony foundation, the host suffers major costs because the original queen and her workers die without producing reproductive offspring.

When the parasitic female enters a colony, the host workers may recognize her via chemical cues and attack her (Lenoir et al. 2001), but in most cases the parasites have evolved chemical mimicry of the host (e.g., Dettner and Liepert 1994; Lenoir et al. 2001) and are not attacked by host workers.

Interspecific nest usurpation is common (e.g., Cervo 2006), although the parasite's behavior and host defenses are similar to those seen in intraspecific cases. When *Polistes nimphus* enter the colonies of *Polistes dominulus*, they stroke their abdomens on the nest surface, saturating the colony with their odor (Cervo et al. 2004).

Contrary to usurper reproductive females, inquiline ones share the queen chamber with the host reproductive female (e.g., in *Advenathrips inquilinus* [Thysanoptera: Phlaeothripidae]; Morris et al. 2000); *Ectatomma tuberculatum* (Hymenoptera: Formicidae; Hora et al. 2005); *Teleutomyrmex schneideri* (Hymenoptera: Formicidae; Hölldobler and Wilson 1990)). Once inside the colony, the parasitic female stays at the host queen chamber (e.g., Hölldobler and Wilson 1990; Hora et al. 2005), which is impregnated with the host queen's odor, with the consequence that the intruder is not attacked by the workers (e.g., Fisher 1987; Hora et al. 2005). The parasitic female

begins to lay eggs that workers carry to the brood chambers as they do with the queen's offspring. The host colony soon becomes a mixed colony in which host workers perform all of the tasks (e.g., Fisher 1987; Hölldobler and Wilson 1990). The costs of this parasitism are very high as host workers have to feed and care for a nonrelated reproductive female and all her reproductive offspring. Sometimes, inquiline species produce individuals of the worker caste, but when this is the case, these workers are few and unproductive. Other inquiline species have lost the worker caste entirely and only produce reproductive offspring (Hölldobler and Wilson 1990).

As in some cases of usurpation (see above), inquiline females usually mimic the chemical signature of the host colony to gain entry to the colony (e.g., Lenoir et al. 2001), but subsequent suffusion with the host queen's odor is necessary. For example, workers of the bee *Psithyrus* sp. (Hymenoptera: Apidae) eject parasitic females in the absence of a host queen (Fisher 1987).

Parasite and host meet with aggression

In all these interactions hosts try to fight off the parasite; thus herein, we have into consideration if the host is able to differentiate between own and foster offspring and consequently drive them off the nest or are not able to differentiate foster offspring and accept them as own.

Without offspring recognition

For many species the nests themselves are a valuable resource requiring a large investment of both time and energy (Collias and Collias 1984; Field 1992a) as well as, sometimes, expensive materials (Brockmann 1993). In some cases both host and parasite fight for the nest, which constitutes a valuable resource that mainly provides protection to the offspring. In these cases, the offspring is not involved while parasitism occurs, thus, no offspring recognition have been developed.

Birds commonly fight over nest boxes or near cavities at the beginning of the breeding season as a consequence of male competition. However, nest stealing between different bird species has rarely been reported. Barrios (1993) observed individual white-rumped swifts (*Apus caffer*) stealing nests from red-rumped swallows (*Hirundo daurica*). Similarly, Prokop (2004) described 40% usurpation of new black-billed magpie (*Pica pica*) nests by Eurasian kestrels (*Falco tinnunculus*) and long-eared owls (*Asio otus*) in an untypical population where competition for nest sites was very high because magpie nests offered the only suitable nesting places.

In other cases, the offspring is involved in the parasitism but recognition has not evolved. For instance within eusocial Hymenoptera, slavery is a form of ant social parasitism in which the slave-making species periodically need to raid nearby host colonies to kidnap pupae and enslave the workers when these hatch (Höldobler and Wilson 1990). To enter the host colony, parasitic species can mimic the host chemical profiles (Brandt et al. 2005) or actively produce specific allomones (chemical weapons) that manipulate the behavior of the host species (Topoff et al. 1988; D'Ettorre et al. 2000; Mori et al. 2000a,b). Some of these allomones protect a parasite queen from host aggression; others play the role of "propaganda substances" that induce attacks against ants that are marked with it (Regnier and Wilson 1971; Allies et al. 1986). Once the raid finishes, slave workers care for and feed the parasitic soldiers and pupae. As one set of host workers ages, parasitic soldiers raid another nest to restore the worker force.

As expected according to the framework of the coevolutionary arms race theory, under such deleterious parasitic consequences, host colonies have developed defenses against parasitic workers. Soldier workers congregate at the nest entrance where they bite and sting parasite workers, even killing them (e.g., Foitzik et al. 2001). A coevolutionary arms race has been reported for the slavemaker *Protomognathus* americanus (Hymenoptera: Formicidae) that mimics its hosts' cuticular profile (Lepthothorax longispinosus; Hymenoptera: Formicidae). The host species has, in turn, evolved specific recognition abilities, which it seasonally adjusts (Brandt et al. 2005). Also in agreement with the coevolutionary arms race theory, Bauer et al. (2009) described a local coadaptation in the Harpagoxenus sublaevis-Leptothorax sp. (Hymenoptera: Formicidae) slave-parasite ant system. In contrast, Zamora-Muñoz et al. (2003) found no

evidence of an arms race within the *Proformica longiseta-Rossomyrmex minuchae* (Hymenoptera: Formicidae) slave-parasite ant system. These authors reported that the slaves showed low aggression toward their social parasites. This could be because as the host species increases its defense, the parasites increase the intensity of its attack, implying a "mafia system", as described by Soler et al. (1998). Thus, the study by Zamora-Muñoz et al. (2003) suggests a different evolutionary direction in which the arms race would reach an evolutionary equilibrium (Zahavi 1979; see General Discussion)

With offspring recognition

In some other parasitic interactions the costly (see General Discussion) behavior of offspring recognition has been developed, which drastically decrease parasitism rate.

One of these interactions is when the nestlings of many bird species themselves abandon their own nest at the end of their nestling period and move to another nest or nesting territory (Riedman 1982). This siteswitching behavior is especially frequent intraspecifically, mainly in semiprecocial species of the orders Charadriiformes (Alcidae, Sternidae and Laridae) and Sphenisciformes (e.g., Pierotti 1991; Saino et al. 1994; Jouventin et al. 1995; Brown 1998). It also occurs in altricial species of the order Ciconiiformes (Ardeidae, Ciconiidae) (Milstein et al. 1970; Redondo et al. 1995), Falconiformes (e.g., Bustamante and Hiraldo 1990; Donázar and Ceballos 1990, Kenward et al. 1993; Tella et al. 1997; Gilson and Marzluff 2000; Arroyo and García 2002) and Strigiformes (Roulin 1999; Penteriani and Delgado 2008). Site-switching behavior is more frequent when population density is high (Bustamante and Hiraldo 1990, Donázar and Ceballos 1990, Kenward et al. 1993), and sometimes can occur during the post-fledging period of dependence (known as brood-switching) (Penteriani and Delgado 2008).

Traditionally, the ornithological literature has treated nest-switching behavior as adoption behavior by foster parents. Here we consider this behavior to be parasitism by chicks because most studies have found that it is the nest-switched chick who gains by moving to a new nest (see general discussion), although Lengyel (2007) reported a benefit of nest-switching in avocets, where nests that adopted chicks were more successful than those of non-adopting parents where the risk of predation was high.

As commented above, eusocial Hymenoptera (ants, some wasps, and bees) are vulnerable to parasitic laying by individual workers (Oldroyd 2002). Beekman and Oldroyd (2008) also described intercolony intraspecific parasitism (worker drifting) (e.g., *B. terrestris, Apis florea*) as worker parasitism. In worker drifting cases, the parasite takes advantage of the fact that failures in nestmate recognition by guard workers are not uncommon. For example, the recognition failure rate in honey bees is 10–

50% (Downs and Ratnieks 2000). When either intracolony or intercolony parasitic eggs are laid, the colony's worker force usually recognizes and destroys them (Ratnieks 1988), a behavior termed worker policing, which has been discussed above.

On the other hand, the clearest cases of parasitism occur where the secondary female totally abandons a nest, as happens with burying beetles *Necrophorus* spp. (Coleoptera: Silphidae). These insects exhibit highly elaborate parental behavior that includes the burial and preparation of a small vertebrate carcass: by removing fur or feathers, burying the carrion and depositing anal secretions on it that prevent rapid decay. The adults also protect and feed their offspring directly until the larvae leave the carcass to pupate in the soil (Müller et al. 1990). When two females find the same small carcass they fight for it. The winner prepares the carrion and oviposits in the surrounding soil, but the excluded female often also oviposits nearby (Wilson and Fudge 1984; Müller et al. 1990). After hatching, parasitic larvae move to the host's buried carcass where, if successful, they will be fed and guarded by the host parents (Müller and Eggert 1990; Müller et al. 1990). However, if parasitic larvae arrive at the carcass more than 20 hours after the host's eggs have hatched, the host parents are able to discriminate and cannibalize them (Trumbo 1994).

But it is in birds where the recognition of foster offspring has been studied in more detail. Intraspecific brood parasitism is widespread in birds, having been documented in 236 avian species (Yom-Tov 2001), being particularly common among precocial birds such as waterfowl. The coevolutionary arms race between members of the same species is not well developed because host defenses based on foreign egg recognition are much rarer than in cases of interspecific parasitism (Davies 2000; see below). Firstly, the eggs of conspecific females are very similar in appearance, which makes egg-recognition ability very unlikely to evolve. Secondly, the costs imposed by intraspecific brood parasitism are much lower than in obligate interspecific avian brood parasitism (see below). As a result, selection pressures are not strong enough for elaborate host defenses to evolve. More detailed information on intraspecific brood parasitism can be found in several reviews (e.g., Petrie and Møller 1991; Johnsgard 1997; Davies 2000).

About 1% of bird species are known to be obligate brood parasites and they are included in four different orders: Cuculiformes, Passeriformes, Piciformes and Anseriformes (Davies 2000). Interspecific brood parasitism has evolved independently seven times in birds (Sorenson and Payne 2002). These obligate avian brood parasites impose significant costs on their hosts. In particular, brood parasitic chicks frequently evict or outcompete host chicks, usually destroying most of them. Furthermore, very often parasitic chicks are larger than host chicks and thus elicit more intensive parental assistance from host parents for a longer time than that provided to young in

nonparasitized nests (Johnsgard 1997; Davies 2000). These costs, and the fact that the breeding success of the parasite is maximized when the breeding success of the host is zero (Rothstein 1990), generate very strong selective pressures that favor the development and rapid spread of defensive adaptations and counteradaptations in this system. Indeed, coevolutionary arms races exist at all stages of the breeding cycle: before laying and during incubation (Johnsgard 1997; Davies 2000; Soler and Soler 2000) and even during the nestling period (see a review in Soler 2009). More detailed information on interspecific brood parasitism can be found in several reviews (e.g., Rothstein 1990; Johnsgard 1997; Davies 2000).

GENERAL DISCUSSION

Parasitic interactions involving parental care are widely distributed within the animal kingdom. Throughout this review we have explored a great variety of cases where parental care provided by parents to their offspring is parasitized by other unrelated young. The variability in both parasitized resources and animal taxa implies that the costs incurred by the victims of parental-care parasitism and the strategies used by the parasites are highly variable.

We have described a new term, parental-care parasitism, and have presented a new classification that resolves an important problem of

imprecise terminology. Hitherto such parasitic behaviors have been described by such terms as reproductive parasitism, brood parasitism, kleptoparasitism, kleptobiosis and social parasitism. Although the boundaries between different types of interspecific interactions are indistinct, we believe that this new classification will be useful and instructive because it assists our understanding of the concepts involved. Parental-care parasitism is defined as "an interaction in which an individual (the parasite) obtains reproductive benefits while reducing or completely eliminating its own costs of parenting by exploiting any type of offspring care provided by other individuals (the hosts)". This definition is more general and includes all the terms given above. Parental-care parasitism does not necessarily imply that hosts have to rear parasitic offspring, diverting resources away from their own young. That is the meaning of the most generally used term, brood parasitism, which should only be applied to those cases where brood parasites fool hosts into raising their parasitic young.

We here offer a novel insight considering nest-switching behavior to be a form of parental-care parasitism promoted by the young themselves rather than comprising adoptions by foster parents, as it is often regarded in the ornithological literature. This point of view, which has previously been suggested by some authors (Pierotti and Murphy 1987; Kenward et al. 1993), is based on several observations. Nest-switching chicks are usually

the younger members of large broods and they move to nests with younger and/or fewer chicks, where they can obtain more food than in their natal nest, thus boosting their probability of survival (Hébert 1988). Also, when foster chicks are accepted, the host parent's fitness is reduced (e.g., Saino et al. 1994; Brown 1998) because parents have to work harder to feed the increased number of chicks (Carter and Spear 1986; Saino et al. 1994; Brown 1998). Chick recognition capacity (see below) by adults has evolved in many colonial and precocial or semiprecocial species within the Charadriiformes (i.e., families Alcidae, Sternidae, and Laridae) and Sphenisciformes (see a review in Soler 2000), where nest-switching is common but no such abilities have been documented for members of the Ciconiiformes, Falconiformes, and Strigiformes (Penteriani and Delgado 2008).

Helping relatives can increase a worker individual's inclusive fitness because it is collaborating in the production of offspring by a close relative and thus transmitting its own genes to the next generation (Hamilton 1964). The workers of many wasp, bee, and ant species have ovaries and could lay unfertilized eggs, which would give rise to males. Thus, it should not be surprising that they would try to produce descendants of their own. We have classified this worker egg-laying behavior as a case of parasitic parental care in spite of the fact that workers are also genetically related to other workers as well as to the queen. However, it has recently been

emphasized that the degree of kinship that exists within colonies in eusocial insects is much lower than previously believed (Ratnieks and Wenseleers 2007) because queens are quite often fertilized by several males and, in many species, there is more than one queen in each colony. Thus, workers may be expected to favor those offspring to whom they are most closely related genetically (Hannonen and Sundström 2003). Consequently, as workers do not necessarily share the same mother and father, they are less related to their sisters' offspring than to those of their mother. Kin selection thus favors investing in the male-producing eggs laid by the queen rather than in the male eggs laid by other workers (Bonckaert et al. 2008). Thus, laying workers can be considered parental-care parasites that are trying to get other workers to care for their own eggs instead of those of the queen, which would bring the latter workers greater genetic benefits.

Indiscriminate care that results in providing energy-costly resources to unrelated offspring results in a reduction of the parents' fitness and in their future fecundity (Clutton-Brock et al. 1989; Johnsgard 1997; Huber et al. 1999; Davies 2000; Koivula et al. 2003). Consequently, parental investment theory predicts that parents should discriminate between their own and unrelated offspring, avoiding parental investment in the latter. For instance, in several species of fishes, it has been reported that males stop care by completely cannibalizing clutches that contain a mix of self-sired and foreign-fertilized eggs (Frommen et al. 2007; Neff 2003b; Rios-Cardenas

and Webster 2005). Also, in avian polyandrous species, beta males provide parental care according to their certainty of paternity (Davies 1992; Whittingham and Dunn 1998). However, the prediction that parents should discriminate between their own and unrelated offspring is only sometimes fulfilled.

The ability to discriminate unrelated offspring can be accomplished through visual, tactile, acoustic, olfactory or gustatory signaling systems or a combination thereof (Sherman et al. 1997). It has been only reported regularly in two groups of species; in those living in communal crèches or groups (Balcombe 1990; Aubin and Jouventin 1998; Aubin et al. 2000; Insley 2000; Charrier et al. 2003; Neff 2003a; Searby and Jouventin 2003; Jesseau et al. 2008; Li and Zhang 2010) and in those that breed in dense colonies with nests close together, which allows hungry chicks to move from their nests to those of neighbors (Buckley and Buckley 1972; Beecher et al. 1981; Jouventin and Aubin 2002; Searby et al. 2004).

Also in those species that are regularly exploited by brood parasites, parents are able to discriminate and reject parasitic eggs (reviewed in Rothstein 1990, Johnsgard 1997; Davies 2000) and sometimes also parasitic chicks (Grim et al. 2003; Langmore et al. 2003; Soler 2009).

In solitary breeding species that are not exploited by brood parasites, indiscriminate care of newborn offspring is not a problem because parents are only likely to encounter their own offspring in their nest or burrow and an ability to discriminate unrelated offspring would not provide any advantage. The selective pressures favoring the evolution of discrimination behavior that can be costly (see below) do not exist in such circumstances.

It can thus be stated that, as a general rule, offspring discrimination has evolved only in those species in which the probability of being exploited by unrelated offspring is high. However, the lack of discrimination ability entails the risk of being parasitized by parental-care parasites, and the ability to recognize offspring would have obvious advantages to parents because it would reduce the amount of care provided to unrelated offspring. Therefore, the lack of discrimination ability may seem to be a maladaptation because parents fail to act in the interest of their genes. However, there also exist risks related to offspring discrimination. Two main types of costs have been described: recognition errors, the risk of mistakenly rejecting or destroying some own eggs; and rejection costs, when parasitized individuals accidentally break their own eggs while trying to eject a parasitic egg or desert the nest or brood in response to the presence of one or more unrelated offspring (Rothstein 1990; Davies 2000; Martín-Vivaldi et al. 2002). Clearly, the costs of discrimination could actually counteract the benefits of refusing to care for parasitic offspring.

Different situations have been described for different host species or populations, which can be explained using the framework of coevolutionary arms race theory (reviewed in Lotem and Nakamura 1998). Some

frequently parasitized species lack offspring discrimination behavior, and this usually is considered to be the consequence of an evolutionary lag (genes responsible for discrimination have not yet appeared). Also, some populations are rejecters while other populations of the same species are acceptors. Furthermore, rejecter and acceptor individuals frequently coexist in the same host population. These last 2 situations arise because the relationship between the costs and benefits of rejection behavior does not favor the rapid spread of the genes responsible for offspring discrimination, a circumstance addressed by the evolutionary equilibrium hypothesis (Rothstein 1990; Davies et al. 1996; Lotem and Nakamura 1998).

As we have seen, offspring recognition has only evolved in species that are exposed to a high risk of being exploited by alien offspring. This implies that absence of discrimination should be the ancestral state. Because discrimination is costly, in the absence of the risk of being exploited by young individuals that are not their genetic offspring, natural selection would penalize discriminating parents because their breeding success would be lower than that of nondiscriminators. In this situation the most adaptive strategy for a parent is to follow a simple behavioral decision-making rule (rule of thumb): to care for any offspring placed in its nest. This rule of thumb has been demonstrated to underlie the observation that most common cuckoo hosts are not able to discriminate against the very different and huge common cuckoo chick (Davies 2000).

There are 2 other adaptive strategies related to parental care that can be exploited by parental-care parasites for their own benefit. As parental investment theory predicts, parents should adjust their parental investment to brood quality and the reproductive value of their offspring (Trivers 1972; Montgomerie and Weatherhead 1988; Clutton-Brock 1991). Consequently, parents should favor larger broods (an indicator of brood quality) and, within a brood, offspring of larger body size (an indicator of offspring quality).

Larger broods have a higher reproductive value than smaller ones and it has been found that parents' readiness to care is higher with larger broods (Magnhagen and Vestergaard 1993; Lissåker et al. 2003; Lissåker and Kvarnemo 2006). This suggests a clear advantage for parental-care parasites because if a female adds its eggs to the existing clutch of the foster parents or some parasitic young join a brood that is being cared for by those parents, these enlarged parasitized clutches or broods will provoke an increase in parental investment and a decrease in the readiness to reject the parasitic offspring. For example, male sand gobies (*Pomatoschistus minutus*) usually recognize their own clutches and, in an experimental study, Svensson et al. (2010) found that in the few cases where males chose to take care of foreign nests, it was a larger clutch size that influenced their parenting decisions.

Larger offspring are better competitors for resources and have a higher probability of survival (Price and Ydenberg 1995; Sogard 1997; Cotton et al. 1999; Bashey 2008). Furthermore, it has frequently been reported that parents preferentially feed larger young (Rivers 2007; Smiseth et al. 2007). For example, larvae of the burying beetle (Nicrophorus vespilloides) can feed themselves from the ball of carrion prepared by the parents for them, but larger larvae additionally receive processed carrion regurgitated by their parents (Smiseth et al. 2007). This also applies with most altricial bird species, the usual hosts of avian brood parasites, where the latter take advantage of this foster parent strategy by usually parasitizing species smaller than they themselves are (Rothstein 1990, Davies 2000). Moreover, where an avian brood parasite uses host species of variable size, as with some cowbirds (Icteridae), parasitic chicks are quite successful with hosts that are smaller or that hatch later (Robinson et al. 1995; Dearborn 1998) but fare poorly with large and/or early-hatching hosts (Lichtenstein 1998; 2001).

Finally, the concept of tolerance can help to explain the fact that parents waste resources caring for unrelated offspring much more frequently than predicted by the coevolutionary arms race theory. As recently emphasized, victims in antagonistic interactions have 2 means of defense against their enemies. One is resistance, which has a direct negative effect on the enemy and selects for counteradaptations (the basic argument

of the coevolutionary arms race theory, see above). The other is tolerance, the ability to minimize the fitness impact of enemy attacks (Svensson and Råberg 2010), which does not provoke selection for counteradaptations, giving rise to a kind of coevolution that will result in stable equilibrium instead of a continuous arms race. The concept of resistance implies that in a continuous coevolutionary arms race some of the interacting species could become extinct, which means, in the case of parental-care parasites and their hosts, that the frequency of broods including unrelated offspring should be low. On the other hand, the concept of tolerance – which has been widely considered in plant studies (Rausher 2001; Svensson and Råberg 2010) but has been completely neglected in the animal literature until recently (Restif and Koella 2003; Svensson and Råberg 2010) involves reducing antagonistic coevolution, which implies that in many parental-care parasite-host systems a state of evolutionary equilibrium could be reached, and so mixed broods including unrelated offspring would be expected much more frequently.

CONCLUSIONS

We have reviewed for the first time different kinds of parental-care parasitism in a great variety of animal groups that live in different ecological conditions which could affect the cost-benefit balance of each parasitic interaction. Furthermore, we have integrated them within a new classification of parental-care parasitism based on behavioral trends, which will allow to a more easy comparison of the same parasitic interactions in different species, genders, families, or even orders.

The inability to discriminate between own and alien offspring found in some species, some populations of the same species and some individuals within the same population, can be explained according to coevolutionary arms race theory as a consequence of 1) the genes responsible for the rejection behavior not yet having appeared (the evolutionary lag hypothesis) or 2) the relationship between costs and benefits not yet having favored further spread of those genes (the evolutionary equilibrium hypothesis).

Because discrimination is costly, the fact that unrelated offspring succeed in being accepted by foster parents is because the most adaptive strategy for parents is to follow simple rules of thumb (to care for any offspring placed in my nest, to care more intensely for larger broods and for offspring of larger body size), which are successfully exploited by parentalcare parasites.

The concept of tolerance, another mechanism by which victims defend themselves against their enemies, also explains the fact that parents care for unrelated offspring much more frequently than coevolutionary arms race theory predicts. Tolerance does not provoke antagonistic coevolution, which implies that in many parental-care parasite-host systems, a state of evolutionary equilibrium would be reached, so that broods including unrelated offspring will be encountered more frequently.

Finally, the information provided about most cases of parental-care parasitism reported in the literature is incomplete and scarce. Much of what has been reported relies on unreplicated studies. Thus more empirical and experimental studies are needed in order to gather the missing information. Four important directions for future research are: 1) determining the frequency and characteristics of parental-care parasitism in different of reported parental-care parasite-host populations systems, 2) experimental assessing of the relationship between costs and benefits in each system, 3) experimental testing of the offspring discrimination capacity of parents in host species and in their closest relatives, and 4) assessing the relative importance of the 2 means of defense used by hosts against their parental care parasites (resistance and tolerance) in each system.

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Geographic variation of host use by the great spotted cuckoo in Spain

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SUMMARY

Avian brood parasites generally select hosts that maximize their own reproductive success. The choice of suitable hosts generally depends on host characteristics such as diet, breeding habitat, abundance, incubation, nestling period and, within species, parental ability in raising nestlings. Because brood parasitism generally decreases host reproductive success, host species evolve defences (such as ejection of alien eggs and active nest defence) to which parasite counter-act, triggering an "evolutionary arm race". In some cases, host defences become so effective that force the brood parasite to switch to a new host. Therefore, changes in host use are usually a consequence of a severe drop of profitability of the so far preferred host. Here we studied the spatiotemporal variation in host use by the great spotted cuckoo Clamator glandarius in Spain. Throughout Europe, the magpie *Pica pica* is used as primary host by this brood parasite while the carrion crow *Corvus corone* is the secondary host and suffers lower parasitism pressure. However, we found that this pattern was reverted in northern Spain, where parasitism on carrion crows increased steadily up to about 70% of nests during the three-years study period, whereas remained low and stable in magpies (about 20%), in spite of their relatively larger abundance. In southern Spain, conversely, parasitism increased proportionally in both hosts during the same time frame. Surprisingly, in the north crows proved to be the least profitable host and magpies were not more proficient in hindering the parasite compared to the southern population. We postulated the existence of separate gens to explain the seemingly maladaptive cuckoo's host choice in northern Spain.

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INTRODUCTION

Avian brood parasites lay their eggs in the nests of other species (the hosts) and have their offspring raised by the foster parents (Rothstein 1990). Some parasites produce a high number of eggs and distribute them among a large variety of host species (generalist brood parasites). For instance, eggs of shiny cowbirds (*Molothrus bonariensis*) and brown-headed cowbirds (*Molothus ater*) have been found in nests of over 200 host species (Wiley 1988; Davies 2000). Other parasites, conversely, use only one high-quality host plus few secondary hosts (specialist brood parasites). This is the case of the great spotted cuckoo (*Clamator glandarius*), which uses a total of 4 host species on its Palaearctic distribution (Cramp 1985).

The reproductive success of a brood parasite is strongly influenced by the choice of suitable host species and nests, because potential hosts vary in their diet, breeding habitat, incubation and nestling period and, within species, individual parents may differ in their ability in raising nestlings (Rothstein 1990; Soler et al. 1995a; Kleven et al. 1999; Soler et al. 1999a; Davies 2000; Langmore et al. 2007). Furthermore, because brood parasitism generally reduces host reproductive success (Davies et al. 1998; Kilner & Davies 1999; Kilner 2003), many host species evolved behavioural defences against parasites, such as aggressive nest defence against parasitic adults and/or recognition and ejection of alien eggs (Davies & Brooke 1989; Soler 1999; Avilés et al. 2004; Spottiswoode & Stevens 2011). As a response against host defence, brood parasites generally evolve counter-strategies such as production of mimetic eggs that closely resemble host's own eggs (Davies & Brooke 1989; Cherry & Bennett 2001), reduced laying time to decrease the risk of host's aggressions (Davies 2000; Soler et al. 2001a) or even "punishment" of host's egg ejection behaviour by destruction of clutches of rejecters in order to prompt them to re-nest and, in the following attempt, to accept the parasitic egg (Soler et al. 1995b; Hoover & Robinson 2007). Over this "evolutionary arms race", the parasite may be forced to change host if its reproductive success drops dramatically. Profitability of a host, however, may vary according to current ecological conditions, which can influence, for example, host population density, effectiveness of defences against the parasite and host diet. As a consequence, parasite's host preferences are expected to change over time and space (Soler et al. 1998, Rothstein 2001). Documenting patterns of spatio-temporal variability in host choice therefore provide important insights to understand parasite/host relationship.

The great spotted cuckoo in the Palaearctic is specialised on corvids, being its primary host the magpie *Pica pica* and its secondary host the carrion crow *Corvus corone corone* (Cramp 1985; Soler 1990). Choughs *Pyrrhocorax pyrrhocorax* and jackdaws *Corvus monedula* are parasitized sporadically (Soler 1990). Great spotted cuckoo chicks do not evict host

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eggs or hatchlings from the nest, and so are raised alongside host nestlings (Soler 1990, Soler et al. 1998). This parasite lays synchronously with its hosts but, due to shorter incubation period of cuckoo eggs, parasitic chicks hatch earlier and gain an age advantage over host nestlings (Soler et al. 1998). As a consequence, parasitic chicks often outcompete magpie chicks for food and starve them (on average, only 0.6 magpie chicks fledge per parasitized nest; Soler et al.1996). Conversely, crow chicks, which are larger than the cuckoo chicks, can cope with the presence of the parasite so that the cost of parasitism for crow parents is usually low (Soler 1990; Soler et al. 1996; Soler et al. 2001b; Canestrari et al. 2009). In Southern Spain, where the great spotted cuckoos has been studied intensively, parasite's reproductive success is higher in magpie than in crow nests because, due to the relative differences in size, cuckoo chicks compete for food better against magpie chicks than crow chicks (Soler 1990; Soler et al. 2001b).

Great spotted cuckoos do not choose host nests at random. When parasitizing magpies, cuckoos prefer high quality pairs, which build nests of larger size (Soler et al. 1995a). Also, magpie nest accessibility influences parasitism rates in Southern Spain, with nests in trees being more parasitized than those placed in scrubs (Soler 1990). When parasitizing a population of cooperatively breeding carrion crows in Northern Spain, great spotted cuckoos use unassisted pairs at higher rates (despite their relative rarity) than cooperative groups, although cuckoo reproductive success does

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not vary with group size. In fact, cuckoos' preference for unassisted pairs is due to the increased opportunities of finding the nest unattended, which favours a better synchronization of parasite/host laying (Canestrari et al. 2009).

Here we report on spatio-temporal variability in the use of magpie and carrion crow nests between a northern and a southern population of great spotted cuckoo in Spain. This study shows that, unlike in the south, the northern population of the great spotted cuckoo reverted the use of the primary and the secondary host, parasitizing the carrion crow with increasing frequency compared to the magpie. In order to explain the different host use between the two areas, we compared cuckoo's reproductive success, host egg rejection behaviour, host nests availability and nest accessibility between the two areas. We expected the geographic variability in host choice to mirror differences in the profitability of the two hosts, with great spotted cuckoos parasitizing locally the host that provided the highest reproductive payoff. Possible explanations for the observed deviation from this prediction are discussed.

MATERIAL AND METHODS

Study areas

We studied brood parasitism by great spotted cuckoos on carrion crows and magpies in two different rural areas in Spain: "La Sobarriba" in the North (42°37' N, 5°26'W; hereafter referred to as Sobarriba) and "La Hoya de Guadix" in the South (37° 18' N, 3°11' W; Guadix hereafter). Sobarriba is characterized by a mosaic of crops, meadows, poplar and pine plantations, scrub, oak *Quercus pyrenaica* forest patches and uncultivated land, while Guadix is a plateaux dominated by cultivated cereals (especially barley) and plantations of almond trees, with some groves of holm oaks *Quercus rotundifolia*.

Host species

Carrion crows breed as unassisted pairs throughout Europe (Cramp and Perrins 1994), but form kin cooperatively breeding groups in both study areas. At Sobarriba and Guadix respectively, about 75% and 66.7% of the territories are occupied by social groups of up to nine individuals, whereas unassisted pairs hold the rest of the territories (Baglione et al. 2002; Roldán & Soler, Chapter 1.). Helping has been studied intensively at Sobarriba (see Canestrari et al. 2005). Helpers contribute to build the nest and to feed the incubating female and the chicks, increasing fledgling production (Canestrari et al. 2008). Crows build open nests in trees (oak, poplar *Populus alba* and willow *Salix fragilis*, in Sobarriba, and holm oak and almond trees *Prunus dulcis* in Guadix). If the nest fails at eggs or hatching stage, crows may re-nest up to 3 times in a season in Sobarriba (Canestrari et al. 2008), whereas re-nesting is rare in Guadix (Roldán & Soler, Chapter 1)

Magpies usually build their roofed nests hidden in brambles, scrubs and thorny bushes at Sobarriba (personal observation), while they mainly use open almond trees in Guadix (Soler et al. 1998a). Magpies breed in unassisted pairs. Both parents feed the chicks and defend the nest and they may re-nest once after a breeding failure (Birkhead 1991). In both study areas the home-ranges of crows and magpies overlap (in Guadix magpies breed in a much larger area than crows but only magpie territories included in the home-range of crows have been used in this study).

Field data collection

In March-July from 2007 to 2009, we surveyed all nests of carrion crows and magpies in both study areas. At Sobarriba, we used extendable poles to reach crow nests up to 15 m high (95% of all nests) to inspect the content with a mirror or a wireless video camera. Higher nests were climbed when possible. At Guadix, all nests were climbed. We followed a total of 167 crow nests belonging to 75 different territories and 153 magpie nests (of

147 breeding pairs) in Sobarriba, and 74 crow nests from 43 territories and 100 magpie nests from 83 pairs in Guadix. For each nest we recorded laying date of the first host egg, number of parasitic and host eggs, number of eggs hatched and number of chicks fledged. In 34 cases, we could not record laying date as the clutch found was already complete. Every time we visited nests for routine data collection (egg-laying activity, nestling hatching, fledging success) we searched in the surrounding areas for new nests or re-nesting attempts.

Egg rejection experiment

In Sobarriba, we introduced experimental model cuckoo eggs in the nests of both hosts. This experiment was carried out in crows in 2009 (n=10 nests) and in magpies in 2007 (n=38) and 2009 (n=17). The model eggs were made of plaster of Paris and painted with acrylic paint imitating the colour and spotted pattern of cuckoo's eggs. Also their size and weight were similar to the real eggs (Soler & Møller 1990). These models were introduced in the nests when at least one host egg was already present and before clutch completion. The nests were visited 7 days after the treatment and model eggs were considered rejected if they had disappeared from the nest. If the nest was depredated during the experiment (i.e., if all eggs had disappeared) we did not include it in the sample size. Rejection rates/data

on Guadix were obtained from Avilés et al. (2004), where the same experimental protocol was followed.

Nest accessibility

In 2009 and 2010, we registered the location of magpies nests at Sobarriba (n=172) and in 2007-2009 at Guadix (n=60) to test whether different accessibility affected the probability of being parasitized. We classified each nest in two categories of accessibility: "difficult", i.e. located at least 50 cm inside Rosa spp, Rubus fruticosus or holm oak bushes, and "easy", located in trees, superficially in bushes or on the top of dense bushes. To investigate this issue further, in 2010 and 2011 at Sobarriba we carried out an experimental manipulation to asses the effect of nest accessibility per se. We chose nests located in dense Rosa spp and R. fruticosus bushes and we pruned a 60° wide truncated conic opening in front of the entrance of the nest. The treatment was carried out when the nest was complete, but before the female started laying. Magpies laid eggs in half of the treated nests. Replacement nest of pairs that abandoned a manipulated nest were left undisturbed. Twenty five nests, where branches were cutted at the bottom of the bush served as control.

Statistical analyses

For statistical analyses we used Genstat 12 (VSN International Ltd., Hemel Hempstead, U.K.). We used Generalized Linear Mixed models (GLMM) and Linear Mixed Models (LMM) with Restricted Maximum Likelihood (REML) to analyse parasitism rates and cuckoo reproductive succes. Territory identity was fitted as random factor in all analyses, because data collected from nests in the same territory across years or from the same territory in one year (re-nesting) are not independent due to intrinsic characteristics of the territory and/or the breeders. Ideally, breeders' identity should have been controlled for too, but this was not possible because many birds were unbanded. However, due low mortality of adults both in crows and in magpies (Baglione et al. 2005, Birkhead 1991), territory identity was likely to control effectively for breeders identity within the relatively short time frame of this study. The final minimal models were obtained by sequentially dropping terms with p > 0.1 using a backwards-stepwise approach. Probability values of significant terms were those provided by the minimal model, whereas p values of non-significant terms were obtained by fitting individually each non-significant term to the minimal model (Crawley 2002).

We analysed the factors that affected spatiotemporal variability of host use by using a GLMM with binomial distribution (presence/absence of cuckoo eggs in a nest) and logit link function. We fitted year, host species, study area as explanatory terms and the two ways and three ways interactions among these variables. Subsequently, we run a LMM to analyze the effect of the same predictors on the number of cuckoo eggs laid per parasitized nest.

We used a LMM (REML) to investigate whether host species influenced cuckoo fledging success (measured as number of cuckoos fledged per parasitized nest) in the two areas. The model included host species, area and year as explanatory terms and the two and three ways interactions among these variables. In addition, we controlled for number of cuckoo eggs laid and total clutch size in the nest (host + cuckoo).

We used Kolmogorov-Smirnov (K-S) test for two samples to compare the distributions of the laying dates (first egg of the clutch) among the cuckoo and its two hosts and between the two areas within the same host. We used Julian dates, being day 1 the 1st of March. We removed 8 outliers corresponding to exceptionally late (invariably unsuccessful) renesting attempts of crows. When the K-S test found a significant within host difference between the two study areas, we analysed the relative dispersion of the data by comparing the coefficients of variation using variance ratio tests ($F=(s^2log)_1/(s^2log)_2$ in Lewontin, 1966 and Zar, 1996).

RESULTS

Parasitism rate in magpies and crows

The temporal pattern of parasitism rate in magpies and crows varied significantly across areas, as indicated by the significant three ways interaction among year, host species and area ($F_{3,468.7} = 10.38$, p <0.01). Throughout the study period, parasitism rate at Sobarriba increased steadily in crows, but remained stable in magpies, which were much less parasitized (Fig. 1). Conversely at Guadix, parasitism rate increased in both hosts, which were eventually used by the cuckoo with similar frequency (Fig. 1). Overall, cuckoos laid the same number of eggs in the nests of the two hosts (effect of host species, $F_{1,202} = 0.79$, p = 0.38). Regardless of the host, the number of eggs laid per parasitized nest varied across years in a different way at Sobarriba and Guadix (year × area interaction, $F_{1,202} = 6.91$, p = 0.01), with a much more dramatic increase in the southern area (Fig. 2).



Figure 1. Parasitism rates on crows (black bars) and magpies (white bars) at Sobarriba and Guadix between 2007 and 2009.



Figure 2. Number of cuckoo eggs laid per parasitized nest in crows (black bars) and magpies (white bars) at Sobarriba and Guadix between 2007 and 2009.

Cuckoo reproductive success

Magpies prove to be a better host for the great spotted cuckoo. Magpie nests fledged more cuckoo chicks than crow nests (F $_{1,82.9} = 30.92$, p < 0.01) regardless of the study area (area × species: F $_{1,80.4} = 1.8$, p = 0.184; Fig.3), after controlling for the significant positive effect of the number of cuckoo egg laid (F $_{1,81.5} = 86.43$, p <0.01) and total clutch size (number of cuckoo eggs + number of host eggs, F $_{1,77.4} = 4.53$, p = 0.04).

Host defence: egg rejection rates

At Sobarriba, magpies showed rejection rates of 26.32% (n=38) and 17.65% (n=17), in 2007 and 2009 respectively (Fisher two-tails Exact test, p = 0.73). The overall rejection rate at Sobarriba (23.6%) was lower than that reported for Guadix (41.7%, n = 36) by Aviles et al. (2004), although the difference was not statistically significant (Fisher two-tails Exact test, p = 0.1). A previous study at Sobarriba showed that, in naturally parasitized crow nests, 9.5% of cuckoo eggs might have been rejected (Canestrari, 2009). The rejection experiment performed in crows in 2009 at Sobarriba confirmed this estimate, with one model egg rejected out of 10. Interestingly, previous works never documented egg rejection in the carrion crow (Yom-Tov 1976; Soler 1990; Soler et al. 1999b).



Figure 3. Average number of cuckoo fledged per parasitized nest \pm SE in crows (black bars) and magpies (white bars) at Sobarriba and Guadix during the three years of study Predictions of LMM. Sample sizes are given above bars.

Host availability: density of nests and laying periods

In Sobarriba, the density of crow nests was 1.85 nests/km², while there were 3.36 magpie nests/km². In Guadix, densities of crows and magpies were 0.71nest/km² and 1.6 nests/ km² respectively. Magpie laying periods did not differ between the two areas (K-S test d_{max} = 0.14, p=0.068), unlike crows (K-S test d_{max} =0.62, p<0.001), which started laying earlier in the south (Fig. 4). However, the relative dispersion of crow laying dates, and therefore the length of crow laying period, did not vary significantly across areas (variance ratio test, p=0.93).

At Sobarriba, cuckoo laying period overlapped only with that of crows (K-S test $d_{max}=0.11$, p=0.22), but not with that of magpies (K-S test $d_{max}=0.46$, p<0.001) or both hosts together (K-S test $d_{max}=0.24$, p<0.001).

In Guadix, in contrast, cuckoo laying dates overlapped with the distribution of both hosts together (K-S test $d_{max}=0.07$, p=0.559) rather than with that of magpies or crows alone (K-S tests $d_{max}=0.36$ and $d_{max}=0.52$ respectively, p<0.001 in both tests; Figure 4).



Figure 4. Laying periods of the great spotted cuckoo and its host at Sobarriba and Guadix. Results of pairwise comparisons with Kolmogorov-Smirnov test are indicated with horizontal lines (n.s.= non significant differences, *** = p < 0.001)

Host defence: nest accessibility

Easily accessible magpie nests (i.e. placed in trees and superficially in bushes) were more frequent at Guadix (63.3% of 60 nests) than at Sobarriba (35.5%, n = 172; Two Tails Fisher Exact Test, p < 0.01). At Sobarriba, parasitism rate was significantly higher in accessible magpie nests than in

difficult ones (18.0% *versus* 7.21% respectively; n=172, χ^2 =4.695, p=0.03), whereas no significant difference was found at Guadix (62,86% vs 64%, n = 60 χ^2 =0,008, n = 60, p=0.93). However, at Sobarriba, parasitism rate did not increased significantly in experimental nests where accessibility had been experimentally augmented (17.6% vs 4.5% in experimental and control nests respectively; Two tails Fisher Exact Test, n = 39, p = 0.3).

DISCUSSION

Our data uncovered spatiotemporal variability of host use in the great spotted cuckoo that challenges the view that magpies are the primary host of this brood parasite (Soler & Soler 1991; Soler et al. 1997). At Sobarriba, the parasitic pressure on carrion crows increased steadily throughout the study period, whereas it remained stable in magpies, which were much less parasitized in spite of their relative higher abundance. Conversely, at Guadix, although magpies were preferred at the beginning of the study, brood parasitism strongly increased in both hosts, reaching eventually similar (very high) levels.

The overall increase of both parasitism rate and the number of cuckoo eggs laid in parasitized nests indicated an increase of the great spotted cuckoo population in both areas, particularly at Guadix where the parasites may have been forced to use the secondary host (crow) because of

increased competition for the primary one (magpie). Increased cuckoo density, however, cannot explain why parasitism rate at Sobarriba augmented in crows only. A plausible hypothesis is that the profitability of the two hosts varies geographically according to current ecological conditions and that great spotted cuckoos' host preference is condition dependent. If so, we would expect crow nests to be more profitable for cuckoos than magpie nests at Sobarriba, either because of better reproductive output or because of constraints on the use of the latter. As far as we could test it, however, this hypothesis does not hold, as we shall discuss below.

Cuckoo reproductive success. Our data show that magpies raised more cuckoo fledglings than crows in both areas, after controlling for cuckoo clutch. This result confirmed previous findings showing that cuckoo chicks easily outcompete magpie chicks in the nest, whereas they are less successful when raised alongside the larger crow chicks (Soler et al. 2002). Therefore, the slightly larger group size of crows at Sobarriba compared to Guadix (Roldan & Soler Chapter 1), which may have resulted in increased brood provisioning in the northern area (Canestrari et al. 2008), did not compensate for the competitive handicap of cuckoos raised by crows. This dismisses the possibility that cuckoo used crows at Sobarriba because of better reproductive output.

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Egg rejection behaviour. The ability to recognise and reject foreign eggs is a widespread defence mechanism developed by hosts against brood parasites (Rothstein 1990; Davies 2000) including magpies (Soler & Møller 1990; Soler & Soler 2000). Over evolutionary times, high parasitism pressures select hosts with the best rejection abilities, and within species that have suffered brood parasitism for long time, populations may plastically vary their rejection behaviour according to current parasitic pressure (Davies & Brooke 1988; Moksnes et al 1993; Davies et al. 1996; Soler et al. 1999; Lindholm & Thomas 2000). When host defences reach a high level of efficiency, parasites may either emigrate to other areas where host defences are less efficient or may use a different host in order to increase reproductive success (Soler et al. 1998; Rothstein 2001). Therefore, the higher use of crow nest in the Sobarriba could have been provoked by better defences of magpies in this area compared to Guadix that forced great spotted cuckoos to increase the use of the secondary host. However, the rejection rate found in magpies in Sobarriba (17.65%-26.32%) was lower than that registered in Guadix (41.7%, nests n=79, in Aviles et al. 2004), which does not support this hypothesis. Interestingly, an event of ejection of a model egg by carrion crows was recorded in Sobarriba, contrasting with previous studies where this behaviour was never observed in this species (Yom-Tov 1976; Soler 1990; Soler et al. 1999b).
However, due low sample size of our experiment, the significance of this anecdotic record is unclear.

Nest accessibility. Magpies can build their nests in places of difficult access for cuckoos, which may in turn increase the use of crow nests. The proportion of magpie nests located in dense bushes was higher at Sobarriba than at Guadix, and cuckoos preferred "easy" magpie nests (in trees or open bushes) at Sobarriba. However, differences in nest accessibility between areas are unlikely to explain the observed variability of host use because: i) only a low proportion of easy magpie nests (less than 20%) were parasitized at Sobarriba, showing that suitable nests were not in short supply, and ii) experimental augmented accessibility of magpie nests did not provoke any significant increase in parasitism rate at Sobarriba.

Availability of host nests and distribution of laying dates. Host use may have been influenced by the relative availability of potential nests at the two study sites, but the fact that magpies were more abundant than crows at both places dismisses the possibility that higher parasitism on crows at Sobarriba was a consequence of a shortage of magpie nests. As magpies laid later than crows (Fig. 4), it may be that cuckoos merely missed their nests at Sobarriba because of an earlier start of the summer migration compared to Guadix. However, data on 19 radiotracked adult showed do not leave until the end of June, thus well beyond the laying season of the magpie. Another possibility may be that crows were more parasitized than magpies at Sobarriba as compared to Guadix because of a longer crow egg laying period in the north that increased the opportunity for cuckoo to find available nests. Similarly, a shorter laying period of magpies at Sobarriba could have been caused the same pattern. However, none of the two hosts showed a significant difference in the length of the egg laying period across areas, so that these possibilities are also dismissed. The distribution of cuckoo laying dates at Guadix, shows that this parasite can extend its laying period to match that of both hosts, and it is therefore unlikely that the preferential use of crows at Sobarriba derived by constraints on cuckoo phenology.

In sum, our data do not support the hypothesis that great spotted cuckoos adjusted the use of crows and magpies to the expected reproductive output, nor that parasitism rate responded to constraints that the hosts posed to the parasite. In other words, as far as we could investigate, cuckoo seemed to behave maladaptively at Sobarriba, using massively the least profitable host and missing opportunities for parasitizing the best one. This scenario may imply that the great spotted cuckoo has separates gentes specialized on a specific host and that a crow gens currently prevails at Sobarriba. The evolution of a crow gens may have taken place in areas where the great

spotted breed in absence of magpies. Although it is known that a single female can use both hosts (Martínez et al. 1998) a nonexclusive preference for either crows or magpies is plausible. Genetic data are urgently needed to investigate this possibility. The occurrence of gentes in generalist brood parasites has been reported several times (for example in the common cuckoo *Cuculus canorus*, Gibbs et al. 2000, and the screaming cowbird *Molothrus rufoaxillaris*, as well as other molothrine species, see Mahler & Adamson 2009 and references therein), and might be more widespread than previously thought. Our study highlights the need of multi-populations studies to uncover complex patterns of host use by brood parasites that, as our data show, can reveal counterintuitive spatiotemporal variability, which is valuable to understand the interactions between cuckoos and their host.

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Great spotted cuckoo nestlings are disfavoured by foster parents in the nests of their larger-size carrion crow host

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SUMMARY

Parents tend to feed preferentially the larger nestlings in the brood and those begging at a higher intensity. Nestlings of non-evicting avian brood parasites have to compete with host chicks for the food delivered by foster parents and usually they enjoy two important advantages: a larger size and a far more exuberant begging than those of host young. Very little is known about the interaction between non-evicting parasites and host chicks when the former are smaller than the latter and this is especially true in the case of brood parasitic cuckoos where the importance of size difference between parasite and host nestlings has never been studied. The great spotted cuckoo (Clamator glandarius) is a non-evictor brood parasite that in the Palearctic uses as its primary host the magpie (Pica *pica*), which is slightly larger than the cuckoo, and as its secondary host the carrier crow (Corvus corone), which is more than twice the size of the cuckoo. Here we study food allocation by carrion crows in both parasitized by the great spotted cuckoo and nonparasitized host nests. This is the first contribution studying a parasitic cuckoo-host system in which host nestlings are considerably larger than brood parasitic ones. We have found that in non-parasitized nests carrion crows preferentially feed nestlings that are closer to the feeding adult, responded more quickly and had a higher begging intensity, and, in parasitized nests, that carrion crows preferentially feed their own nestlings instead of parasitic chicks. This implies that in spite of their parasitic adaptations, which are effective in nests of hosts of a similar or smaller size, great spotted cuckoo chicks are not able to overcome the size advantage of carrion crow nestlings.

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INTRODUCTION

Theoretical studies have shown that begging might be a means of scramble competition for food or it might be an honest signal of need (Parker & Macnair 1979; Godfray 1995; Royle et al. 2002). Both models of sibling scramble competition and honest signalling yield very similar predictions (Royle et al. 2002). However, under scramble, competitive asymmetries between chicks can determine food gains which are not predicted for honest signalling (Parker et al. 2002). Size asymmetries in nestlings are established mainly by asynchronous hatching (Magrath 1990; Stenning 1996; Mock & Parker 1997). Larger nestlings are able to access a greater proportion of food as a consequence of their larger size (Rydén & Bengtsson 1980; Göttlander 1987; McRae et al. 1993; Kacelnik et al. 1995; Price & Ydenberg 1995; Cotton et al. 1999) while the smallest nestlings in a brood are usually the poorest competitors growing more slowly and dying more often (Magrath 1990). Empirical evidence also shows that size asymmetries also affect nestling begging, as junior often receive less food than do seniors even though the former beg more intensively (Cotton et al. 1999; Kilner 1995; Lotem 1998; Price & Ydenberg 1995). For these reasons it has been suggested that parents may follow different provisioning rules according to the breeding strategy. In clutch-adjusters (where all chicks usually survive to fledge) parents tend to distribute food equitably among their chicks, preferentially feeding young that are in poorer condition, whereas in brood reducers (where some chicks starve) parents selectively feed larger chicks independently of their begging intensity (Soler 2001; Soler 2002).

Brood parasitism is a type of parental care parasitism (Roldán & Soler 2011) in which a female lays eggs in the nest of a conspecific or heterospecific host female that then care for the parasite's eggs and young (Davies 2000). Obligate interspecific avian brood parasites never have nests of their own and depend entirely on the host species that incubate their eggs and care for their young (Rothstein 1990). Because of the lack of relatedness between brood parasitic chicks and their nest mates and foster parents (Briskie et al. 1994), begging displays by brood parasitic chicks are far more exuberant than those of individual host young (e.g., Dearborn 1998; Davies et al. 1998; Lichtenstein & Sealy 1998; Soler et al. 1999; Rivers 2007), and thus brood parasitic nestlings enjoy a begging advantage. On the other hand, as brood parasites tend to use host species of smaller size than themselves, usually parasitic offspring also enjoy a size advantage.

Because brood parasitism reduces hosts fitness, hosts has evolved some efficient defense mechanisms giving rise to a coevolutionary arms race (Rothstein 1990; Davies 2000; Soler & Soler 2000; Stokke et al. 2005). Traditionally it was thought that this arms race was confined to the egg

stage of the breeding cycle because most host species are able to reject even highly mimetic parasitic eggs but they seemed unable to reject strongly different parasitic chicks (Rothstein 1990; Davies 2000). In fact, it was assumed that parasitic nestlings efficiently cheat their foster parents (Davies 2000), even providing them with a supernormal stimulus impossible to ignore (Dawkins and Krebs 1979). However, this point of view has dramatically changed during the last years because many cases of parasite chick discrimination by hosts have been reported (reviewed in Grim 2006; Soler 2009).

The great spotted cuckoo (*Clamator glandarius*) is a specialist brood parasite that in the Palearctic uses mainly two corvid species as hosts (Cramp 1985; Soler 1990). Its primary host is the magpie (*Pica pica*), which is slightly larger than the cuckoo and shows defensive mechanisms against the parasite (namely, aggressive response towards adult great spotted cuckoos and the ability to eject cuckoo eggs laid in their nests; reviewed in Soler & Soler, 2000). Brood parasitism by the great spotted cuckoo strongly affects the breeding success of its magpie host (Soler et al. 1996). The reproductive failure of the magpie is caused by egg destruction by adult cuckoos, but also by nestling cuckoos out-competing magpie chicks for food, especially when the cuckoo nestling hatches several days before magpie chicks (Soler et al. 1996), which occurs frequently. In this case all cuckoo chicks survive to fledge (Soler et al. 1998). However, when cuckoo eggs are laid after clutch completion, cuckoos hatch at the same time or after the host nestlings, suffering a relevant reduction in their breeding success (Soler et al. 1998).

The secondary host of great spotted cuckoos is the carrion crow (*Corvus corone*), which is more than twice the size of the cuckoo and lacks defensive mechanisms (i.e., crows do not attack adult great spotted cuckoos and do not eject even strongly non-mimetic eggs) (Yom-Tov 1976; Soler 1990; Soler et al. 2001; Canestrari et al. 2009). However, in spite of this absence of defences, the costs of crows of successful parasitism was half as high in crow nests (1.5 fewer nestlings in parasitized compared to unparasitized nests) than in magpie nests (3.0 fewer magpie nestlings fledged) (Soler et al. 2001).

Surprisingly, in spite of the lack of defences by carrion crows, great spotted cuckoo fitness is higher in magpie than in carrion crow nests. This does not depend on lower hatching success of the parasite, but on higher mortality of cuckoo chicks in carrion crow nests, which is more than double than in magpie nests (Soler et al. 2001). Soler *et* al. (2001) suggested that the lower fitness of great spotted cuckoos in carrion crow nests was due to the superior competitive ability of crow nestlings compared to cuckoo chicks due to host's larger size, because crow nestlings, even when hatching later, soon become larger and sometimes out-compete cuckoo chicks.

In non-evicting parasite species, the size difference between parasitic and host nestlings has important implications for both intra-brood food allocation by foster parents and the fate of both parasitic and host chicks in their competition for food. In brood parasitic American cowbirds (*Molothrus spp.*) it has been shown that parasitic nestlings usually outcompete young of smaller-sized species (reviewed in Robinson et al. 1995; Lorenzana & Sealy 1999), but when cowbirds parasitize larger-sized hosts they are not able to overcome the size advantage of host nestlings (Lichtenstein 1998, Dearborn & Lichtenstein 2002; Rivers et al. 2010) because of hosts' increased competitive ability.

In general, very little is known about the interaction between nonevicting parasites and host chicks when the former are smaller than the latter, as most studies on the relationships between brood parasite and host chicks sharing a host nests have focused on small and similar-sized hosts. In particular, in brood parasitic cuckoos, though many papers have been published on this topic, the importance of size difference between parasite and host nestlings has never been studied, because most cuckoo species are evictors and because they usually parasitize host species smaller than themselves. The only exception is the study by Soler et al. (1995) in which they demonstrated that great spotted cuckoo chicks were fed at a higher rate than host chicks by their magpie foster parents. Though both species are of a similar size, cuckoos hatch earlier and enjoy a size advantage.

In this paper we study food allocation by carrion crows, the secondary host of the great spotted cuckoo, which is much larger than the parasite, in both parasitized and non-parasitized nests. This parasite-host system provides a unique opportunity to examine food allocation and the interactions between a cuckoo nestling and hosts nestlings of a much larger host species. The aims of this paper are to determine whether (i) the presence of a parasitic great spotted cuckoo chick affects feeding rate, (ii) carrion crow nestlings obtain food more easily in non-parasitized than in parasitized nests, (iii) in parasitized nests, carrion crow foster parents preferentially feed the cuckoo chick, and (iv) carrion crow parents discriminate against great spotted cuckoo chicks.

MATERIAL AND METHODS

Study area and general field procedures

The study was carried out in a 45 Km² rural area in Northern Spain ("La Sobarriba 42°37' N, 5°26'W") characterized by a mosaic of cultivated fields, small forest patches and poplar and pine plantations. Here crows breed cooperatively in about 75% of territories (Baglione et al. 2002) where they form groups of 3-9 individuals composed by a resident breeding pair, 1-4 previous offspring that delay dispersal for up to four years and/or 1-3 immigrants that are related to the same-sex resident breeder (Baglione et al.

2002; Baglione et al.2003). Up to five individuals may contribute to nestling provisioning (Canestrari et al. 2005).

In this area, great-spotted cuckoos parasitize carrion crows besides magpies. Since 2004, parasitism rate on crows has steadily increased reaching 31.4% of nests in 2006 (Canestrari et al. 2009).

Since 1995, we have been following reproduction in all territories in the study area. All nests were monitored regularly to record the time of egg laying, number of parasitic eggs and final clutch size. Between 2004 and 2007, we have video-recorded activity at 13 nests (7 parasitized, 6 non parasitized) where in most cases group members were individually banded with patagial wing tags and/or coloured rings (for details see Canestrari et al. 2005; Canestrari et al 2007) using camouflaged micro-cameras placed 1.5-3 m away from the nests (for details see Canestrari et al. 2005). In this study, we selected recordings from 6 non-parasitized and 4 parasitized nests that had the sufficient quality to analyse crow provisioning and nestling begging behaviour in detail (see below). The nests included in the sample were filmed when crow chicks were 10-15 days old. One to four recording bouts of 4 hours each were collected for each nest, for a total of 116 hours of recording.

Nestlings were not weighed previously to video recording because great spotted cuckoo chicks were in an advanced stage of development and our approximation could provoke their flight out of the nest. However,

carrion crow nestlings were about double the size of great spotted cuckoo nestlings (about 125g when they are between 15 and 20 days old, Soler & Soler 1991).

Analysis of the video recordings

The recordings were analysed with a VHS player which allowed still-bystill examination. Recordings were run until adult(s) reached the nest, after which the tape was carefully analysed still-by-still and the number of begging nestlings was noted. We differentiate adult visits (if the adult did not feed any nestling) from feedings, and simple feedings (when food was delivered to only one nestling) from multiple feedings (when food was delivered to several nestlings or to one nestling several times).

For each feeding event a score was assigned to each nestling which begged for each of the following variables: (1) 'Order'. The relative begging sequence, that is, the order in which each nestling begged for food following a parent's arrival. (2) 'Position'. Relative position in the nest with respect to the adult, estimated as the distance from a begging nestling's beak to its parent's body. (3) 'Intensity'. Relative begging intensity: an order of begging intensity following the gradient described in other studies (Redondo and Castro 1992; Soler et al. 1999), from begging with the beak open and legs flexed to begging with the neck and legs completely extended, but considering also the possibility of an intensity of begging = 0, when the fed chick was not begging

but was wake up by the feeding adult (purple feedings, Soler et al. submitted). We also calculated (4) the duration of the nestling begging since the adult reach the nest until the nestling is fed. And finally, when the nestlings begin to beg after the adult reach the nest, we calculated (5) "latency": the time elapsed since the adult reach the nest to the nestling begins to beg. As great spotted cuckoo nestlings were more developed than carrion crow ones, they could be in or out of the nest. Thus, we also annotated when the cuckoo nestling were positioned into the nest, on the rim of the nest or out of the nest. For each nest we calculated the number of feedings per nestling per hour, as well as the feeding time per nestling per hour. We did not analyze vocal begging because it was impossible to distinguish individual nestling's vocalizations from our recordings.

Statistical analyses

Firstly, we explored the differences between parasitized and non-parasitized nests for all variables described above. We calculated mean values of every variable for each nest and include it in a GLM where the variable was set as dependent, and the condition of being or not being parasitized as independent variable. We also included in the model the number of nestlings in the nest as random variable to control the effect of nestlings' competence for food.

Secondly, we explored the begging behaviour of the nestlings in the nest. On the one hand, we compared carrion crow nestlings in parasitized and non-parasitized nests. For these analyses we calculated the average values of each variable described above for each species in each nest. We run a GLM analysis for each variable setting as independent variable the condition of being or not parasitized. As commented above, we set the number of nestlings in the nest as random variable. On the other hand, we compared the behaviour of great spotted cuckoo and carrion crow nestlings in parasitized nests. To this aim we run a GLM analysis for each variable, including only parasitized nests, and set as independent variable the nestling species. Number of nestlings in the nest was included as random variable.

Thirdly, we wanted to analyze which aspect of nestling begging behaviour influences most the decision of the adult to feed a nestling. We calculated the average position of the nestling in the nest, begging order, begging intensity and latency as variables for each species in each nest for those occasions in which were fed and those in which were not fed. As these variables are inter-correlated, in order to prevent problems of collinerity in our analyses, we performed a principal components' analysis and use PCA scores. We set the maximum number of factors at 4 and choose varimax rotation for loadings. In the analyses were included only those factors including eigenvalues higher than 0.70.

After the analysis we obtained two factors statistically significant. Factor 1 was positively correlated to position in the nest, begging order and latency. Factor 1 explained 58.6% of the variability. Factor 2 was negatively correlated to begging intensity, and explained 24.1% of the variability.

We run a GLM analysis in which we included as dependent variable if the nestling were fed or not and as independent variables nestling species, territory and the factor scores obtained from the PCA analysis. Territory was set as random variable.

RESULTS

In unparasitized nests, about half of the visits by an adult carrion crow to the nest finished in a multiple feed (50.5%, n = 592) and 48.0% in a single feed (in 1.5% of the visits the adult did not provide any food). In parasitized nests the percentage of multiple feedings was higher (66.2%, n = 219) and percentage of single feeds lower (26.9%) than in unparasitized nests. Differences in multiple feedings between parasitized and unparasitized nests were not significant (*t* test (1, 10) = -1.91; p = 0.09) but reached significance in single feedings (*t* test (1, 10) = 2.47; p = 0.04). Visits without providing any food were more frequent in parasitized (6.9%, n = 219) than in unparasitized nests, (1.5%, n = 592), but differences were not significant (*t* test (1, 10) = -1.17, p = 0.28). In parasitized nests carried crow and cuckoo nestlings received a very similar percentage of multiple (66.5% and 67.4%, respectively) and single feedings (26.7% and 26.6%, respectively).



Figure 1. Number of feedings (1a) and duration of food transfer (1b) in parasitized and unparasitized carrion crow nests.

On average, parasitized carrion crow nests received more feeds/hour/nestling than unparasitized nests, and the duration of food transfer to chicks was also higher in parasitized than in unparasitized nests (see Figure 1a and 1b), but after controlling for the number of nestlings on the nest, differences did not reached significance (F(1,4) = 4.67; p = 0.097 and F(1,4) = 5.76; p = 0.07 for feeds/hour/nestling and duration of food transfer, respectively.



Figure 2. Duration of food transfer (2a) and time spent begging before being fed in parasitized and unparasitized carrion crow nests.

Even after controlling for the number of nestlings on the nest, carrion crow nestlings received food for a longer time in parasitized than in unparasitized nests (F(1,4) = 11.06; p = 0.03; Figure 2a) and begged for a longer time before being fed in unparasitized than in parasitized nests (F(1,4) = 6.98; p = 0.02; Figure 2b).



Figure 3. Number of feedings received by great spotted cuckoo and crow nestlings in parasitized nests.

In parasitized nests carrion crow nestlings received a similar number of feedings than cuckoo nestlings (F(1,3) = 2.91; p = 0,19; Figure 3). After feeding events cuckoo nestlings remained begging at a higher intensity than carrion crow nestlings (F(1,3) = 22.52, p = 0.02; Figure 4).



Figure 4.Begging intensity after feeding events by great spotted cuckoo and crow nestlings in parasitized nests.

When carrion crow parents arrived to the nest, their offspring were always into the nest, but great spotted cuckoo chicks, which were more developed, could be positioned into the nest (81.5% of the cases), on the rim of the nest (16.6%) or even out of the nest (1.9%). However, these different positions are equally successful, the cuckoo chick was fed in approximately 50% of the cases in each position (50.8%, 50.8% and 57.1%, for the into, the rim and out of the nest positions, respectively).



Figure 5. Relative position in the nest with respect to the feeding adult (5a), relative begging sequence (5b) relative latency (5c) and relative begging intensity (5d) of unfed and feed great spotted cuckoo and crow nestlings in parasitized nests.

The preference in nestling feeding of carrion crows is mainly determined by the nestling position with respect to the feeding adult, begging order and latency (Factor 1; F(1,12) = 7.77; p = 0.02). Carrion crows preferentially fed those nestlings that were closer to the adult (Figure 5a), those that first respond to the arrival of parents to the nest (Figure 5b) and those showing shorter latency (Figure 5c). Begging intensity also influenced significantly carrion crow's feeding preference (F(1,12) = 26.68, p < 0.001; Figure 5d) being preferentially fed those nestlings that begged

more intensely. Finally, nestling species significantly influences feeding preference (F(1,12) = 12.82, p < 0.01), carrion crows fed preferentially crow nestlings.

DISCUSSION

In non-evictor brood parasites, parasitic nestlings have to compete with host chicks for the food delivered by foster parents. It is well known that parents tend to feed nestlings that are begging at a higher intensity (Teather 1992; Leonard & Horn 1996; Lichtenstein 2001) and that the largest nestling in the brood receives most of the food from provisioning parents (Bengtsson & Ryden 1983; Teather 1992; Price & Ydenberg 1995; Lichtenstein & Sealy 1998; Smiseth et al. 2003; Rivers 2007). Usually, brood parasite chicks enjoy a size advantage (see references above), but what happens when host nestlings are significantly larger than brood parasitic nestlings? This study is the first contribution trying to answer this question in a brood parasitic cuckoo – larger host system.

We have found (Figure 1) that, though not significantly (surely due to the small sample size) after controlling for the number of chicks in the nests, broods with great spotted cuckoo nestlings elicited a higher delivery rate by adult carrion crows than unparasitized broods. This finding is consistent with other studies that have reported increased host provisioning

in parasitized than in unparasitized nests (Dearborn et al. 1998; Hauber and Montenegro 2002; Kilner et al. 2004; Martín-Gálvez et al 2005; Hoover & Reetz 2006; Hauber & Moskát 2008). This probably is the consequence of the higher begging intensity in parasitized nests due to the fact that parasitic nestlings beg at a higher intensity than host nestlings (see references above) being this also the case for great spotted cuckoo chicks that beg at a far higher call rate and for much longer than host chicks do (Soler et al. 1999; Rodríguez-Gironés et al. 2002).

Assuming that nest visitation rates are positively correlated with food delivery to the nest, an interesting question here is who benefit from this increase of food delivery rates for parasitized broods in nests of evicting parasites where hosts and parasite chicks share the nest. Kilner et al. (2004) found that in parasitized nests of eastern phoebe, *Sayornis phoebe*, the benefit was for the larger brown-headed cowbird nestling. However, Rivers et al. (2010) have recently reported that the beneficiary depends on the size difference between parasite and host nestlings, being the larger nestling in a brood the one that received the majority of the food provisioned independently of their identity (host or parasite). This suggestion is in agreement with numerous studies that have shown that the largest nestling in the brood is preferentially fed by parents (see references above). This is also the case in the present study, in which, first, carrion crow nestlings received more feeds and were fed for a longer period of time in parasitized than in non-parasitized nests (Fig. 2) and, second, carrion crow nestlings were fed at a similar frequency but during a longer period of time than great spotted cuckoo chicks (Fig. 2). This suggestion is also supported by the fact that great spotted cuckoo nestlings, after being fed, remains begging at a higher intensity than carrion crow nestlings (Fig. 3).

All these results together mean that, contrary to what happens when parasitizing smaller host species, great spotted cuckoo nestlings, in spite of their more exuberant begging behaviour (and in this study higher activity), are not stronger competitors for parental provisioning than host nestlings because their smaller size, which is in agreement with previous findings (Soler et al. 2001).

Similar results have been found in parasitic cowbirds of the genus *Molothrus*, which suffer a reduction in breeding success when using larger host species because cowbird chicks frequently starve (Eastzer et al. 1980; Dearborn 1998; Lichtenstein & Sealy 1998; Lorenzana & Sealy 1999; Payne et al. 2001, Dearborn & Lichtenstein 2002; Kilner 2003). Thus, contrary to traditional belief (Davies 2000), our results support empirical evidence showing that frequently non-evictor brood parasitic nestlings are less effective at eliciting care from their foster parents than host nestlings (Lichtenstein 2001; Payne et al. 2001; this paper).

Carrion crows preferentially fed nestlings that are closer to the feeding adult, responded more quickly and had a higher begging intensity

as it has been reported in many other species (see references above), including the magpie (Moreno-Rueda et al. 2007). However, magpies preferentially fed great spotted cuckoo chicks instead of magpie chicks (Soler et al. 1995) while here we have found that carrion crows preferentially feed their own nestlings instead of great spotted cuckoo chicks. This is surely the consequence of the fact that later in the nestling period -the period when our nests were video recorded- carrion crow nestlings have a size double than that of great spotted cuckoo nestlings (see above) and, as have been shown in many species, parents preferentially feed larger nestlings (see references above) especially in brood reducer species in which the smallest nestling usually starve soon after hatching as is the case of most corvids. In fact, when a great spotted cuckoo chick of the same size or a little smaller than magpie nestlings was experimentally introduced in magpie nests, the parasitic chick was then not preferentially fed (Soler et al. 1995).

Linchtenstein (2001) found that shiny cowbird (*Molothrus bonariensis*) chicks were also disfavoured when parasitizing a larger host species (rufous-bellied thrushes, *Turdus rufiventris*) and she found evidence of parental discrimination. Recently it has also been reported certain evidence of parental discrimination against great spotted cuckoo by magpie foster parents as they sometimes ignore begging signals of great spotted cuckoo chicks while waking up one of their own nestlings to feed it –purple

feedings (Soler et al. submitted). Recently, frequent cases of chick discrimination or even chick ejection have been reported (Langmore et al. 2003; Sato et al. 2010; Shizuka & Lyon 2010), which is in agreement with the strong selection pressures imposed by brood parasites on hosts for nestling recognition (Soler 2009). An interesting question arises mainly taken into account the extreme morphological differences existing between great spotted cuckoo and carrion crow nestlings (size, colouration and begging behaviour): Do carrion crow foster parents discriminate against great spotted cuckoo chicks? The response is not. Neither purple feedings (only in one occasion a non-feeding chick was wake up and it happened in a non-parasitized nest) nor any other indication of cuckoo discrimination has been observed in our video recordings. Thus, the conclusion is that great spotted cuckoo chicks are disfavoured in carrion crow nests because their advantages of a more exaggerate begging behaviour and greater activity are not enough to overcome the size advantage of their larger brood mates.

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Vocal begging display of great spotted cuckoo (*Clamator glandarius*) nestlings in nests of its two main host species

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SUMMARY

Begging behaviour of nestlings is a communication system by which nestlings request food from their parents. In the case of brood parasitic species, nestlings in nests of different host species could achieve the appropriate begging calls through three different ways: (i) mimicking the host begging calls, (ii) emitting a begging call that stimulates a wide range of hosts, or (iii) tuning the begging call to parental food provisioning through learning. All three ways could be determined genetically, if parasitic females specialize on particular host species, and/or by posthatching environmental factors. In this study we analyze begging calls of great spotted cuckoo (Clamator glandarius) nestlings in nests of its two main hosts, magpies (Pica pica) and carrion crows (Corvus corone corone). We did not find support for the previously suggested mimetic call of cuckoo nestlings since the structure of begging calls did not differ independently of the host species. In addition, the number of notes per call was the only trait of cuckoo begging calls that differed when parasitizing different host species but it was in the opposite direction from that of the begging calls of the nestlings of the two host species. Furthermore, cross-fostering experiments with nestlings that hatched in nests of the two host species did not support the possibility of a genetic component (e.g. host species of origin) of begging calls of cuckoos parasitizing different host species. Rather, we found a significant effect of nest of rearing explaining variation in the number of notes per call. Therefore, our results suggest that cuckoo nestlings are able to adjust their begging calls after hatching in nests of different host species.

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INTRODUCTION

Begging behaviour is part of a communication system by which offspring request food from their parents. Variation in the begging calls of parasitic nestlings in nests of different host species is determined by genetics and environmental components (those related to particularities of host nest environment); this not only includes those factors related to particularities of the host species, but also ecological factors shaping begging calls of non-parasitic species (Grim 2005), including nest predation (Haskell 1994) and relatedness (Briskie et al. 1994). Further environmental factors influencing begging behaviour of nestlings include pre-hatching parental effects through hormone deposition in the egg yolk (Schwabl 1993), or through trans-shell invasion of androgens from parental faces (Hinde et al. 2009).

Obligate interspecific avian brood parasitism is a type of parental-care parasitism (Roldán & Soler 2011) in which brood parasitic females lay their eggs in the nests of other species (Davies 2000). Brood parasitism is often costly for hosts, and therefore, hosts that are able to reject the parasitic eggs and/or nestlings from their nests are favoured by natural selection (Rothstein 1990; Davies 2000). Those host defences develop counter-adaptations in the parasite (e.g. the evolution of mimetic eggs or chicks), which in turn provoke new host defences in the coevolutionary arms race in which hosts and brood parasites are engaged (Rothstein 1990; Davies 2000; Soler & Soler 2000).

Vocal begging display of great spotted cuckoo

Recently, studies have provided strong evidence of parasitic nestling discrimination by hosts (Sato et al. 2010; Tokue & Ueda 2010; previous cases reviewed in Grim 2006, Soler 2009) challenging the classical view that even host species able to reject mimetic parasitic eggs are unable to reject strongly different parasitic chicks. According to predictions by the coevolutionary theory, it has been found that visual (Payne & Payne 2002; Langmore et al. 2011) and vocal (i.e. begging; Langmore et al. 2003) mimicry of host young by nestling brood parasites has evolved in response to nestling discrimination. Apart from host discrimination, parasitic nestlings have to confront another important problem, namely to elicit appropriate parental care from their foster parents. Brood parasitic nestlings can trigger foster parental care in three different ways:

First, nestlings can present begging calls that mimic those of host nestlings, this has been found in several brood parasitic-host systems (McLean & Waas 1987; Payne & Payne 1998; Dearborn & Lichtenstein 2002; Langmore et al. 2008; Anderson et al. 2009). Host-specific mimetic begging calls could have evolved genetically being an inflexible display innately encoded or, alternatively, could be acquired after parasitism by learning to match hosts' begging calls. The first possibility seems more probable to evolve in evictor-cuckoo species, in which parasitic nestlings evict host eggs or chicks soon after hatching and so do not have the opportunity to imitate host offspring. However, there is no empirical evidence of begging signals being innately encoded, but some studies have shown that it could be the consequence of a nestling learning process (Payne & Payne 1998; Langmore et al. 2008).

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Second, parasitic nestlings may trigger parental care of foster parents by using begging calls with traits that elicit feeding behaviour in many host species. This is apparently the case of the exaggerated frequency of calls of some generalist brood parasites of the genus *Molothrus* (Broughton et al. 1987; Lorenzana & Sealy 1996).

The third possibility consists of emitting begging calls that do not mimic those of host nestlings but that are tuned to host parental provisioning. This means that a newly hatched brood parasitic nestling could rapidly modify its begging calls according to its experience in frequency of food provisioning received from the host parents (McLean & Waas 1987; Butchart et al. 2003; Madden & Davies 2006). This ability of modification of begging calls according to provisioning rewards by foster parents is an adaptation based on phenotypic plasticity (West-Eberhard 2003), because different host species probably have different preferences of begging voices and thus begging calls of parasitic nestlings should change depending on the host species (McLean & Waas 1987; Butchart et al. 2003).

All these three possibilities can have both a genetic and an environmental component, so differentiating genetic and environmental influences of vocal begging behaviour of brood parasites is essential for understanding parasitic strategies that may help minimize the probability of recognition of foreign nestlings by adult hosts and/or maximize received parental care.

In this context, we study the begging calls of great spotted cuckoo (Clamator glandarius), an obligate brood parasite that in Europe mainly

parasitizes nests of magpies (Pica pica; its primary host) and carrion crows (Corvus corone corone) (Soler 1990). Great spotted cuckoo nestlings do not evict hosts' eggs or nestlings, and consequently may share the nests with host foster siblings (Cramp & Perrins 1988). Parasitism by great spotted cuckoos is very costly for magpies and several adaptations and counter-adaptations have been described in this coevolutionary system (for a review see Soler & Soler 2000). For carrion crows, the cost of brood parasitism is greatly reduced mainly because the larger size of carrion crow nestlings makes the cuckoo chick usually unable to outcompete crow chicks even when hatching several days earlier (Soler et al. 2002). Characteristics of great spotted cuckoo vocalization were first studied by Mundy (1973) using a single individual and concluded that great spotted cuckoo nestlings mimic the begging call of chicks of its pied crow host (Corvus albus; its main host in South Africa, where the study was carried out). Afterwards, Redondo and Arias de Reyna (1988) reported that nestlings from naturally parasitized nests of its two main hosts in Europe (magpie and carrion crow) produced different begging calls resembling host nestling calls. Therefore, these two previous works indicated differences in begging calls of great spotted cuckoo nestlings when parasitizing different host species (resembling begging calls of each host species). Furthermore, Mundy (1973) suggested that vocal mimicry found in great spotted cuckoos could be due to an innate tendency of this cuckoo species to imitate any bird that it hears, but Redondo & Arias de Reyna (1988) suggested that nestling cuckoos could learn to emit a mimetic begging call. Here, we use cross-fostering experiments, which is a commonly used approach for

quantifying the genetic and environmental influences of nestling traits in avian literature (Merilä 1996), for exploring the possible role of genetic and environmental factors associated to the use of different host species determining vocal begging traits of great spotted cuckoo nestlings. Briefly, we analyze differences in begging calls of great spotted cuckoo nestlings reared in nests of their two main host species and explore the influence of environmental (i.e., posthatching learning, estimated by the effect of species of nest of rearing) and genetic (i.e., innate, estimated by the effect of species of nest of laying) factors explaining variation in begging calls associated with the use of different host species.

MATERIAL AND METHODS

Study site, general methods and experimental design

The study was performed during the breeding seasons of 1995, 2000, 2004, and 2009 in the Hoya de Guadix (southeast Spain; 37°20'20.00" N, 3°04'13.04" W; elevation about 1100 m a.s.l.) where parasitism by the great spotted cuckoo of magpie (55.7%) and carrion crow (25.5%) nests is frequent (Soler 1990; Soler et al. 2002).

At the beginning of each breeding season we surveyed magpie and carrion crow territories to find the nests that we then followed to detect brood parasitism by the great spotted cuckoo. We inspected nests daily during laying and hatching, and twice or three times per week afterwards. Laying date, host clutch size and number of parasitic eggs were recorded for all nests. To ensure the survival of host nestlings in parasitized magpie nests, we exchanged parasitic eggs laid in nests of magpies or carrion crows that match expected hatching dates with these of their hosts (see Martín-Gálvez et al. 2011 for a similar approach). In the case of carrion crow nests, hatching dates of exchanged cuckoo eggs were adjusted to two to four days before the expected hatching dates of nestling crows. All sampled cuckoo nestlings therefore shared the experimental nest with host nestlings.

Begging calls were recorded in the field using two different recorders: a Sanyo M-1270C Compact Cassette Recorder during 1995, 2000 and 2004, and a Marantz PMD-660 Solid State Recorder (set at a sample rate of 44.1 Hz and 16 bit resolution) with a Sennheiser MKH-416-P48 microphone during 2009. The Marantz recorder was also used to digitize cassette tape recordings. Analog recordings were digitized with Sound Tools software and hardware (sample rate of 44.1 Hz and16 bit resolution). Briefly, each individual nestling was placed in an artificial nest and stimulated by gently touching the border of the nest and by moving our fingers above their heads until begging commenced. If the nestling did not beg immediately, we repeated the stimulus every 5 minutes up to two and a half hours. After recording, the nestling was fed *ad libitum* and placed back in the nest.

Sample sizes of inter-specific cross-fostering experiments were low because laying dates of the two species barely overlaps, carrion crows begin laying in mid-March and magpies begin to lay eggs in early April (Soler 1990; Soler et al.

2002).Also, the parasitism rate on carrion crows is relatively low (25.5%; Soler 1990) with early-laying nests of carrion crow being more heavily parasitized (Soler et al. 2002). We successfully recorded begging calls of five day old great spotted cuckoos from interspecific cross-fostered eggs in 3 nests of magpies and in 5 nests of carrion crows. Additionally, we recorded begging calls of great spotted cuckoos from eggs that were laid and hatched in nests of crows (n = 7) and in nests of magpies (n = 9). All host nests included chicks of the host species. Finally, we also recorded begging calls of five-day-old magpie (n=6) and crow (n=11) nestlings from parasitized nests.



Figure 1. Spectrogram of 3 s of duration of begging calls of nestlings of great spotted cuckoo reared in nests of carrion crows and magpies and those of host nestlings. Main traits of begging calls (peak frequency, silence, note and pulses within note) are shown. Spectrograms were obtained from Raven Pro1.3.

Audiospectrogram and statistical analyses

Audiospectrograms from the recordings of the begging calls were obtained with the sound analysis software "Raven Pro" version 1.3 (www.birds.cornell.edu/raven; settings: Hanning, window size 11.6 ms, 3-dB bandwidth of 124 Hz, frequency grid DFT size 512 samples and 86.1 Hz). For each audiospectrogram we differentiated several calls divided into notes, and in the case of great spotted cuckoos, several short pulses of sound within each note (i.e., this trait was absent in host nestlings calls; see Fig. 1). With the information in the spectrogram we were able to estimate the following 7 variables that we used in subsequent analyses: (1) the number of notes per call; (2) the duration in seconds of inter-calls (hereafter, silence); (3) the duration in seconds of notes; (4) peak average frequency (Hz) of notes, (i.e., maximum frequency measured at the point of highest amplitude) of notes; (5) the proportion of time that a nestling is producing sound during calls (hereafter, duty cycle); (6) the number of pulses per note, and (7) number of pulses per second. Before the analyses, variables 4 and 7 were square-root transformed, while all other variables, with the exception of number 1, which was normally distributed, were logarithmically transformed to reach approximately normal distributions. To avoid pseudo-replication only a single nestling was used per studied nest. We used mean values per nestling, the analyses were weighed by the number of calls analyzed per nestling, and degrees of freedoms were adjusted to the number of nestlings.

To avoid problems of co-linearity of variables describing begging calls and reduce number of independent variables in the analyses, we performed principal

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components analyses with varimax normalized factor rotation and used PCA scores in the analyses. Begging calls of great spotted cuckoos, but not those of magpies or carrion crows showed pulses within a note (see above). Thus, for inter-specific comparisons we did not include related variables (i.e., numbers 6 and 7 above) in the PCA. A second PCA was therefore performed for reducing the seven intercorrelated variables describing begging calls of great spotted cuckoos reared in nest of the two host species.

The PCA that included the five variables describing begging calls of magpie and crow nestlings resulted in three factors that explained 47.2%, 19.4% and 14.2% of variance, respectively. Factor 1 was positively related to number of notes per call (factor loading 0.89) and negatively to the silence of the call (factor loading = -0.80). Factor 2 described the duration of notes (factor loading = 0.95), and factor 3 the peak average frequency of notes (factor loading = 0.97). The second PCA including the seven variables describing begging calls of great spotted cuckoos resulted in three factors that explained 55.2%, 17.9% and 12.8% of the variance respectively. Factor 1 was positively correlated to note duration (factor loading = 0.96), duty cycle (factor loading = 0.97), and number of pulses per note (factor loading = 0.90). Factor 2 described the peak average frequency of notes (factor loading = 0.93).

Interspecific comparisons were carried out by means of Multivariate General Linear Models (MANOVAs) with PCA scores as dependent variables and species identity as the independent factor. Only cuckoos from eggs that were laid and hatched in nests of the same species (i.e. control nestlings) were used in these analyses. We therefore differentiated four groups of nestlings: two groups of cuckoos and one of each host species. Similarly, the experimental effects of host species explaining variation in begging calls of cuckoos were explored by using Multivariate General Lineal Models (MANOVAs) with the PCA scores as dependent variables and two independent factors: the identity of the host species where the parasitic egg was laid (i.e., nest of origin), and that where the egg hatched and the chick grew (i.e., nest of rearing) nested within species identity of nest of origin. These models allow us to quantify the pre-hatching (i.e., genetic) and post-hatching (i.e., environmental) influences determining phenotypic variation in begging calls of great spotted cuckoos parasitizing magpies and carrion crows.

All analyses were performed with Statistica 8.0 software.

RESULTS

The begging calls of nestlings of the three studied species differed with respect to the number of notes per call and the duration of silence in the call (Factor 1; $F_{3,30}$ = 13.99 p < 0.001; Bonferroni post-hoc analyses: p < 0.01 ; Fig 2a), Peak average frequency of notes also differed among species (Factor 3; $F_{3,30}$ = 9.55 p < 0.001) but this was due to crow nestlings begging at a statistically significant lower frequency than magpie and cuckoo nestlings (Bonferroni post-hoc analyses: p < 0.05; Fig 2c). Finally, interspecific differences in note duration did not reach

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statistical significance (Factor 2; $F_{3,30} = 2.82 \text{ p} = 0.058$; Fig. 2b). All these results indicated that in general, begging call characteristics of nestlings of the three studied species differ (MANOVA, Wilk's $\lambda = 0.10 \text{ F}_{9,60} = 10.75 \text{ p} < 0.001$).



Figure 2. Species differences in begging call studied variables described by all three PCA factors. Figure 2a shows factor 1 described by the number of notes per call (circles) and silence (triangles). Figure 2b shows factor 2 described by notes duration and figure 2c shows factor 3 described by the peak average frequency of notes. Graphs show mean \pm SE. Means denoted by different letters are significantly different at the 0.01 level according to Bonferroni post-hoc test.

Similarly, we compared the great spotted cuckoo nestlings' begging calls from the inter-specific cross-fostering experiments. We included both nest of origin and species of rearing (nested in nest of origin). From the three PCA factors included, only Factor 3 (number of notes per call) showed statistically significant differences (Factor 3; $F_{3, 20} = 5.95 \text{ p} < 0.01$), while the other two factors did not (Factor 1; $F_{3, 20} = 1.13 \text{ p} = 0.36$ and Factor 2; $F_{3, 20} = 1.87 \text{ p} = 0.17$). Species of origin failed to explain differences in the variability of begging calls (MANOVA, Wilk's $\lambda = 0.85 \text{ F}_{3,18} = 1.06 \text{ p} = 0.39$;), while the nest of rearing (nested within nest of origin) did explain a significant proportion of variance in begging call properties (MANOVA, Wilk's $\lambda = 0.37 \text{ F}_{6,36} = 3.91 \text{ p} < 0.005$). The detected effects of nest of rearing were mainly due to variation in the number of notes per call (Factor 3; $F_{2, 23} = 8.30 \text{ p} < 0.01$; Table 1). Begging calls of cuckoos reared in magpie nests showed higher number of notes per call, note duration and duty cycle than those reared in crow nests (Table 1). Peak average frequency of notes and the number of notes per call did not differ significantly (Factor 1; $F_{2, 23} = 1.42 \text{ p} = 0.26$; Factor 2; $F_{2, 23} = 2.72 \text{ p} = 0.09$; Table 1).

Table 1 Begging calls properties of great spotted cuckoos reared in magpie and carrion crow nests. PCA factor in which each variable is encoded is shown in brackets. Variables in bold correspond to PCA factor with statistically significant differences between both groups (p < 0.01). Mean ± SE values are shown.

	In magpie nests	In carrion crow nests
Pulses per note (F1)	3.69 ± 0.96	1.88 ± 0.21
Note duration (F1)	0.29 ± 0.09	0.17 ± 0.03
Duty cycle (F1)	0.39 ± 0.08	0.26 ± 0.03
Peak average frequency (F2)	5386.90 ± 360.85	5649.44 ± 401.26
N. notes per call (F3)	18.14 ± 3.30	14.83 ± 4.04

DISCUSSION

Our results show that great spotted cuckoo begging calls differed when reared by two different hosts while identity of the species selected for parasitism for females' cuckoo did not explain significant proportion of variance of cuckoo begging calls. These results are in agreement to empirical evidence showing that nestlings can learn and modify their begging displays after hatching according to the social situation they found in their nest (Kedar et al. 2000; Kölliker & Richner 2004; Budden & Wright 2005), evidence that has also been reported for great spotted cuckoo nestlings (Rodríguez-Gironés et al. 2002).

The detected differences were exclusively due to the number of notes per call (Table 1), and none of the variables describing call structure of great spotted cuckoo nestlings varied when reared in nests of different species. Nestlings of generalist brood parasitic species often modify the structure of their begging calls when parasitizing different hosts (Madden & Davies 2006; Langmore et al. 2008), but those of specialist brood parasitic species (as it is in the case of the great spotted cuckoo) do not (Payne & Payne 1998). Our results are therefore in accordance with different capacities of nestlings of specialist and generalist brood parasites species, showing a limited degree of modification (notes per call) in a specialist brood parasitic species but with two alternate hosts.

Previous studies of the begging displays of great spotted cuckoos claimed that nestling cuckoos mimic the begging calls of host young (Mundy 1973; Redondo & Arias de Reyna 1988). We have found that cuckoo begging calls differ depending on the host species, but it is not clear that these differences increase mimicry (see Fig 1 and 2). Both previous studies had extremely low sample sizes (one cuckoo chick in Mundy (1973) and low numbers in Redondo & Arias de Reyna (1988; T. Redondo, personal communication) and used chicks older than those studied by us. Possible differences in begging calls in relation to nestling age, however, cannot explain the absence of evidence in favour of begging mimicry in great spotted cuckoo nestlings in our results. Visual inspection of sonograms of begging calls of cuckoo nestlings of age similar to that used in Redondo & Arias de Reyna (1988) reared by both host species also confirmed the absence of similarity between sonograms of cuckoo nestlings and those of their host nestmates (see Fig. 3). Thus, our results do not clearly support the existence of mimetic begging in great spotted cuckoo nestlings as suggested in previous articles (Mundy 1973; Redondo & Arias de Reyna 1988). The absence of evidence supporting the expected mimicry of begging calls of parasitic nestlings to those of their host species should not be surprising since in a comparative work, Ranjard et al. (2010) did not find consistently correlated similarity between begging calls of several passerine species and specialist brood parasitic cuckoos that supposedly evolved to mimic their hosts.



Figure 3. Spectrogram of 3 s of duration of begging calls of nestlings. (a) Cuckoo nestling reared by crows (10 days old) (b,c) Cuckoo nestlings reared by magpies (10 days old) (d) Crow nestling (8 days old). (e,f) Magpie nestlings (9 and 8 days old respectively). Spectrograms were obtained from Raven Pro 1.3.

Differences in begging calls between great spotted cuckoo nestlings reared in nests of their two main host species could be due to genetic (i.e., innate, Mundy 1973) or environmental (i.e., learning, Redondo & Arias de Reyna 1988) factors. The statistical analyses of our cross-fostering experiments failed to detect an effect of the nest in which the egg was laid, which means that detected differences in begging calls of cuckoos reared in different host species are not genetically determined. This result suggests the absence of specialization processes occurring in great spotted cuckoo females, which is in agreement with previous results showing that the same great spotted cuckoo female can lay eggs in both magpie and crow nests (Martínez et al. 1998). Furthermore, the nature of the call parameter differring between great spotted cuckoo nestlings reared in different species' nests (notes per call) is a stricktly behavioral trait, a mere change in the temporal rate and pattern of emission of the notes. No changes in parameters related to call apparatus structure (such as frequency, which would be related to vocal chord morphology) were observed.

Thus, the first possibility suggested in the introduction by which brood parasitic nestlings could emit the appropriate stimulus to trigger foster parents to feed them by mimicking host's begging calls, does not work in great spotted cuckoos. What about the other two possibilities? The second possibility, that the use of begging calls is generally adapted to many host species, is unlikely to be applied to great spotted cuckoos, because although it could be adaptive in generalist brood parasites (Lorenzana & Sealy 1996) it is highly improbable in a brood parasite as specialized as the great spotted cuckoo (see above). However, if the environmental component represents an important influence in the development of vocal begging behaviour, this second possibility would be very similar to the third one (see below).

The third possibility, that newly hatched cuckoo nestlings can modify their begging calls according to provisioning rewards obtained from foster parents, is the most frequently suggested mechanism explaining changes in vocal begging displays presumably developed to more efficiently exploit foster parents. For example, West & King (1998) proposed that differences in begging call found in brown-headed cowbirds (*Molothrus ater*) when reared in different hosts could be due to a trial and error mechanism of learning, and Butchart et al. (2003)

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suggested that this mechanism would explain the differences in begging calls found in different races of common cuckoo (Cuculus canorus). However, the strongest support for this possibility has been reported by Madden & Davies (2006) working on the common cuckoo and its passerine hosts. By crossfostering cuckoo eggs between host species they demonstrated that the different structure of cuckoo nestling begging calls found in each host species was acquired by modification soon after hatching and that the resulting structure of begging calls is the most effective in exploiting foster parents (Madden & Davies 2006). This plastic mechanism of learning by trial and error responding to positive feedback may allow parasitic nestlings an efficient exploitation of foster parents that would allow even specialist brood parasites to explore the possibility of sporadically parasitizing new host species. In our cross-fostering experiment we found that nest of rearing was the only factor explaining variation in begging calls of nestling reared in magpie and in carrion crow nests, and thus it suggests that nestlings adjust their begging call to the parasitized species. This plastic underlying mechanism, as occurs in other species, is likely to be a learning process mediated by trial and error responding to positive feedback, which would allow the exploitation by great spotted cuckoos of sporadically parasitized potential hosts such as jackdaws (Corvus monedula) and red-billed choughs (Pyrrhocorax pyrrhocorax) (Soler 1990).

In conclusion, reported differences in begging calls between great spotted cuckoo nestlings reared in nests of magpies and carrion crows are not the consequence of more closely resembling those of foster siblings and are not

genetically determined, but rather are the result of phenotypic plasticity allowing parasitic nestlings to learn efficient begging displays when exploiting foster parents of different species.

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DISCUSIÓN INTEGRADORA

En la presente tesis doctoral hemos descrito una segunda población de corneja negra que presenta cría cooperativa y que sufre parasitismo de cría por parte del críalo europeo, relacionando así las asociaciones animales beneficiosas y perjudiciales principales que podemos describir con respecto a los costes que supone la reproducción y el cuidado de la descendencia. Por otra parte, hemos llevado a cabo una revisión en la que abarcamos y clasificamos el parasitismo de los cuidados parentales desde el punto de vista de los costes que produce y en base a las estrategias que los parásitos desarrollan, principalmente desde el punto de vista de la descendencia parásita. En lo que respecta a este tema también nos centramos en el parasitismo del críalo europeo en los nidos de corneja para estudiar las estrategias parásitas que desarrolla el pollo parásito para competir por el alimento con los pollos hospedadores.

Cría cooperativa

La población de corneja negra que hemos estudiado (situada en la Hoya de Guadix, Granada) presenta una alta tasa de cooperación (66,5%) muy similar a la encontrada en la población de La Sobarriba (León; 75%; Baglione et al. 2005). Una de las características comunes para las especies

en las que existe cría cooperativa es que los tamaños de puesta suelen ser más reducidos que en las especies no cooperativas (Brown 1987; Arnold & Owens 1998; Arnold & Owens 1999). Sin embargo, en ninguna de las dos poblaciones cooperativas de corneja el tamaño de grupo afecta al tamaño de puesta (Canestrari et al. 2008, Capítulo 1). Incluso, ambas presentan un tamaño de puesta ligeramente mayor que el resto de poblaciones europeas (Cramp & Perrins 1988; Canestrari et al. 2008), contradiciendo, por tanto, la predicción general. Sin embargo, este hecho puede ser consecuencia de la latitud sureña a la que se encuentran ambas poblaciones, ya que se ha visto que algunos córvidos incrementan su tamaño de puesta conforme disminuye la latitud a la que se reproducen (Soler & Soler 1992).

La principal diferencia que encontramos entre ambas poblaciones cooperativas de corneja negra reside en la tasa de puestas de reposición cuando el nido ha sido depredado con huevos o pollos pequeños. Mientras que en la población de La Sobarriba la tasa de reposición es elevada (70,3% en territorios cooperativos y 29,7% en no cooperativos; Canestrari et al. 2008), en la población de Guadix la tasa de reposición es bastante baja (10,42%). Esta diferencia entre ambas zonas puede ser debida principalmente al efecto de los factores meteorológicos. Como muestran nuestros resultados, la temperatura máxima durante la etapa de pollos en el nido incrementa el número de pollos muertos por inanición. Puesto que en Guadix se alcanzan temperaturas de hasta 36°C al final de la primavera, la

disponibilidad de presas para cebar a los pollos disminuiría y esta disminución podría haber desembocado en una adaptación local que limitase la fecha de puesta debido a que los pollos de puestas más tardías presentarían una baja probabilidad de supervivencia.

Otra de las ventajas descritas para las especies que presentan cría cooperativa es el incremento en el éxito reproductor (ej., Boland et al. 1997; Brown et al. 1982; Emlen and Wrege 1991; Komdeur 1994; Mumme 1992 in Hatchwell et al. 2004). En la población de La Sobarriba, Canestrari et al. (2008) encontraron un incremento en el éxito reproductor en los grupos cooperativos con dos ayudantes, mientras que en nuestra población no hemos encontrado un efecto del tamaño de grupo en el éxito reproductor. Esta ausencia de efecto en nuestra población de estudio pudiera ser debido a que se necesiten más años de estudio o un mayor tamaño de muestra para poder detectarlo, aunque también podría ser explicado por otros factores. Baglione et al. (2006) demostraron experimentalmente que los territorios de mejor calidad son los que presentan un mayor retraso en la dispersión de los juveniles, lo que sugiere que los territorios cooperativos son de mejor calidad que los no cooperativos. Por tanto, podría ser esta mayor calidad del territorio y no el tamaño del grupo lo que estuviese incrementando el éxito reproductor de los territorios cooperativos.

Por otra parte, en nuestra población encontramos que el tamaño de grupo no sólo no incrementa el éxito reproductor, sino que está influyendo

positivamente en el número de pollos que mueren por inanición. Canestrari et al. (2004) describieron una elevada proporción de cebas falsas (llegar al nido sin comida, comer parte de la ceba, o recuperar ceba de la garganta de un pollo recién cebado; Canestrari et al. 2004) por parte de los ayudantes, pero principalmente de la hembra. Aunque nuestro tamaño de muestra no es alto, podemos argumentar que en nuestra población de estudio, si la hembra llevase a cabo un elevado número de cebas falsas y los ayudantes no compensasen esas cebas, esto podría provocar un mayor número de muertes por inanición entre los pollos de los territorios cooperativos.

Otra de las principales causas de muerte de los pollos en los nidos es la depredación. Varios estudios en diferentes especies que presentan cría cooperativa han encontrado que la tasa de depredación en los nidos con ayudantes es menor que en los nidos sin ayudantes (Brown 1987; Emlen 1991; Cockburn 1998; Dickinson & Hatchwell 2004). Nosotros no encontramos diferencias en la tasa de depredación entre los territorios defendidos por parejas y los defendidos por grupos, pero quizá la ausencia de efecto en nuestra población de estudio sea debida a la baja tasa de depredación que encontramos (19,35%).

Por último, cabe destacar que las condiciones meteorológicas de cada población pueden hacer variar el efecto del tamaño de grupo sobre el éxito reproductor de las especies con cría cooperativa. En nuestra población de estudio, hemos encontrado que las condiciones meteorológicas pueden

influir en la biología reproductiva de una especie tanto como los factores biológicos. Así, aparte del ya comentado efecto de la temperatura máxima sobre la mortalidad de los pollos, la precipitación puede tener efectos contrarios dependiendo del estadio reproductor: durante la incubación de los huevos disminuye la tasa de eclosión, mientras que durante la etapa de pollos en el nido incrementa el número de volantones producidos, probablemente debido a una mayor disponibilidad de presas como sugirió Rofstad (1988). Por tanto, el incluir variables meteorológicas en los estudios de la biología reproductiva de las especies con cría cooperativa podría ayudarnos a encontrar esa "pieza clave" que propicia la cooperatividad y que nos ayudase a entender las diferencias encontradas entre las distintas poblaciones (e incluso especies) cooperativas.

Parasitismo de los cuidados parentales y cría cooperativa

En el Capítulo 2 definimos un nuevo término: "parasitismo de los cuidados parentales". Este nuevo término aúna todos aquellos comportamientos parásitos que involucran cuidados parentales y, puesto que la clasificación que presentamos está basada en comportamientos y no en taxones como las propuestas hasta el momento, elimina las imprecisiones terminológicas que los términos utilizados hasta ahora imponían. Por primera vez se clasifican estos comportamientos parásitos en función de los costes que provocan para
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el hospedador, haciendo así posible la comparación entre estrategias parásitas y taxones diferentes. Otra de las ventajas del nuevo término es que incluye aquellos comportamientos parásitos promovidos directamente por la descendencia parásita, como sería el caso del "switching" o cambio de nido de los pollos que se ha descrito en algunas especies de aves nidícolas.

Uno de los comportamientos parásitos que engloba el parasitismo de los cuidados parentales es el parasitismo de cría, estudiado principalmente en aves (ej. Rothstein 1990; Johnsgard 1997; Davies 2000). Aunque el parasitismo de cría en aves ha sido muy estudiado, se sabe muy poco de su interacción con la cría cooperativa. Los parásitos de cría deberían preferir parasitar grupos cooperativos puesto que su descendencia sería alimentada a una tasa mayor (Poiani & Elgar 1994). Aunque, por otra parte, el parasitismo de esos nidos sería más difícil puesto que se trataría de territorios mejor defendidos (Dickinson & Hatchwell 2004) y el nido quedaría menos tiempo solo ya que la presencia de ayudantes permitiría a la hembra pasar más tiempo incubando los huevos (Canestrari et al. 2009).El caso concreto del parasitismo de cría del críalo europeo a la corneja negra ha sido estudiado en las dos poblaciones de corneja con cría cooperativa descritas hasta ahora. A diferencia de lo encontrado en la población de La Sobarriba, en la de Guadix no encontramos diferencias en la tasa de parasitismo de los territorios defendidos por parejas o por grupos, lo que concuerda con los resultados encontrados por Langmore & Kilner (2007) en otra especie de paseriforme que presenta cría cooperativa y que es parasitada por otra especie de cuco. Por otra parte, el parasitismo del críalo en corneja en ambas poblaciones parece estar sujeto a patrones diferentes. Mientras que en Guadix la tasa de parasitismo tanto en el hospedador primario (urraca) como en el secundario (corneja) en los últimos años ha incrementado de forma paralela alcanzando en ambas especies tasas de parasitismo muy similares (llegando al 90% en 2009); en La Sobarriba, la tasa de parasitismo en urraca se ha mantenido constante a un nivel bajo (20%) mientras que en corneja ha ido incrementado sucesivamente en los últimos años llegando a alcanzar valores similares a los de la población de Guadix (70%). El incremento en la tasa de parasitismo en ambas especies hospedadoras en Guadix parece responder a un incremento en la densidad poblacional del críalo, mientras que el incremento del parasitismo exclusivamente sobre la corneja en La Sobarriba no está tan claro. El hecho de que el éxito reproductor del críalo en corneja sea más bajo en ambas poblaciones indica que debe haber otros factores que estén influenciando la preferencia por la corneja como hospedador en La Sobarriba. En ambas poblaciones las cornejas no presentan el mecanismo de defensa de expulsar los huevos extraños, mientras que las urracas sí lo presentan, aunque en la población de La Sobarriba el porcentaje de expulsión es más reducido que en Guadix, por lo que este no sería el factor que marcaría la preferencia del críalo por la corneja como hospedador en la población del Norte de España.

Otra posible explicación de esta preferencia vendría dada por la accesibilidad de los nidos: que los nidos de urraca en La Sobarriba fuesen menos accesibles que en Guadix podría ser un motivo de la preferencia por las cornejas como hospedadores. Pero tan sólo un 20% de nidos de urraca de fácil accesibilidad fueron parasitados en La Sobarriba. Por otra parte, el experimento llevado a cabo incrementando la accesibilidad de algunos nidos no aumentó el parasitismo en dichos nidos. Ambos resultados sugieren que la preferencia por la corneja como hospedador encontrada en La Sobarriba no es debida a la mayor accesibilidad de los nidos.

Por otra parte, cabría la posibilidad de que la fecha de puesta de los críalos y los hospedadores en ambas poblaciones fueran muy diferentes. Los resultados muestran que en La Sobarriba la fecha de puesta del críalo se ajusta a la de la corneja, difiriendo significativamente respecto a la de urraca y a la de ambos hospedadores considerados juntos; mientras que en Guadix, la fecha de puesta del críalo difiere de la de ambos hospedadores por separado pero se ajusta a la fecha de puesta de ambos hospedadores juntos. Puesto que en Guadix se observa que el críalo amplía su fecha de puesta para adaptarla a ambos hospedadores, parece poco probable que la fenología del parásito sea la causa del parasitismo principal en la corneja en la población de La Sobarriba.

Otras dos potenciales explicaciones serían posibles aunque, desafortunadamente, aún no tenemos datos suficientes para poder ponerlas a prueba. La primera de ellas sería que las urracas defendiesen de forma más eficiente sus nidos en la población de La Sobarriba que en Guadix. Aunque son necesarios estudios más detallados para comprobar esta hipótesis, los estudios preliminares llevados a cabo en la población de La Sobarriba parecen sugerir que en ambas poblaciones la defensa de las urracas frente al críalo es similar, mientras que en cornejas esta defensa no existe, por tanto esta hipótesis no explicaría el mayor porcentaje de parasitismo de las cornejas en La Sobarriba.

La segunda explicación hace referencia a la existencia de una posible diferenciación genética de los críalos en dos razas especializadas cada una en una especie hospedadora diferente, como ocurre en el cuco común (Gibbs et al. 2000). Por un lado, las diferencias encontradas en las llamadas de petición de alimento de críalos criados en nidos de ambos hospedadores indican que en la población de Guadix no habría tal diferenciación genética (Capítulo 5), lo que coincidiría con los resultados de Martínez et al. (1998) que encontraron que una misma hembra de críalo puede parasitar nidos de ambas especies hospedadoras. Por otra parte, el hecho de que el críalo sea una especie migradora y la falta de datos que apoyen que presenten una tendencia a volver a la zona de cría del año anterior (E. Macías, J. G. Martínez y M. Soler datos no publicados), hace difícil aceptar que esta opción sea la que explique el aparente cambio de hospedador en la población de La Sobarriba, aunque serían necesarios estudios en

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profundidad sobre la genética y la distribución de la especie para conseguir conclusiones fiables.

Petición de alimento de los pollos parásitos

En los parásitos de cría cuyos pollos no expulsan huevos y/o pollos del hospedador, los pollos parásitos han de competir con los pollos hospedadores por el alimento llevado por los padres al nido. Varios estudios han demostrado que los padres ceban preferentemente a aquellos pollos que piden con mayor intensidad (Teather 1992, Leonard & Horn 1996, Lichtenstein 2001) y que los pollos de mayor tamaño reciben la mayoría del alimento llevado por los padres (Bengtsson & Ryden 1983; Teather 1992; Price & Ydenberg 1995; Lichtenstein & Sealy 1998; Lichtenstein 2001; Smiseth et al 2003; Rivers 2007). El críalo europeo parasita especies hospedadoras de su mismo tamaño o mayores. En el caso de la urraca los pollos hospedadores son aproximadamente del mismo tamaño que los parásitos, pero, puesto que el críalo eclosiona antes, disfruta de un mayor tamaño que le otorga una ventaja sobre los pollos hospedadores (Soler et al. 2002).

En el caso de la corneja, una especie mucho más grande que el críalo, el pollo parásito, aunque eclosiona antes, no disfruta durante mucho tiempo de la ventaja de un mayor tamaño porque los pollos de corneja crecen muy rápido y pronto alcanzan y superan el tamaño del pollo de críalo (Soler et al. 2002). Nuestros resultados indican que los nidos parasitados presentan una mayor tasa de ceba que los no parasitados (aunque este resultado no es estadísticamente significativo, probablemente por el bajo tamaño de muestra). Este resultado puede ser debido a la mayor intensidad de petición que emana de los nidos parasitados como consecuencia de la alta frecuencia e intensidad de petición que generalmente desarrollan los pollos parásitos de cría (Davies 2000). A pesar de esta elevada tasa de petición, nuestros resultados indican que los pollos de críalo son cebados a una menor tasa que los pollos de corneja. Estos resultados concuerdan con otros estudios que han encontrado que los pollos parásitos que comparten nido con los hospedadores, cuando no son de mayor tamaño, son menos efectivos consiguiendo comida que los pollos hospedadores (ej. Dearborn 1998; Davies et al. 1998; Lichtenstein & Sealy 1998; Soler et al. 1999; Rivers 2007). Nuestra conclusión es que los pollos de críalo son desfavorecidos en los nidos de corneja porque, a pesar de su exagerado comportamiento de petición y su mayor actividad en el nido, no son capaces de competir con la ventaja que supone para los pollos hospedadores su mayor tamaño.

Muchos pollos parásitos presentan modificaciones en sus llamadas de petición de alimento que estimulan a los padres hospedadores a alimentarlos preferentemente y/o con una mayor frecuencia (ej., Davies 1998; Langmore et al. 2008). Los parásitos de cría generalistas modifican

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sus llamadas de petición de alimento en cada hospedador (Madden & Davies 2006; Langmore et al. 2008), pero no ocurre lo mismo con los especialistas (Payne & Payne 1998), como es el caso del críalo europeo. Puesto que, como ya hemos discutido, la mayor intensidad de petición no le reporta una ventaja, cabría esperar que los pollos de críalo hayan modificado su llamada de petición de alimento de la manera que resulte más "atractiva" a los padres hospedadores que la de sus propios pollos. En el Capítulo 5 comparamos las llamadas de petición de pollos de críalo criados en nidos de urraca con las de los criados en nidos de corneja. Nuestros resultados muestran que no existen diferencias estructurales de la llamada de petición de alimento, lo cual, junto con los resultados de los experimentos de intercambio de huevos de críalo entre especies hospedadoras que llevamos a cabo, indica la ausencia de influencia genética en dichas diferencias. Puesto que las llamadas de petición de alimento de los pollos de críalo muestran diferencias según el hospedador, podríamos descartar la hipótesis de que el críalo emitiese una llamada de petición que estuviese adaptada a cualquier hospedador, como sugieren algunos estudios publicados (ej., Broughton et al. 1987; Lorenzana & Sealy 1996). Otra posibilidad sería que el críalo mimetizase las llamadas de petición de sus hospedadores (McLean & Waas 1987; Payne & Payne 1998; Dearborn & Lichtenstein 2002; Langmore et al. 2008; Anderson et al. 2009). Al contrario que estudios anteriores sobre el críalo europeo (Mundy 1973; Redondo & Arias de Reyna 1988), nuestros resultados no muestran una tendencia de las modificaciones de las llamadas de petición del críalo a mimetizar las del hospedador. Por último, podríamos pensar que el críalo modifica su llamada de petición de alimento en función de las condiciones medioambientales (nido en el que está siendo criado), como ha sido descrito para otros parásitos de cría (McLean & Waas 1987; Butchart et al. 2003; Madden & Davies 2006). Esta explicación es la que nos parece más plausible por los motivos anteriormente señalados. Si aceptamos esta hipótesis como cierta, nuevos estudios en profundidad serían necesarios para discernir si el pollo parásito modifica su llamada de petición como respuesta a pruebas de ensayo y error según la tasa de cebas aportadas por los padres, o en función de la llamada de petición de los otros pollos hospedadores.

CONCLUSIONES

1. La población de corneja negra (*Corvus corone*) estudiada en la comarca de Guadix (provincia de Granada) presenta un sistema de cría cooperativa similar al descrito en la única población cooperativa de esta especie conocida hasta el momento (La Sobarriba, España). La diferencia más importante está en la tasa de puestas de reposición cuando el nido es depredado, siendo en Guadix casi inexistente.

2. En la población cooperativa de corneja negra de la comarca de Guadix no se han detectado beneficios relacionados con el tamaño de grupo. Por el contrario, se ha puesto de manifiesto una relación positiva del tamaño de grupo con la mortalidad de pollos por inanición.

3. Los factores meteorológicos (temperatura máxima, temperatura mínima y precipitación) presentan, en las diferentes fases del periodo reproductivo de la corneja negra en Guadix, una influencia sobre el éxito reproductor tan importante como la de los factores bióticos.

4. En nuestra revisión de los comportamientos animales que implican algún tipo de parasitismo de cuidados parentales, proponemos un nuevo término: "parasitismo de cuidados parentales" que definimos como la interacción en la cual un individuo (el parásito) obtiene beneficios reproductivos reduciendo o eliminando los costes mediante la explotación de cualquier tipo de cuidado parental proporcionado por otros individuos (los hospedadores) a sus descendientes. Este nuevo término conlleva una clasificación basada en los costes provocados por el parasitismo al hospedador en lugar de basarse en los taxones que interactúan, como había sido hasta ahora. La clasificación que proponemos también incluye, por

primera vez, comportamientos parásitos de los cuidados parentales propiciados directamente por los descendientes.

5. En nuestra revisión sobre el parasitismo de cuidados parentales hemos puesto de manifiesto que existen evidencias de adaptaciones y contraadaptaciones en bastantes sistemas de parásitos de cuidados parentales y sus hospedadores, lo que indica que las carreras de armamentos coevolutivas también están funcionando en algunos de estos sistemas.

6. La tasa de parasitismo del críalo europeo (*Clamator glandarius*) en urraca (*Pica pica*) y corneja negra durante los años 2007 a 2009 difieren en las poblaciones de Guadix y La Sobarriba. En Guadix las tasas de parasitismo han incrementado de forma paralela respondiendo, probablemente, a un incremento en la densidad de críalo europeo en la zona. En La Sobarriba, la tasa de parasitismo en corneja negra ha incrementado, mientras que la de urraca se ha mantenido constante. Estas diferencias en las tasas de parasitismo de las urracas en ambas poblaciones parecen estar correlacionadas con los periodos de puesta del críalo, aunque esta correlación no determine causalidad. Otras posibilidades tendrán también que ser estudiadas.

7. Las cornejas, al contrario de lo que ocurre en el resto de las especies de aves hospedadoras de cucúlidos parásitos, no alimentan preferentemente al pollo parásito, sino a los pollos que están más cerca del adulto, que comienzan a pedir antes y que piden con mayor intensidad. Alimentan preferentemente a los pollos de corneja.

8. Los pollos de críalo europeo, cuando parasita nidos de corneja negra, a pesar de que su petición de alimento es de una intensidad más elevada que

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la de los pollos hospedadores, no resulta más exitoso que los pollos de corneja consiguiendo alimento.

9. La llamada de petición de alimento de los pollos de críalo europeo varía según la especie hospedadora. Difieren en el número de notas por llamada, pero no muestran mimetismo con la llamada de petición de alimento de los pollos hospedadores. Un experimento de intercambio de pollos nos ha permitido concluir que las diferencias encontradas no son debidas a factores genéticos, sino que parecen encajar con un patrón de modificación de la llamada como consecuencia del aprendizaje una vez eclosionado el pollo.

CONCLUSIONS

1. The population of carrion crow (*Corvus corone*) studied in Guadix (Granada, Spain) shows a similar cooperative breeding system to that found in the only cooperative population of the species described at the moment (La Sobarriba, Spain). The main difference between both is the re-nesting rate after nest depredation, which in Guadix is almost nonexistent.

2. No benefits related to group size have been detected in the cooperative population of carrion crow studied in Guadix. On the contrary, there is a positive correlation between group size and the number of starved nestlings.

3. Meteorological factors (maximum temperature, minimum temperature, and precipitation) studied at the different stages of the reproductive period of carrion crow in the population of Guadix showed a similar influence on reproductive success to that of biotic factors.

4. In our review of animal behaviours that imply any kind of parasitism of parental care, a new term is proposed: "parental-care parasitism" that we define as an interaction in which an individual (the parasite) obtains reproductive benefits while reducing or completely eliminating the costs of parenting by exploiting any type of offspring care provided by other individuals (the hosts). This new term entails a new classification based on the costs produced by parasitism to hosts instead of the taxa-based classification that is used at the moment. The classification that we proposed includes parasitic behaviours sought by the offspring for the first time.

5. In our review of parental-care parasitism we show that in many of the described parasite-host systems, adaptations and counter-adaptations to the

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parasitism could exist, what indicates that in some of these systems an arms race is also occurring

6. Parasitism rate of great spotted cuckoo (*Clamator glandarius*) on magpie (*Pica pica*) and carrion crow during years 2007 to 2009 shows differences between the populations of Guadix and Sobarriba. In Guadix parasitism rates have augmented equally in both hosts, probably due to an increase of cuckoo density in the area. But in Sobarriba, parasitism rate on carrion crow has increased while in magpie has not changed.

7. Crows do not preferentially feed parasitic nestlings starving their own nestlings, as it happens in most avian host species. Adult crows preferentially feed those nestlings closer to the adult, that respond earlier, and that beg at a higher intensity, feeding preferentially crow nestlings.

8. Great spotted cuckoo nestlings, when parasitizing carrion crow's nests, do not manage to get more food from their foster parents than host nestlings, in spite of their higher begging intensity.

9. Great spotted cuckoo begging calls vary depending on host species. The calls differ in the number of notes per call, but do not mimic host nestlings begging calls. A cross-fostering experiment allowed us to determine that the differences found are not due to genetic factors, but seem to be in accordance with a modification of the begging call as a consequence of a learning process after hatching.

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