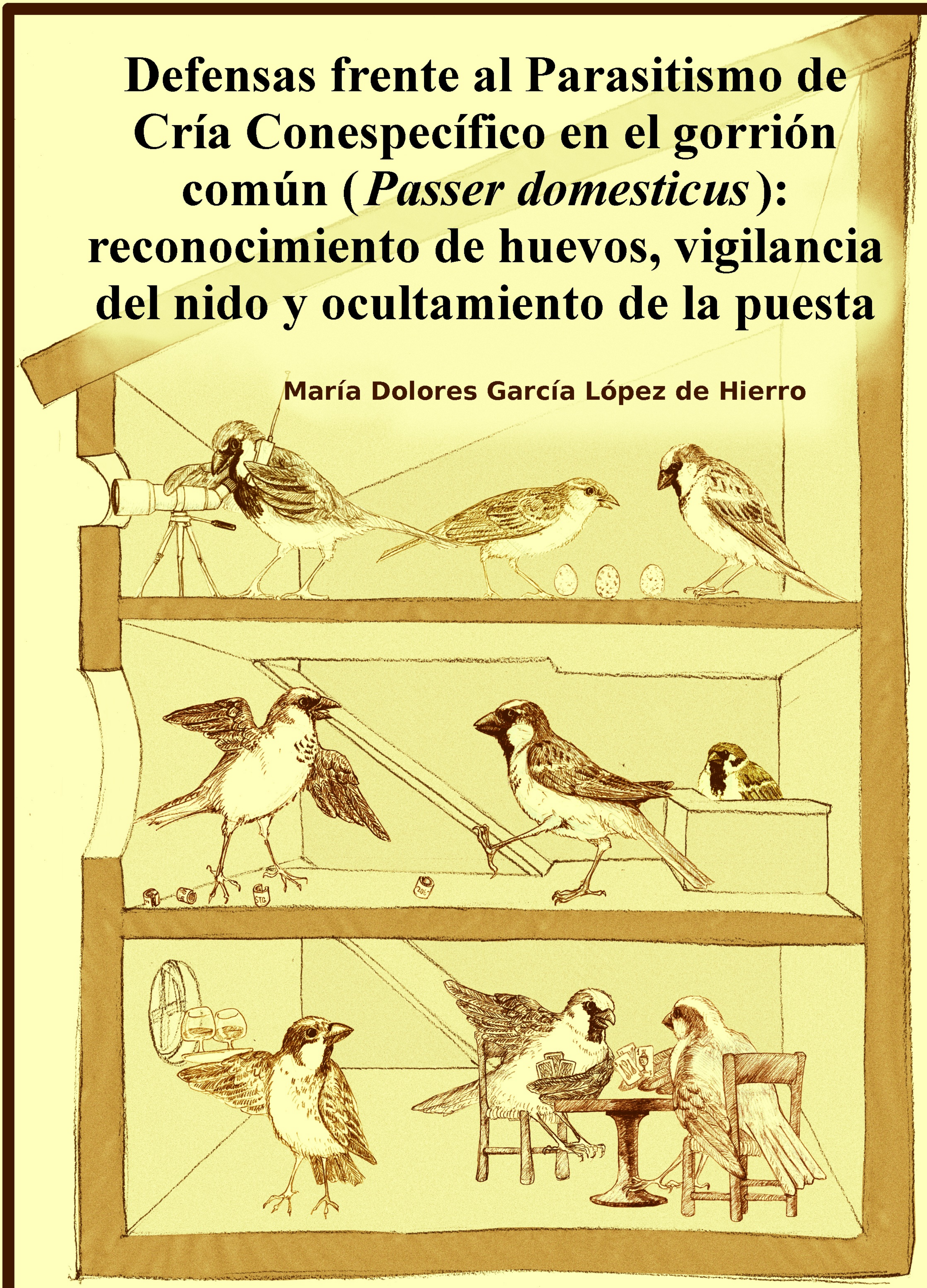
Defensas frente al Parasitismo de Cría Conespecífico en el gorrión común (*Passer domesticus*): reconocimiento de huevos, vigilancia del nido y ocultamiento de la puesta

María Dolores García López de Hierro



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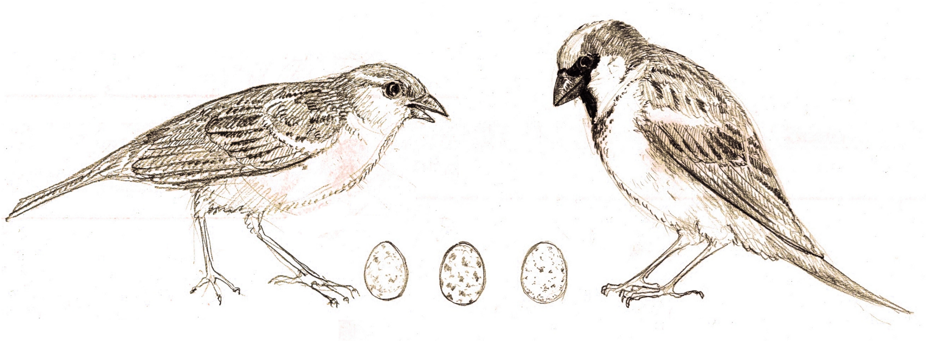

María Dolores García López de Hierro

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Defensas frente al Parasitismo de Cría Conespecífico en el gorrión común (Passer domesticus): reconocimiento de huevos, vigilancia del nido y ocultamiento de la puesta

Memoria presentada por Dña. María Dolores García López de Hierro para optar al Grado de Doctor por la Universidad de Granada.

Directores: Doctoranda:

Dr. Gregorio Moreno Rueda Dr. Marcos Moleón Páiz María Dolores García López de Hierro

En Granada, a Julio de 2009

“Y aunque intentó parecer adecuadamente severo ante sus alumnos, Pedro Gaviota les vio de pronto tal y como eran realmente, sólo por un momento, y más que gustarle, amó aquello que vio. ¿No hay límites, Juan?, pensó, y sonrió. Su carrera hacia el aprendizaje había empezado.”

Richard Bach. Juan Salvador Gaviota.

Contenidos

Lista de Manuscritos

I. **Pigment limitation and female reproductive characteristics influence egg shell spottiness and ground colour variation in the house sparrow (*Passer domesticus*)**
María Dolores García López de Hierro & Liesbeth De Neve
En revisión en Journal of Ornithology

II. **Egg-spot pattern rather than egg colour affects conspecific egg rejection in the house sparrow (*Passer domesticus*)**
María Dolores García López de Hierro & Gregorio Moreno-Rueda
Aceptado en Behavioral Ecology and Sociobiology

III. **Nest defence and egg rejection in the house sparrow (*Passer domesticus*) as protection against conspecific brood parasitism**
María Dolores García López de Hierro & Peter G. Ryan
Behaviour 145, 949-964

IV. **Egg covering behavior in the house sparrow (*Passer domesticus*) is a consequence of carrying feathers by males to insulate the nest**
María Dolores García López de Hierro & Peter G. Ryan
En preparación

Abstract

This thesis deals with behaviours happening during bird reproduction in the framework of brood parasitism: recognition and rejection of foreign eggs, nest defence, and egg covering.

Hosts show several defences to reduce the costs of parasitism, including defending their nests against parasitic females, and the recognition and rejection of parasitic eggs. The egg recognition and rejection is based in egg features. Several non-mutually exclusive hypotheses attempt to explain intraspecific egg variability in birds. A function of variability in egg colour and spot pattern may be to facilitate egg recognition of foreign eggs in species with interspecific or conspecific brood parasitism. Therefore, brood parasitism could be a selective pressure for each female to have a type of egg that permits recognition. Nevertheless, variation in egg colour between females is due to a combination of genetic, environmental and maternal influences. The extensive between-female variation in egg colouration, compared with the low within-clutch colour variation found in numerous studies, suggests that, in general, egg colour has an important genetic component. Beside of this, egg colour is probably also affected by environmental conditions and/or female physical condition. With regard to the hypothesis that egg colouration may signal female physical condition, a growing number of studies provide support to the hypothesis that the deposition of the antioxidant pigment biliverdin in the eggshell may depend on the higher antioxidant capacity of laying females, and thereby be indicative of female quality. Due to the pro-oxidant properties of protoporphyrins, it has been proposed that they could either signal female quality because increased pigmentation would indicate oxidative tolerance or, alternatively, be an indicator of poor condition, since high levels of protoporphyrins produce physiological stress that may be reflected in females' condition. In the present thesis we investigated the egg colour patterns of the same females over several consecutive years in a captive population of house sparrows (Passer domesticus). The objectives were (1) estimate the importance of genetic influences, (2) study whether pigment deposition may be limited for laying females, and (3) explore whether indicators of female quality (i.e. clutch size) affected egg colour patterns. We analyse the effect of relative size in experimental parasitic eggs compared to the host eggs on egg recognition in this species. In addition, we modified egg ground colour and the spot pattern to determine the influence of these characteristics on egg rejection. Furthermore, we examine whether egg rejection increases when more than one egg characteristic is modified ("stimulus summation").

On the other hand, both nest defence and the recognition and rejection of parasitic eggs are costly strategies for the hosts, because time invested in nest guarding is lost to other functions, such as foraging. Moreover, the process of recognising and rejecting parasitic eggs may lead to rejection costs, in which a host may inadvertently expel one of its own eggs during the course of rejecting parasitic ones. These costs of parasitism have been studied and received much attention predominantly in the context of the coevolutionary arms-race between obligate brood parasites and their hosts (interespecific brood parasitism). In some of these host species, nest defence and egg rejection are positively correlated, but in others they are antagonistic responses due to the costs involved. In this thesis we test whether the presence of an intruding conspecific female generates an additive stimulus or whether nest guarding and egg rejection are antagonistic responses.

Otherwise, another antiparasitic defence could be covered the eggs to hide information about the nest content and stage (i.e. egg laying, start of incubation) making the nest less attractive to other females. Nevertheless, other hypotheses exist to explain the egg covering behaviour

like thermoregulation, reducing predation, reducing hatching asynchrony, or hiding information about the female fertile period. In a population of house sparrow (Passer domesticus) located on Dassen Island (South Africa), a high proportion of sparrows build domed nests in the branches of trees. The typical tree nest in Dasen Island is a more or less spherical structure where the nestcup is composed by a lot of feathers. The feathers are also part of the basin where the eggs are deposited, and it is usual to find them covering the eggs. We examined the specific time pattern of egg cover during the egg-laying sequence, daily and breeding season to test the predictions for brood parasitism, thermoregulation, nest predation, hatching asynchrony, and hide information about the their fertile period hypotheses. We explored whether carrying feathers is part of the male courtship display, is an indicator of male phenotypic or genetic attributes, or an indicator of male parental care.

Our results showed the eggs color pattern is determine for the females identity, suggesting the existence of a rank of variability of these features due to genetic factors in the house sparrows. Furthermore, egg ground colour and the colour intensity and size of spots diminished according to the position in the laying sequence, suggesting a limited capacity to deposit these pigments for each reproductive event. Moreover, young females and females with larger clutches laid more densely spotted eggs, with more intensely coloured and larger spots, as well as a larger proportion of eggs with a bluish ground colour, suggesting that both pigmentations may be related to female physical condition. Our results also indicated that the distribution of spots is the egg characteristic less variable within females.

We found that egg rejection is not affected by relative egg size between the species' own eggs and the experimental parasitic egg. However, the change in the spot pattern proved to exert the highest influence on egg rejection (32.4% of trials), significantly higher than when only egg colour was changed (3.8%). Probably, the low illumination inside hole-nests favours the use of spot patterns vs egg colour in the egg-recognition process. Therefore, our results suggest that brood parasitism may be a pressure favouring the maintenance of spotted eggs among hole-nesting birds.

However, nest guarding was not related to egg recognition and rejection. Egg rejection did not appear to depend on the probability of nests being parasitised or on an inability to assume the costs associated with nest guarding/defence and with egg rejection.

On the other hand, egg covering in the house sparrow is not related to the risk of conspecific brood parasitism, external environmental variables, or to the risk of predation. It neither prevents hatching asynchrony, nor hides information about female fertile period. Nevertheless, the amount of nest feathers appears to be related to internal nest temperature. The carrying feathers behaviour is primarily performed by males, and the amount of feathers increased significantly during the incubation period and with newly hatched chicks, when more important is thermoregulation. When males brought feathers called to females and showed typical displays. Normally females were watching males. Although the amount of feathers in the nest was not correlated with other parental cares, it positively influenced the investment in reproduction by females (i.e. clucth size). We suggest that carrying feathers could be a kind of parental care, enhancing the insulating quality of nest and so reducing the trade-off between the energy needs to thermoregulation and the energy needs to adults' survival. This behavior seems to be moreover interpreted by females as a signal of male quality, consequently conditioning the reproductive investment of the former.

Resumen

En esta tesis doctoral se han estudiado comportamientos que se producen durante la reproducción de algunas especies de aves en el marco del parasitismo de cría conespecífico (PCC): el reconocimiento y el rechazo de los huevos extraños, la defensa del nido y el ocultamiento de la puesta. El PCC es una estrategia reproductiva que consiste en la puesta de huevos de las hembras parásitas en nidos de conespecíficos por no poder asumir los costes de la reproducción o por disminuir los costes asociados a los cuidados parentales.

La gran variación en coloración existente en los huevos de diversas especies de aves ha despertado tradicionalmente el interés de numerosos biólogos evolutivos desde el siglo XIX, los cuales, especialmente en las últimas décadas, han propuesto múltiples hipótesis para intentar comprender los patrones encontrados. Una de estas hipótesis propone que el parasitismo de cría ejercería una presión selectiva que favoreciese un tipo de huevo para cada hembra facilitando, así el aprendizaje de sus características y el reconocimiento y rechazo de huevos que difieran de ellas. No obstante la variabilidad del tipo de huevo entre hembras se debe a una combinación de factores genéticos, ambientales y a la influencia materna.

La variabilidad de las características de los huevos entre hembras se debe a una combinación de factores genéticos y ambientales. La amplia variabilidad de la coloración de huevos que existe entre las hembras de una misma especie, en comparación con la baja variabilidad dentro de una puesta, sugiere que, según muestran numerosos estudios, el color del huevo tiene un componente genético. Aún así, la coloración de los huevos también está afectada en parte por las condiciones ambientales. La biliverdina y la protoporfirina son los principales pigmentos responsables de la coloración de los huevos en las aves. La biliverdina es el pigmento responsable de los colores azul y verde, mientras que la protoporfirina es responsable de los colores rojizo y marrón. La biliverdina es un pigmento con importantes propiedades antioxidantes, mientras que la protoporfirina es un pro-oxidante (genera radicales libres). Basándose es estas propiedades de los pigmentos, recientemente se ha propuesto que las hembras pueden señalizar su condición por medio de la coloración de los huevos, hembras en buena condición pudiendo invertir más cantidad de biliverdina en la cáscara de sus huevos. Respecto a la protoporfirina, se ha propuesto que también puede servir como indicador de la condición de las hembras, bien porque una mayor cantidad de este pigmento podría mostrar su tolerancia oxidativa, o bien porque mostraría la mala condición de las hembras ya que altos niveles de protoporfirina indicarían estrés fisiológico.

En esta tesis doctoral se estudió (I) el patrón de coloración a lo largo de varios años consecutivos de las mismas hembras de gorrión común (Passer domesticus) de una población mantenida en cautividad. Además, se analizó (II) el efecto del tamaño, y del color y el patrón de las motas (tamaño y densidad) de los huevos sobre el reconocimiento y rechazo de huevos extraños, así como si la variación de dos características en el mismo huevo incrementa la frecuencia de rechazo debido al efecto llamado “suma de estímulos”.

Por otro lado, una de las estrategias seguidas para evitar los costes del parasitismo es impedir que éste se produzca mediante la vigilancia del nido y el ataque y expulsión de las hembras potencialmente parásitas. No obstante, la defensa del nido es una estrategia costosa para los hospedadores, ya que el tiempo invertido en guardar y defender el nido se resta del tiempo necesario para desarrollar otras funciones biológicas. El rechazo de huevos parásitos también es costoso al producirse la expulsión de huevos propios por error. En algunas especies, la defensa del nido y el rechazo de huevos están correlacionadas positivamente, pero en otras son respuestas antagónicas debido a la suma de los costes involucrados en cada

estrategia. En esta tesis doctoral se estudió (III) si la presencia de una hembra conespecífica de gorrión común cerca del nido de los hospedadores incrementaba la frecuencia de rechazo de huevos introducidos, o si por el contrario las parejas que presentaron un mayor grado de defensa de los nidos rechazaban con menor frecuencia.

Otra de las defensas frente al parasitismo de cría es cubrir la puesta con material del nido, ocultando información sobre el contenido del nido y la fase del evento reproductor (periodo de puesta o incubación). No obstante, existen otras hipótesis que pueden explicar el cubrimiento y ocultamiento de la puesta: termorregulación, evitar la depredación, reducir la asincronía de eclosión, u ocultar información sobre el periodo fértil de las hembras a los machos. En una población de gorrión común localizada en Dassen Island (Sudáfrica) con nidos construidos en los árboles y cuyas plumas cubren la puesta frecuentemente, se examinó (IV) el patrón de cubrimiento de huevos durante la secuencia de puesta, a lo largo del día y durante la temporada de cría, para comprobar cuál podría ser la función de este comportamiento según las hipótesis anteriores. Además, se estudió si el transporte de las plumas que forman el nido y cubren la puesta formaba parte del cortejo de los machos, y si este comportamiento podría indicar la calidad de los machos y su inversión en los cuidados parentales.

Los resultados mostraron que el patrón de coloración de los huevos estuvo determinado por la identidad de las hembras, lo que sugiere que en el gorrión común estas características se mantienen dentro de un rango de variación debido a factores genéticos. Por otro lado, tanto el número, tamaño e intensidad de color de las motas como la intensidad del color de fondo disminuyen con el orden de puesta, lo que indicaría que la deposición de pigmentos puede estar limitada en cada evento reproductor. Las hembras de esta especie que tienen un mayor tamaño de puesta, y no son de edad avanzada (a partir de cuatro años), tuvieron huevos con mayor número de motas, de mayor intensidad de coloración y que fueron de mayor tamaño. Además pusieron una mayor proporción de huevos azulados. Estos resultados sugieren que la deposición de pigmentos en la cáscara de los huevos en el gorrión común podría estar relacionada con la condición de las hembras. La densidad de motas es la característica que se encuentra menos influenciada por factores externos, ya que mostró menor varianza dentro de cada hembra.

El rechazo de huevos parásitos en el gorrión común no estuvo determinado por las diferencias en el tamaño ni en el color entre los huevos del hospedador y los huevos parásitos, pero sí por el patrón de las motas. La modificación del patrón de motas generó hasta el 38 % de rechazo, mientras que el cambio en el color de los huevos tan sólo dio lugar a un 3,8 %. Probablemente, la baja iluminación que existe dentro de los nidos de esta especie favorece el uso del contraste del patrón de motas sobre el fondo de los huevos en el proceso de reconocimiento de huevos parásitos. Según este resultado, el PCC podría actuar por tanto, como presión selectiva favoreciendo el mantenimiento de las motas en los huevos de esta especie.

Por otro lado, ni la presencia de una hembra conespecífica cerca del nido, ni el nivel de defensa del nido, alteraron la probabilidad de rechazo de huevos parásitos. Por tanto, el gorrión común mostró una defensa generalizada del nido con ausencia de estrategias particulares contra el PCC.

En el gorrión común, el cubrimiento de los huevos no parece tener la función de evitar el parasitismo de cría o la depredación, ni de disminuir la asincronía de eclosión u ocultar información sobre el periodo fértil de las hembras. Por el contrario, la cantidad de plumas que forman el nido sí parece estar relacionada con su termorregulación interna, para mantener el calor y permitir que los padres pasen más tiempo fuera del nido, ya que esta cantidad aumentó de forma significativa durante el periodo de incubación y con pollos recién eclosionados (fases del evento reproductor con mayor requerimiento térmico).

Teniendo en cuenta que las plumas que forman parte de los nidos fueron transportadas por los machos, este transporte podría ser en sí mismo un tipo de cuidado parental que podría indicar la calidad de los mismos. El transporte de plumas al nido por parte de los machos de gorrión común podría ser un rasgo seleccionado sexualmente, ya que las hembras incrementan su inversión reproductiva (tamaño de puesta) en respuesta a un mayor transporte de plumas.

Estructura de la Tesis

La tesis doctoral que se presenta consta de dos bloques principales. A lo largo del primer bloque se realiza una introducción general en la que se expone el marco teórico en el que se encuadra el trabajo presentado. En primer lugar, se discute resumidamente sobre la definición y tipos de parasitismo de cría, y se exponen las distintas hipótesis que intentan explicar el origen del parasitismo de cría conespecífico en aves. Se describen los tipos de costes que genera este tipo de parasitismo a los hospedadores, y por consiguiente, las defensas que han desarrollado los hospedadores frente a él. Se incluye un resumen de los conocimientos que se tienen de la especie de estudio (el gorrión común *Passer domesticus*) en relación con el trabajo que se desarrolla posteriormente, y se abordan sus aspectos comportamentales que nos han llevado a la realización de los diversos estudios que se presentan en esta tesis doctoral. En el apartado de Material y Métodos que se expone en este primer bloque se destacan los aspectos más importantes y generales de la metodología empleada para la realización de la tesis. Para los aspectos más concretos, los métodos utilizados se especifican con más detalles en cada uno de los manuscritos (ver más abajo). En el apartado de Resultados y Discusión se exponen los resultados más destacados encontrados en los estudios realizados, los cuales se discuten de forma resumida. Posteriormente, se exponen las conclusiones alcanzadas y una serie de sugerencias para futuros estudios. Al finalizar se encuentra un listado de toda la bibliografía citada en este primer bloque.

En el segundo bloque se presentan los cuatro manuscritos resultantes de esta investigación, en los que se describen los trabajos realizados con mucho más detalle. El primero de los manuscritos aborda cuáles son los posibles factores que influyen sobre la variabilidad de las características de coloración de los huevos en la especie de estudio. El segundo manuscrito describe una serie de experimentos en los que se modifican diversas características de coloración de los huevos, y se examina cómo influyen sobre el comportamiento de rechazo de los huevos extraños. En el tercer y cuarto manuscrito se abordan, también experimentalmente, otros dos tipos de defensa frente al parasitismo, la defensa del nido y su relación con el rechazo de huevos parásitos (Manuscrito III), y el ocultamiento de la puesta (Manuscrito IV).

Facilitar la propagación y evolución del conocimiento científico es el argumento fundamental que justifica la organización propuesta en la presente tesis. En consecuencia, publicar los principales resultados y conclusiones de cada apartado como artículos independientes en revistas de carácter científico constituyó una prioridad desde el principio. Para ello, cada uno de los manuscritos se estructuró en general siguiendo las secciones que definen la fisonomía convencionalmente aceptada para una publicación científica: “introducción”, “material y métodos”, “resultados”, “discusión” y “referencias”, lo que los hace plenamente autónomos en su entendimiento.

Introducción General

Parasitismo de cría: Definición y Tipos

El parasitismo de cría es un tipo de interacción biológica entre dos organismos en la que uno de ellos (el parásito) explota los cuidados parentales del otro (el hospedador). El parasitismo de cría aparece en varios grupos de vertebrados (peces, Sato, 1986; Baba et al., 1990; aves, Payne, 1977; Rothstein, 1990; Payne, 1997; Davies, 2000; Yom-Tov, 2001), y en varios órdenes de insectos, como Himenoptera (Zamora-Muñoz et al., 2003; Fanelli et al., 2005), Coleoptera (González-Megías & Sánchez-Piñero, 2003; Rasa & Heg, 2004), o Heteroptera (Mónaco et al., 1998).

El parasitismo de cría puede ser **facultativo**, si el parásito es capaz de criar a parte de su descendencia además de parasitar a otros individuos (Payne, 1997), u **obligado** si toda la descendencia del parásito es criada por los hospedadores (Wyllie, 1981).

Si el parasitismo de cría se produce entre individuos de diferentes especies, se denomina **parasitismo de cría interespecífico** (PCI). Este tipo de parasitismo se ha detectado en unas cien especies de aves parásitas (Davies, 2000). En el PCI, el parásito puede ser **especialista**, si utiliza una o muy pocas especies hospedadoras, o **generalista**, si éste parasita a un gran número de especies (Friedman, 1971). En cambio, si parásito y hospedador pertenecen a la misma especie, se trata de **parasitismo de cría intraespecifico o conespecífico** (PCC). Este tipo de parasitismo se encuentra bastante extendido en aves con pollos nidífugos o especies coloniales (Rohwer & Freeman, 1989; Arnold & Owens, 2002). Hasta la fecha, se han encontrado 234 especies en 16 órdenes de aves en los que se produce PCC (Yom-Tov, 2001).

Orígenes del Parasitismo de Cría Conespecífico en aves

El PCC apareció en numerosos linajes de forma independiente (revisión en Petrie & Møller, 1991; Davies, 2000). Modelos matemáticos sugieren que el PCC es un paso evolutivo intermedio entre una estrategia reproductiva en la que los padres realizan todos los cuidados parentales y el PCI obligado (Cichoń, 1995; Yamaguchi, 1995; Magali & Sorci, 2001). No obstante, otros estudios concluyen que en todos los casos de PCI obligado en aves altriciales (aves en las que los pollos necesitan cuidados parentales durante largo tiempo), probablemente este tipo de estrategia reproductiva evolucionó directamente sin tener como paso intermedio al PCC (Slagsvold, 1998; Yom-Tov & Geffen, 2006).

Actualmente existen varias hipótesis no mutuamente excluyentes que intentan explicar el origen y el valor adaptativo del PCC (revisión en Yom-Tov, 1980; Andersson, 1984; Eadie et al., 1988; Petrie & Møller, 1991; Sorenson, 1991; Rothstein & Robinson, 1998; Davies, 2000; Lyon & Eadie, 2008):

1- "La mejor opción dentro de lo malo"- Las hembras ponen huevos parásitos cuando los factores ambientales o fenotípicos limitan otro tipo de reproducción, o cuando las condiciones ambientales son tan desfavorables que las perspectivas de éxito reproductor cuidando de sus propios pollos son bajas. Un ejemplo del primer caso es cuando las hembras pierden su nido durante el periodo de puesta y optan por depositar los huevos en los nidos de otras hembras. En estos casos, las hembras que optan por parasitar otros nidos verían aumentada su eficacia biológica respecto a la eficacia que hubiesen tenido al realizar su propia puesta o no reproducirse esa temporada.

2- "Incremento de la fecundidad"- Esta hipótesis considera que este tipo de parasitismo sería una estrategia adicional y simultánea a la del cuidado de su progenie. Consiste en que algunas hembras pondrían huevos en otros nidos para disminuir algunos de los

costes asociados a los cuidados parentales (estrategia mixta), como el coste de incubación, el número de pollos que alimentar, la competencia en el nido, o el riesgo de perder toda la descendencia por depredación, maximizando así su éxito reproductor.

3- "Parásitos especialistas"- Se daría en casos en los que, dentro de una misma especie, existen individuos (hembras) que no cuidan de su propia progenie y utilizan sólo una estrategia de parasitismo Estas hembras conseguirían una mayor eficacia biológica a lo largo de la vida cuando existe una baja proporción de ellas en la población, debido a las ventajas de evitar todos los cuidados parentales y el consecuente aumento de su fecundidad a lo largo de sus vidas (invierten más en fecundidad porque no tienen costes asociados a la reproducción). Sin embargo, como estas hembras parásitas dependen completamente de las parejas nidificantes para sacar adelante a su descendencia, se produciría una presión selectiva de frecuencia-dependencia negativa que estabilizase la frecuencia de hembras parásitas y no parásitas en la población (estado mixto de estabilización evolutiva). No obstante, hasta hoy ningún estudio ha demostrado la existencia de estas hembras (Lyon & Eadie, 2008).

Sorenson (1991) publicó un modelo donde conceptualiza sobre cuatro opciones reproductivas en las que las hembras pueden criar a sus propios pollos o no: a) si se ocupan de sus propios pollos, pueden a su vez a.i) poner huevos en otros nidos o a.ii) no hacerlo; b) si no crían a sus propios pollos, pueden b.i) optar por ser parásitas o b.ii) por no reproducirse. Estas opciones serían "decididas" por cada hembra en cada estación de cría, y la "decisión" óptima dependería del contexto en el que se encuentra cada hembra en un año determinado. Según el modelo conceptual de Sorenson (1991), cuando el éxito reproductor de una hembra que cría a su propia descendencia podría ser bajo y/o los costes asociados a la reproducción son altos, las hembras llevarían a cabo estrategias que impliquen una baja inversión reproductiva (no criar o poner huevos parásitos). Sin embargo, cuando las perspectivas son buenas, las hembras aumentarían su inversión reproductiva tanto maximizando la inversión en sus propios nidos, como parasitando otros nidos. Por lo tanto, la estrategia reproductiva óptima supondría una decisión continua basada en condiciones externas e internas de la hembra. Este contexto implica que ser parásita es una opción para todas las hembras de una población y que se trata de un comportamiento plástico. Observaciones empíricas y trabajos realizados a largo plazo con individuos marcados muestran que las mismas hembras varían entre las opciones reproductivas descritas anteriormente a lo largo de los años, apoyando la idea de que el PCC es un comportamiento plástico (Heusmann et al., 1980; Eadie, 1989; Sorenson, 1991; Lyon, 1993; Forslund & Larsson, 1995; McRae, 1998; Åhlund & Andersson, 2001).

Lyon & Eadie (2008) proponen una modificación de la estructura conceptual de las hipótesis que explican el origen y valor adaptativo del PCC, basada en los tres componentes fundamentales de la eficacia biológica que influyen sobre la inversión reproductiva óptima: (a) fecundidad actual, (b) supervivencia de la descendencia y (c) supervivencia de los adultos (y, por tanto, la fecundidad futura). Esta modificación se basa en que los compromisos entre los distintos componentes de la eficacia biológica varían entre las distintas estrategias reproductivas de las hembras, y según las condiciones ecológicas, sociales y/o fisiológicas, en las que se encuentran las hembras. Por ejemplo, utilizarían una estrategia de solo parasitismo aquellas hembras que no sean capaces de asumir los costes reproductivos (incubación, alimentación de nidada, etc.), como hembras jóvenes, inexpertas o con un elevado estrés fisiológico (Eadie, 1989; Lank et al., 1989; Semel & Sherman, 2001; Sorenson, 1991, 1993; Weigmann & Lamprecht, 1991), hembras que pierden sus nidos durante el periodo de puesta (Emlen & Wrege, 1986; Eadie, 1989; Lank et al., 1989; Stouffer & Power, 1991; McRae 1997; Sandell & Diemer, 1999), o no tienen lugar para nidificar (Eadie, 1991; Gowaty & Bridges, 1991; Lyon, 1993). Por otro lado, las hembras también

pueden incrementar la fecundidad total al poner huevos parásitos antes de empezar su propia puesta (Møller, 1987; Sorenson, 1991; Lyon 1993; Brown & Brown, 1998; McRae, 1998; Åhlund & Andersson, 2001). En resumen, las hembras pueden basar su decisión de nidificar o poner todos sus huevos de forma parásita en función del éxito que tendrían sus propios nidos en relación al éxito que tendrían los huevos parásitos en la población (Lyon & Eadie, 2008).

Todo lo descrito anteriormente (excepto hipótesis de los parásitos especialistas), implicaría que en una población todas las hembras tendrían la capacidad de parasitar, por lo que el PCC estaría fijado genéticamente y se expresaría con plasticidad fenotípica. Sin embargo, la hipótesis de "parásitos especialistas" implicaría que en una población existen hembras que son parásitas siempre y hembras que no lo son, estando entonces el PCC determinado de forma polimórfica. En este caso, las hembras parásitas se mantendrían en una población cuando su eficacia biológica fuese al menos igual que la de las hembras nidificantes. Sin embargo, debido a los costes que produce el PCC en los hospedadores, al aumentar la frecuencia de PCC en la población, los hospedadores aumentarían las defensas frente al parasitismo de cría (ver más abajo). Este aumento de defensas antiparasitarias disminuiría la eficacia biológica de las hembras parásitas y, por consiguiente, la frecuencia de PCC. Puesto que es costoso mantener el nivel de defensa frente al PCC (ver más abajo), al disminuir la tasa de parasitismo disminuiría la inversión de los hospedadores en defensas antiparasitarias. Esta relación entre costes y beneficios tanto de PCC en las hembras parásitas como de defensas en los hospedadores, generaría ciclos de parasitismo y de estrategias antiparasitarias según el momento, o se generaría una presión selectiva de frecuencia-dependencia negativa que estabilizase la frecuencia de hembras parásitas y no parásitas en la población (estado mixto de estabilización evolutiva; revisión en Petrie & Møller, 1991; Lyon & Eadie, 2008).

Costes del Parasitismo de Cría Conespecífico en aves

Como normal general, en las interacciones parásito de cría-hospedador el hospedador ve disminuido su éxito reproductor como consecuencia del parasitismo, debido a la inversión en una descendencia con la que no está (totalmente) emparentada genéticamente, en detrimento de la suya propia (Yom-Tov, 1980). A parte de este coste, el parasitismo de cría puede reducir la eficacia biológica de los hospedadores por otras razones (revisión en Yom-Tov, 1980; Rohwer & Freeman, 1989; Petrie & Møller, 1991; Lyon & Eadie, 2008):

1- La puesta del hospedador puede verse reducida por la rotura o expulsión de uno de sus huevos cuando el huevo parásito es depositado (Lombardo et al., 1989).

2- Al aumentar el número de huevos en una puesta se reduce la eficacia de incubación, lo que incrementa el tiempo de incubación (mayores costes energéticos para los padres hospedadores, mayor riesgo de depredación, etc.; Thomson et al., 1998; Conway & Martin, 2000a, b) y disminuye el éxito de eclosión (Eadie, 1989; Weigmann & Lamprecht, 1991; Semel & Sherman, 2001; Gibbons, 1986; Nielsen et al. 2006a).

3- Se puede producir una disminución del número de pollos del hospedador que llegan a volar por el aumento de competitividad entre hermanos y el reparto de alimento (Møller, 1987; Brown & Brown, 1998; Lyon et al., 2002). Además, el aumento del tamaño de nidada reduce la tasa de crecimiento de los pollos y, por tanto, la probabilidad de supervivencia al salir del nido (Martin, 1987; Magrath, 1991).

4- Dado que el PCC incrementa el tamaño de nidada, los hospedadores pueden ver reducida su capacidad para reproducirse en el futuro, e incluso su supervivencia (Brown & Brown, 1998), debido a los costes de los cuidados parentales (Clutton-Brock, 1988). Como consecuencia de ello, en especies que sufren altas tasas de

parasitismo el PCC puede ser una presión selectiva que favorezca un menor tamaño de puesta (Power et al., 1989; Lyon, 1998).

Diversos estudios muestran evidencias del coste del parasitismo de cría al comparar el éxito reproductor de los individuos parasitados y no parasitados. Muchos de estos trabajos demuestran que los hospedadores sufren menor éxito de eclosión y menor número de pollos que llegan a volar (Møller, 1987; Lank et al., 1990; Romagnano et al., 1990; Brown & Brown, 1991, 1998; Sorenson, 1991; McRae, 1998; Semel & Sherman, 2001; Lyon et al., 2002). Además, Brown & Brown (1998) encontraron una menor tasa de supervivencia de los adultos que han sido parasitados en comparación con los no parasitados (aunque ver Lank et al., 1990, para el caso de aves con pollos nidífugos). No obstante, habría que tener en cuenta que las diferencias encontradas pueden ser el resultado de la menor calidad de los hospedadores o de sus territorios, lo que podría a su vez hacerles más vulnerables al parasitismo (Eadie, 1989; Lank et al., 1990). Sin embargo, en contra de este argumento, algunos parásitos seleccionan como hospedadores a individuos de elevada calidad reproductiva (Brown & Brown, 1991; Soler et al., 1995).

Por otro lado, estos costes se reducen o desaparecen si los hospedadores son aves precociales (con pollos nidífugos) en lugar de altriciales, ya que es posible que el aumento en el número de pollos genere un beneficio en la eficacia biológica de los hospedadores, por la disminución del riesgo de depredación de un pollo propio al aumentar el número de pollos con los que no están emparentados, o bien por el aumento de la vigilancia frente a los depredadores (Andersson, 1984; Eadie & Lumsden, 1985; Eadie et al., 1988; pero ver Amat, 1987). Estos beneficios podrían explicar la aceptación de los huevos parásitos así como la adopción de pollos no emparentados tras su eclosión (Eadie et al., 1988; Eadie, 1989).

Otro de los contextos en los que los hospedadores obtienen beneficios a través del PCC es el caso de la selección de parentesco. Si los hospedadores y parásitos están emparentados, los costes directos del PCC de los hospedadores podrían compensarse (al menos parcialmente) al aumentar su eficacia biológica inclusiva por el incremento de eficacia reproductiva de sus parientes parásitas. No obstante, sólo se obtendrían beneficios al aceptar los huevos de las hembras parientes si el PCC es poco costoso para los hospedadores (Lyon & Eadie, 2000). En caso contrario, la frecuencia de PCC disminuiría al aumentar la relación de parentesco entre parásitos y hospedadores ya que las hembras parásitas verían reducida su eficacia biológica indirecta más de lo que aumentaría su eficacia biológica directa (Zink, 2000). Estudios empíricos muestran que en algunas especies las hembras tienden a parasitar a parientes con más frecuencia (Andersson & Åhlund, 2000; Nielsen et al., 2006b; Waldeck & Andersson, 2006), aunque otros estudios indican que el parentesco entre parásitos y hospedadores no juega un papel importante en los patrones de PCC (McRae & Burke, 1996; Semel & Sherman 2001; Pöysä, 2004).

La existencia de “cuasi-parasitismo”, que consiste en que el huevo parásito es el resultado de la cópula del macho hospedador con la hembra parásita (Wrege & Emlen, 1987), varía la distribución de los costes del parasitismo. En estos casos, la hembra hospedadora, pero no el macho, es la que sufre los costes de la presencia de un huevo parásito en su nido. No obstante, el cuasi-parasitismo es muy raro en la naturaleza (revisión en Griffith et al., 2004).

Defensas frente al Parasitismo de Cría Conespecífico en aves

Con el fin de reducir los costes asociados al PCC, los hospedadores han desarrollado numerosas defensas (revisión en Davies, 2000) incluyendo el reconocimiento y rechazo de los huevos extraños (p.ej. Victoria, 1972; Rothstein, 1975, 1982), la defensa de los nidos contra los parásitos (Emlen & Wrege, 1986; Møller, 1987, 1989; Brown & Brown, 1989;

McRae, 1996) y el ocultamiento de la puesta (Clark & Robertson, 1981; Briskie & Sealy, 1988). A continuación revisamos en más detalle las diferentes estrategias:

Reconocimiento y rechazo de huevos

El rechazo de huevos parásitos basado en el reconocimiento de sus características es una defensa efectiva pero poco extendida en la mayoría de las especies que sufren PCC (Lyon & Eadie, 2008). La mayoría de estas especies son capaces de rechazar huevos conespecíficos si estos son depositados en los nidos antes de que los hospedadores comiencen su propia puesta, pero no después (Stouffer et al., 1987; Brown & Brown, 1989; McRae, 1995). El rechazo de huevos basado en el reconocimiento se produce al menos en dos grupos, gallinetas y fochas (Rallidae: Lyon, 1993, 2003; Jamieson et al., 2000) y tejedores (Ploceidae: Jackson, 1998; Lahti & Lahti, 2002). Estas especies presentan una alta variabilidad en las características de los huevos entre hembras, y el rechazo se produce con mayor frecuencia cuanto más difiera el huevo parásito de las características de los huevos del hospedador (Victoria, 1972; Lahti & Lahti, 2002; Lyon, 2003). El gorrión común (*Passer domesticus*) es otra de las especies capaz de reconocer y rechazar huevos conespecíficos, incluso tras haber comenzado su propia puesta (Kendra el al., 1988; Moreno-Rueda & Soler, 2001).

Según Rensch (1925), el reconocimiento de huevos basado en sus características puede producirse por discordancia (comparación de las características de los huevos y rechazo de aquéllos que difieren de los que sean mayoritarios en el nido) o por auténtico reconocimiento (los hospedadores aprenden las características de sus huevos, y reconocen la presencia de un huevo extraño aunque sus huevos estén en menor proporción). Por lo tanto, el auténtico reconocimiento implica el aprendizaje de las características de los huevos propios. Los estudios experimentales realizados muestran que las especies hospedadores presentan rechazo de huevos por auténtico reconocimiento (Victoria, 1972; Rothstein, 1975, 1978; Moksnes, 1992; Lotem et al., 1995; Sealy & Bazin, 1995; Peer & Sealy, 2001; Lahti & Lahti, 2002; Lyon, 2007).

El patrón de coloración y el tamaño de los huevos poseen una gran variación entre las especies de aves (revisión en Underwood & Sealy, 2002; Kilner, 2006). La variación en el patrón de coloración puede ser el resultado de presiones selectivas como el riesgo de depredación (Wallace, 1889; Lack 1958; Solís & de Lope, 1995; Lloyd et al., 2000; Blanco & Bortellotti, 2002; Sánchez et al., 2004; pero ver Tinbergen et al., 1962; Montevecchi, 1976; Götmark, 1992; Weidinger, 2001). Otra de las presiones selectivas que pueden influir sobre la coloración de los huevos es un proceso de selección sexual donde el color de los huevos indique la condición física de las hembras debido a las propiedades antioxidantes de la biliverdina (pigmento responsable de la coloración azul de los huevos: Moreno & Osorno, 2003; Moreno et al., 2006; Soler et al., 2005; Siefferman et al., 2006). No obstante, existen evidencias de que la cantidad de biliverdina invertida en algunas especies depende de determinadas condiciones ambientales, como la precipitación o la temperatura (Avilés et al., 2007).

La protoporfirina es el pigmento que dota de color marrón-rojizo a los huevos y es el que es utilizado para formar las motas. Este pigmento tiene propiedades pro-oxidativas (Afonso et al., 1999, Shan et al., 2000). Por ese motivo, se ha propuesto que la cantidad de protoporfirina podría mostrar la calidad de las hembras, de manera que un incremento de pigmentación estaría indicando la tolerancia oxidativa de las hembras (Moreno & Osorno, 2003). De forma alternativa, podría indicar una mala condición física, ya que altos niveles de protoporfirinas producirían estrés fisiológico que podrían reflejarse en la condición y respuesta fisiológica de las hembras (Martínez-de la Puente et al. 2007).

Por otro lado, Joseph et al. (1999) muestran que la cantidad de protoporfirina invertida en la cáscara de los huevos depende del tipo de dieta, en la cual puede faltar algún elemento esencial. Gosler et al. (2005) propusieron que la deposición de protoporfirinas servía para compensar la falta de calcio en la alimentación, de forma que estos pigmentos ocupaban las zonas más frágiles de la cáscara y que serviría para reducir la permeabilidad de los huevos y la pérdida de agua durante la incubación (Véase: Higham & Gosler, 2006; Sanz & García-Navas, 2009).

Otra de las presiones selectivas que puede dar lugar a la variabilidad en las características de los huevos es el parasitismo de cría (Freeman, 1988; Øien et al., 1995; Soler & Møller, 1996; Stokke et al., 1999, 2002, Davies, 2000; JJ Soler et al., 2000; Lahti 2005, 2006). En el parasitismo de cría interespecífico, la capacidad de reconocer y rechazar huevos parásitos por parte de los hospedadores basada en las características de los huevos, ha generado que las especies parásitas pongan huevos cada vez más semejantes a los huevos de los hospedadores (Moksnes & Roskaft, 1995; Davies, 2000). Por otro lado, los hospedadores desarrollarían la capacidad de poner huevos con características muy determinadas que dificultasen el mimetismo por parte de los parásitos (revisión en Davies, 2000) y que facilitase su reconocimiento y rechazo disminuyendo la posibilidad de error (Swynnerton, 1918; Davies & Brooke, 1989b; Soler et al., 2000). Esta interacción entre parásitos y hospedadores aumentaría la variabilidad de las características de los huevos (Stokke et al., 1999, 2002, Davies, 2000; Soler et al., 2000; Lahti, 2005, 2006).

Si el PCC es muy frecuente en una especie y genera un elevado coste para los hospedadores, esta estrategia reproductora podría tener el mismo efecto sobre las características de los huevos (Victoria, 1972; Collias, 1984; Freeman, 1988). Para que las características de los huevos puedan evolucionar en respuesta al parasitismo, un requisito imprescindible es que la variación fenotípica en los rasgos de los huevos tenga un componente genético. En apoyo de esta idea, Gosler et al. (2000) encontraron que, en una población natural de la carbonero común (Parus major), el patrón de los huevos se encontraba bajo control genético, explicando más del 80% de la variación de todas las características de color de los huevos estudiadas, y que la heredabilidad de los patrones está vinculada al sexo femenino en esta especie. Collias (1993) llegó a la conclusión de que la presencia o ausencia de motas en el huevo del tejedor común (Ploceus cucullatus) está controlada por más de un par de alelos autonómicos, pero, dada la gran variación en la abundancia de motas, su distribución y tipos, es probable que este patrón esté bajo control poligénico en esta especie.

Por lo tanto, el parasitismo de cría podría favorecer la aparición de un tipo de huevo para cada hembra dentro de una misma especie, de forma que se reduciría al máximo la variabilidad dentro de una puesta, y aumentaría la diferencia en el tipo de huevos entre las hembras de una población (Victoria, 1972; Collias, 1984; Freeman, 1988). De hecho, si el componente genético del color y el patrón de motas en los huevos favorece una baja variabilidad en estas características dentro de cada hembra, facilitaría su aprendizaje (Rothstein, 1978; Lotem et al., 1995), y serviría para detectar más fácilmente huevos que difieran de ellas reduciendo los costes de rechazo y errores de reconocimiento (Soler et al., 2000).

Entre las características de los huevos que podrían facilitar el reconocimiento y rechazo de los huevos parásitos se encuentran el tamaño (Payne, 1974; Marchetti, 2000), el color de fondo (Victoria, 1972; Moskat et al., 2008) y el patrón de motas (Soler et al., 2000). En el tejedor común, cada hembra pone un huevo diferente de las demás durante toda su vida, con diferentes colores de fondo, y presencia o no de motas (Victoria, 1972; Collias, 1984). Las hembras rechazan principalmente los huevos que difieran de los suyos en el color de fondo, y cuando el color de fondo de los huevos del parásito se encuentra dentro de la

gama de la puesta hospedadora, la presencia o ausencia de motas determina el rechazo (Victoria, 1972).

No obstante, el proceso de reconocer y rechazar huevos parásitos puede generar costes. Estos costes consisten en que los hospedadores pueden perder involuntariamente alguno de sus propios huevos en el transcurso del rechazo (costes de expulsión; Davies et al., 1996; Lotem & Nakamura, 1998; Røskaft & Moksnes, 1998), perder toda su puesta si la respuesta frente al parasitismo es el abandono del nido (Fenske & Burley, 1995; McRae, 1995; Moreno-Rueda & Soler, 2001), o bien sufrir errores de reconocimiento y expulsar algún huevo propio a pesar de que no hayan sido parasitados debido a que hayan visto una hembra parásita cerca de sus nidos (Davies & Brooke, 1988, 1989a; Davies et al., 1996). El compromiso existente entre los costes de rechazo y los costes del parasitismo podría ser el responsable de que, respecto al PCI, las especies hospedadoras en Europa tengan una frecuencia de rechazo entre 40 % y el 80 %, nunca del 100 % (Øien et al., 1995), y de que este tipo de defensa antiparasitaria sea poco frecuente en especies que sufren PCC (revisión en Petrie & Møller, 1991; Lyon & Eadie, 2008).

Defensa del nido

Otra de las estrategias para evitar los costes del parasitismo es impedir que éste se produzca mediante la vigilancia del nido y el ataque y expulsión de las hembras potencialmente parásitas (Emlen & Wrege, 1986; Møller, 1987; Brown & Brown, 1989; McRae, 1996). Por ejemplo, los hospedadores potenciales de los cucos (*Cuculidae*) generan gritos de alarma y ataques hacia las hembras de cuco cuando éstas se encuentran cerca de los nidos (Payne et al., 1985; Davies & Brooke, 1988; Briskie et al., 1992; Gill et al., 1997). Møller (1989) muestra que, en la golondrina común (*Hirundo rustica*), la defensa de los nidos reduce el riesgo de PCC.

El grado de defensa de los hospedadores frente a los parásitos varía, entre otros factores, en función del hábitat seleccionado por los hospedadores para nidificar (Røskaft et al., 2002a,b). Por ejemplo, las especies hospedadoras del cuco que sólo nidifican en los árboles o cerca de ellos, los hábitat donde el cuco parasita con más frecuencia, son más agresivas frente a la presencia de los modelos disecados de cuco que las especies que nidifican lejos de los árboles (Røskaft et al., 2002a,b). Por otro lado, la etapa del evento reproductor también influye sobre el grado de defensa de los nidos (p.ej. Moreno-Rueda, 2003). El parasitismo de cría se produce con mayor frecuencia durante el periodo de puesta de los hospedadores, con el fin de que el huevo parásito reciba el mismo tiempo de incubación que el resto de la puesta y se produzca un buen desarrollo embrionario (Yom-Tov, 1980; Petrie & Møller, 1991). Por lo tanto, cabe esperar que la defensa del nido sea mayor en esta etapa para evitar el PCC.

No obstante, la defensa del nido es una estrategia costosa para los hospedadores, ya que el tiempo invertido en guardar y defender el nido se resta del tiempo necesario para desarrollar otras funciones biológicas como la búsqueda de alimento. Así, por ejemplo, la tasa de defensa del nido por la hembra de golondrina es mínima durante el período de puesta de huevos, ya que durante este periodo las hembras ven constreñido su tiempo disponible para vigilar por los altos requerimientos energéticos que le supone la producción de huevos (Møller, 1987).

Defensa del nido y rechazo de huevos

En algunas de las especies hospedadoras, la defensa del nido y el rechazo de huevos están correlacionadas positivamente (Moksnes et al., 1990), pero en otros son respuestas antagónicas debido a los costes involucrados en cada estrategia (Neudorf & Sealy, 1992;

Soler et al., 1999; ver arriba). La presencia del parásito cerca del nido puede sugerir la posibilidad de ser parasitados, aumentando la tasa de rechazo de huevos (Davies & Brooke, 1988; Moksnes & Røskaft, 1989; Moksnes et al., 1993, 2000). Bártol et al. (2002) muestran que la presencia del cuco (*Cuculus canorus*) cerca del nido del carricero tordal (Acrocephalus arundinaceus) puede aumentar su tasa de rechazo porque se produce una suma de estímulos al observar al parásito cerca del nido y la presencia de un huevo extraño en la puesta (ver también Moksnes & Røskaft, 1989; Moksnes & Elbertø, 2006). Además, estos autores observaron que las parejas hospedadoras que rechazaban con mayor frecuencia los huevos experimentales fueron más agresivas frente al modelo disecado del parásito. Sin embargo, Moksnes & Røskaft (1989) no observaron ninguna relación entre el grado de agresividad y la tendencia a abandonar el nido en la bisbita común (Anthus pratensis), que es la respuesta frente al parasitismo más frecuente en esta especie. El único estudio experimental sobre la influencia de la presencia del parásito cerca del nido hospedador sobre el rechazo de huevos en el contexto de PCC se realizó con el estornino pinto (Sturnus vulgaris), pero no encontró ninguna influencia de la proximidad de un conespecífico sobre la respuesta de los hospedadores, que nunca rechazaron los huevos parásitos, incluso tras responder de forma agresiva frente al modelo (Moksnes & Elbertø, 2006).

Cuando la defensa del nido es suficientemente eficaz contra el parasitismo de cría, la selección natural podría favorecer una disminución del reconocimiento y rechazo de huevos parásitos, con el fin de reducir los costes totales de las defensas antiparasitarias (defensas antagónicas: Soler et al. 1999). Por lo tanto, los hospedadores que sufren parasitismo de cría podrían evitar ser parasitados al exhibir altos niveles de defensa contra el parásito durante el período de puesta (Folkers & Lowther, 1985; Neudorf & Sealy, 1992). Un alto nivel de defensa del nido puede asegurar el no haber sido parasitado, por lo que los hospedadores invertirían menos tiempo en revisar su puesta para detectar los huevos parásitos y se reducirían los costes asociados al rechazo de huevos (Davies & Brooke, 1988). Por ejemplo, Soler et al. (1999) muestran cómo en la urraca (*Pica pica*), una especie que sufre parasitismo de cría por parte del críalo (*Clamator glandarius*), capaz de reconocer y rechazar los huevos parásitos, las parejas con mayor frecuencia de rechazo de huevos presentan menor nivel de defensa y vigilancia del nido frente al modelo de críalo que aquellas parejas que aceptan más frecuentemente los huevos extraños.

Por lo tanto, ambos tipos de defensa antiparasitaria pueden estar correlacionadas de forma positiva (Moksnes et al., 1990; Bártol et al., 2002), o bien, debido a los costes asociados a cada tipo de defensa antiparasitaria, éstas pueden estar correlacionadas de forma negativa (Neudorf & Sealy, 1992; Soler et al., 1999).

Ocultamiento de la puesta

El ocultamiento de la puesta es un comportamiento común en numerosas especies (revisión en Champhell & Lack, 1985; Welty & Baptista, 1988). Algunos autores sugieren que uno de los beneficios del ocultamiento de huevos es la defensa de la puesta para evitar el parasitismo de cría (Clark & Robertson, 1981; Briskie & Sealy, 1988). En especies que sufren parasitismo de cría, las hembras parásitas suelen poner los huevos durante el periodo de puesta del hospedador, antes de que comience la incubación, o en los primeros días de incubación. Esto permitiría un buen desarrollo embrionario y que el pollo parásito sea uno de los primeros pollos en eclosionar, lo que le permite ser alimentado antes que el resto de los pollos que eclosionen después y ganar tamaño, con la consiguiente ventaja competitiva (Petrie & Møller, 1991; M Soler et al., 1998; Moreno-Rueda, 2006). Además, en caso de escasez de alimento suele morir el pollo más pequeño (Magrath, 1989; 1990; Stenning, 1996; Forbes et al., 2001). Por lo tanto, la eclosión temprana de los pollos parásitos asegura en mayor medida su supervivencia (Petrie & Møller, 1991; M Soler et al., 1998; Moreno-

Rueda, 2006). De esta manera, el ocultamiento de huevos podría servir para ocultar información sobre el contenido y fase del evento reproductor (periodo de puesta y comienzo de incubación), con lo que se consigue dificultar la puesta de un huevo parásito (Clark & Robertson, 1981; Briskie & Sealy, 1988).

Otros autores sugieren que el cubrimiento de la puesta tiene una función termorreguladora, favoreciendo el aislamiento térmico de la puesta y reduciendo la pérdida de calor (Bochenski, 1961; Caldwell & Cornwell, 1975; Haftorn, 1978). Existe un compromiso entre el tiempo invertido por parte de los padres para generar el calor necesario que permita el buen desarrollo embrionario o la termorregulación de los pollos recién eclosionados, y las necesidades energéticas de los adultos (p.ej. la búsqueda de alimento; Williams, 1996; Conway & Martin, 2000a, b). Un nido bien aislado y el cubrimiento de los huevos permite que el calor generado se mantenga durante más tiempo, lo que disminuye el gradiente de pérdida de calor con el medio ambiente (Haftorn, 1978; Skutch, 1983). Esto favorecería el éxito de eclosión (Caldwell & Cornwell, 1975) y reduciría el compromiso energético existente (Walsberg, 1981; Collias & Collias, 1984; Conway & Martin, 2000a, b).

Una estrategia para reducir el riesgo de depredación es cubrir la puesta con material de nido (Broeckhuysen & Frost, 1968; Götmark & Åhlund, 1984; Keller, 1989; Shimoda et al., 1994; Orizaola & Braña, 2003; Kreisinger & Albrecht, 2008), de forma que aparentaría estar vacío (Perrins, 1979). Diversos estudios, de hecho, muestran que el cubrimiento de la puesta disminuye el riesgo de depredación (Götmark & Åhlund, 1984; Salonen & Penttinen, 1988; Opermanis, 2004). Kreisinger & Albrecht (2008) comprobaron experimentalmente que las plumas y el material vegetal utilizados por el ánade azulón (*Anas platyrhynchos*) para cubrir la puesta tenían una clara función de ocultamiento y mimetismo, y las puestas que estaban cubiertas sufrieron menor riesgo de depredación al ser menos visibles a los depredadores.

Stenning (1995) sugiere que el cubrimiento de los huevos durante el periodo de puesta puede retrasar la incubación hasta la puesta del último huevo, y disminuir así la asincronía de eclosión, por las ventajas que ello implica para las hembras (véanse Slagsvold & Lifjeld, 1989; Slagsvold et al., 1994, 1995).

Por otro lado, en especies en las que se produce la deserción de algún miembro de la pareja tras la puesta de los huevos, las hembras podrían ocultar esta información a sus machos cubriendo los huevos y así ser ellas las primeras que abandonen la puesta, obligando a los machos a sacarla adelante mientras ellas emparejan con otro macho, o simplemente evitan los costes de la crianza de la nidada (Valera et al., 1997).

El cubrimiento de la puesta también puede estar relacionado con la selección sexual. Un rasgo comportamental normalmente relacionado con adornos morfológicos es el uso de materiales extraños durante la construcción del nido. Los machos de numerosos grupos de aves se han especializado en llevar materiales que proporcionan señales de su estatus o calidad genética (Borgia & Gore, 1986; Moreno et al., 1994; Gwinner, 1997; JJ Soler et al., 1998; Duffy & Gregory, 2002; Brouwer & Komdeur, 2004). La demanda de plumas como material de construcción del nido puede ser habitual en diversas especies de aves para conservar mejor el calor en el nido (p.ej Hansell, 1995, 2000). El uso de plumas con función de señalización se ha considerado siempre como una parte del cortejo de los machos (Collias & Collias, 1984; Borgia & Gore, 1986; pero véase en el caso de las hembras: Polo & Veiga, 2006). Por tanto, puede existir una relación entre la tasa de transporte de plumas por parte de un macho y el cubrimiento de la puesta como consecuencia de dicho transporte.

Especie Objeto de Estudio

El gorrión común (*Passer domesticus*) es un paseriforme granívoro comensal del hombre, originario de oriente próximo (revisión en Summers-Smith, 1988; Anderson, 2006). El gorrión común se extendió por las poblaciones humanas al mismo tiempo que el hombre fue domesticando los cereales y se produjo la expansión de la agricultura (revisión en Summers-Smith, 1988; Anderson, 2006). Se trata de una especie que nidifica normalmente en agujeros o en nidos cerrados construidos en las ramas de los árboles (Kulczycki & Mazur-Gierasinsk, 1968; Heij, 1986; Summers-Smith, 1988; Indykiewicz, 1991; Anderson, 2006). Pone normalmente 4-5 huevos (revisión en Summers-Smith, 1988; Anderson, 2006), que varían en tamaño, color de fondo, y patrón de motas (Seel, 1968; Lowther, 1988; Harrison, 1991). El tamaño de los huevos varía considerablemente dentro de una población, pero tiende a ser repetible para una misma hembra (Anderson, 2006), y no parece estar influenciado por el avance de la temporada de cría (Veiga, 1990; Anderson, 1998; pero ver Lowther, 1990), o el tamaño de puesta (Lowther, 1990; Veiga, 1990; Marcos & Monrós, 1994), aunque tiende a variar un poco dentro de una puesta debido a que el último huevo es diferente a los demás (Lowther, 1990; Marcos & Monrós, 1994). El color de fondo de los huevos varía desde el blanco puro hasta tonalidades azuladas, y su superficie está cubierta por motas de coloración marrón, de diverso tamaño y densidad. La distribución de las motas también varía considerablemente, pudiendo constar de una única mancha en la parte roma del huevo, hasta estar uniformemente distribuidas por toda la superficie (Seel, 1968; Lowther, 1988; Harrison, 1991).

El gorrión común es una especie colonial, siendo habitual que en la zona de nidificación de una pareja existan nidos conespecíficos adyacentes. Es esencialmente monógama con baja frecuencia de pollos extra-pareja (p.ej. Veiga & Boto, 2000). Esta especie sufre PCC en un rango del 0-10 % (Manwell & Baker, 1975; Kendra et al., 1988; Cordero et al., 1999) y muestra capacidad de reconocer y rechazar los huevos parásitos (Kendra et al., 1988; Moreno-Rueda & Soler, 2001). No obstante, el rechazo de huevos es muy costoso para los hospedadores, ya que durante el proceso de expulsión suelen romper hasta un 44,4 % de sus huevos, y pueden abandonar la puesta cuando han sido parasitados (Moreno-Rueda & Soler, 2001).

El gorrión común presenta altos niveles de agresividad frente a individuos (de la misma o de otras especies) que se encuentran cerca de sus nidos (revisión en Anderson, 2006). Cada miembro de la pareja defiende el nido frente a los individuos conespecíficos de su mismo sexo, y ambos lo defienden frente a individuos de otras especies sin diferenciar el sexo (Summers-Smith, 1958). Además, el grado de agresividad está positivamente correlacionado con la densidad poblacional (revisión en Anderson, 2006). En el gorrión común, las hembras invierten más tiempo en vigilar el nido durante la puesta de huevos, el momento con mayor riesgo de PCC, que durante la incubación o tras la eclosión de los pollos (Moreno-Rueda, 2003). En esta especie, la temperatura tiene un efecto positivo sobre los patrones de vigilancia de las hembras, ya que disminuye los requerimientos energéticos, permitiendo un menor requerimiento de tiempo en la búsqueda y obtención de alimento (Moreno-Rueda, 2003). Además, al aumentar el tamaño de puesta (y por tanto el valor reproductivo de la nidada), incrementa la vigilancia del nido por parte de la hembra (Moreno-Rueda, 2003).

Los nidos que se sitúan en los árboles son más o menos esféricos con una cúpula construida a base de material vegetal y plumas. La construcción de los nidos depende principalmente de los machos, siendo éstos los que transportan mayor cantidad de material (revisión en Anderson, 2006). Las plumas adquieren mayor protagonismo en la cúpula y en

la taza donde se depositan los huevos, y es habitual encontrarlas cubriendo la puesta y a los pollos pequeños (obs. pers.).

Justificación

Reconocimiento y rechazo de huevos parásitos

Como hemos explicado en la Introducción General, la variación en el patrón de coloración y el tamaño de los huevos entre las especies de aves puede ser el resultado de diversas presiones selectivas (Wallace, 1889; Joseph et al., 1999; Stokke et al., 1999, 2002, Davies, 2000; Soler et al., 2000; Moreno & Osorno, 2003; Gosler et al., 2005; Lahti 2005, 2006; Higham & Gosler, 2006). La mayoría de las especies de aves que nidifican en agujeros o nidos cerrados poseen huevos blancos e inmaculados (Wallace, 1889; Lack, 1958; Kilner, 2006), por lo que la aparición de pigmentos (biliverdina y protoporfirina) en los huevos del gorrión común podría ser resultado de alguna o varias de las presiones selectivas descritas anteriormente. Por ejemplo, la cantidad de biliverdina depositada en los huevos podría ser un indicador de la condición física de la hembra por sus propiedades anti-oxidantes, como ha sido demostrado en otras especies (Moreno & Osorno, 2003; Moreno et al., 2005, 2006; Siefferman et al., 2006; Krist & Grim, 2007; Jagannath et al., 2008; Soler et al., 2008). Además, la presencia de motas (acumulo de protoporfirina en diversas zonas de la cáscara de los huevos) podría indicar del mismo modo la calidad de las hembras (Moreno & Osorno, 2003), debido a las propiedades pro-oxidativas de este pigmento (Afonso et al., 1999, Shan et al., 2000). Altos niveles de protoporfirina producirían estrés fisiológico, por lo que sólo hembras en buena condición podrían soportar estos niveles (Moreno & Osorno, 2003), o bien la presencia de protoporfirina en los huevos reflejaría la baja condición de las hembras (Martínez-de la Puente et al., 2007). Aunque se han realizado diversos estudios sobre la función de la biliverdina en la cáscara de los huevos como señal de la condición de la hembra (Moreno et al., 2005, 2006; Siefferman et al., 2006; Krist & Grim, 2007; Jagannath et al., 2008; Soler et al., 2008), pocos estudios han abordado la cantidad de protoporfirina como señal de esta condición (Martínez-de la Puente et al., 2007; Sanz & García-Navas, 2009).

Por otro lado, la aparición de zonas pigmentadas en los huevos de esta especie puede ser resultado de la presión que ejerce el PCC y el reconocimiento y rechazo de huevos parásitos (Stokke et al., 1999, 2002, Davies, 2000; JJ Soler et al., 2000; Lahti 2005, 2006). En este caso, aquellas características que sean más repetibles en los huevos de una hembra y que se encuentren menos influenciadas por condiciones externas (p.ej. condiciones ambientales o la condición física de las hembras), y que se mantengan en un rango de variación limitado, facilitarían el proceso de aprendizaje de los huevos propios, y así poder reconocer y rechazar los huevos parásitos cometiendo menos errores y disminuyendo los costes de rechazo (revisión en Davies, 2000; Lyon & Eadie, 2008). Por tanto, cabe esperar que este tipo de características sean las más importantes en el proceso de reconocimiento de huevos parásitos.

Hasta la realización de esta tesis doctoral, no se había estudiado si la cantidad de pigmentos en la cáscara de los huevos (biliverdina y protoporfirina) está relacionada con la condición de las hembras en el gorrión común. Además, tampoco se había estudiado cuales de las características de los huevos que se encuentren menos influenciadas por condiciones externas, y cómo afectan al reconocimiento y rechazo de los huevos parásitos en esta especie.

Defensa del nido

En algunas especies, la presencia de una hembra potencialmente parásita cerca del nido de otros individuos aumenta la intensidad de defensa y agresividad, y genera que se revise más atentamente la puesta y, en caso de parasitismo, aumente la frecuencia de rechazo (Davies &

Brooke, 1988; Moksnes & Røskaft, 1989; Moksnes et al., 1990, 1993, 2000). Sin embargo, debido a los costes asociados a cada una de las estrategias antiparasitarias, en otras especies se produce una respuesta antagónica entre ambas estrategias antiparasitarias (Neudorf & Sealy, 1992; Hochberg, 1997; Soler et al., 1999). Como hemos explicado anteriormente, el gorrión común es una especie que defiende el nido de forma agresiva frente a individuos de la misma o de otras especies (revisión en Anderson, 2006). Además, es una especie que tiene la capacidad de rechazar huevos parásitos (Kendra et al., 1988; Moreno-Rueda & Soler, 2001). No obstante, hasta la realización de esta tesis doctoral, en esta especie no se había estudiado la relación existente entre ambos tipos de defensas.

Ocultamiento de la puesta

Este comportamiento ha sido descrito en diversas especies en función de las hipótesis existentes (Bochenski, 1961; Broeckhuysen & Frost, 1968; Caldwell & Cornwell, 1975; Haftorn, 1978; Perrins, 1979; Clark & Robertson, 1981; Götmark & Åhlund, 1984; Briskie & Sealy, 1988; Keller, 1989; Shimoda et al., 1994; Stenning,1995; Valera et al., 1997; Orizaola & Braña, 2003; Kreisinger & Albrecht, 2008). No obstante, no había sido descrito anteriormente en el gorrión común, al igual que la danza que realizan los machos al llevar las plumas al nido, mostrándoselas a las hembras de forma intensa. Por esto interpretamos que podría ser algún tipo de señalización de su calidad o capacidad de invertir en cuidados parentales.

Objetivos

El objetivo principal de esta tesis doctoral es contribuir al conocimiento de algunos aspectos comportamentales y evolutivos del gorrión común. Ésta es una especie habitual de nuestro entorno y, sin embargo, tiene una serie de comportamientos que han sido poco estudiados. Por ejemplo, cuál es la función de la presencia de pigmentos en sus huevos, qué características reconoce para rechazar los huevos extraños, o bien, como se describe por primera vez en esta tesis doctoral, cuál es la función del cubrimiento de la puesta o nidada con plumas, o la función del transporte de plumas por parte de los machos. A continuación enumeraremos los objetivos de esta tesis doctoral detalladamente:

Objetivo 1 - debido a la importancia que tienen las características de los huevos en el contexto evolutivo, en esta tesis doctoral nos propusimos estudiar el **mantenimiento del patrón de coloración** de los huevos para una misma hembra. Esto sugeriría una base genética del patrón de coloración en el gorrión común. Además, para inferir si la traslocación de los pigmentos a la coloración de los huevos es costosa para las hembras (Moreno & Osorno, 2003), analizamos la variación del patrón de motas y color de fondo según el orden de puesta de los huevos y según el número de puestas, lo que nos indicaría una posible limitación de estos pigmentos. Por último, estudiamos la variación de coloración de los huevos en función de dos parámetros reproductivos que indicarían la calidad de las hembras (tamaño de puesta y edad de las hembras; Martin, 1987; Christians, 2002; Garamszegi et al., 2004; Martínez-de la Puente et al., 2007; Manuscrito I).

Objetivo 2 - tras los resultados del estudio anterior, nos propusimos estudiar cuáles de las **características de los huevos** favorecen en mayor medida el **reconocimiento y rechazo de huevos** extraños (tamaño del huevo, color del huevo y patrón de motas). Dado que la influencia que una sola característica de los huevos ejerce sobre el rechazo puede ser menos importante que la suma de varias características (debido al efecto del denominado "suma de estímulos" o "estímulo sumatorio"; Rothstein, 1982), analizamos además si la variación simultánea de más de una característica incrementaba la frecuencia de rechazo de los huevos extraños (Manuscrito II).

Objetivo 3 - en una población natural con aparente falta de enclaves para nidificar (razón por la que se puede producir el PCC, ver Introducción General), nos propusimos estudiar la **incidencia de parasitismo de cría y la frecuencia de rechazo de huevos extraños** en esta población. Además, debido a que los costes de las defensas antiparasitarias pueden influir sobre la estrategia seguida por las especies capaces de rechazar huevos parásitos (Soler et al., 1999), se estudió si el rechazo de huevos está positivamente correlacionado con la **defensa del nido**, o bien se produce una relación antagónica entre ambos tipos de defensas. Si la presencia de una hembra intrusa de gorrión común cerca del nido junto a la introducción de un huevo parásito experimental actúa como un estímulo aditivo, las parejas que defiendan sus nidos más vigorosamente presentarán mayor frecuencia de rechazo. Alternativamente, si existe una relación antagónica entre ambos tipos de defensas antiparasitarias, las parejas que presenten mayor grado de defensa del nido -lo que aseguraría en mayor medida no haber sido parasitado- presentarán menores frecuencias de rechazo (Manuscrito III).

Objetivo 4 - en una población natural de gorrión común con nidos construidos en los árboles y cuyas plumas cubren la puesta frecuentemente, examinamos el **patrón de cubrimiento de huevos** durante la secuencia de puesta, a lo largo de un día y durante

la temporada de cría, para comprobar cuál podría ser la función de este comportamiento. A la luz de las hipótesis preexistentes, podemos plantear las siguientes predicciones (Manuscrito IV):

Hipótesis 1 - si el ocultamiento de huevos se produce para evitar el PCC, los huevos estarán más frecuentemente cubiertos durante el período de puesta y al principio de la incubación (Haftorn & Slagsvold, 1995).

Hipótesis 2 - si el cubrimiento de los huevos está relacionado con la termorregulación de la puesta, se espera que los huevos estén cubiertos menos frecuentemente al ir avanzando la temporada de cría, ya que es esperable que las condiciones meteorológicas serán más favorables (Valera et al., 1997). Además, esperaríamos que los huevos estuviesen más frecuentemente cubiertos cuando existan condiciones ambientales desfavorables (Haftorn & Slagsvold, 1995).

Hipótesis 3 - si el ocultamiento de los huevos se produce para evitar la depredación, cabría esperar que este comportamiento se ajuste al valor relativo de la puesta (tamaño de puesta; Broekhuysen & Frost, 1968; Keller, 1989), y sería más frecuente que las parejas cubriesen los huevos al abandonar el nido durante el período de puesta y de incubación (Broekhuysen & Frost, 1968; Haftorn, 1981; Keller, 1989). Y sobretodo, este comportamiento sería más frecuente al aumentar el riesgo de depredación (Haftorn & Slagsvold, 1995).

Hipótesis 4 y 5 - si el ocultamiento de huevos se produce para reducir la asincronía de eclosión u ocultar información acerca del periodo fértil de las hembras, los huevos deberían estar cubiertos durante el periodo de puesta, y no se esperaría una interrupción de este comportamiento a lo largo del día o de la temporada de cría (Valera et al., 1997).

Objetivo 5 - en función de la importancia que tiene en algunas especies el uso de materiales extraños durante la construcción del nido, que proporcionan señales del estatus o calidad del macho (Borgia & Gore, 1986; Moreno et al., 1994; Gwinner, 1997; Soler et al., 1998; Duffy & Gregory, 2002; Brouwer & Komdeur, 2004), en esta tesis nos propusimos conocer si el **transporte de plumas** es parte del cortejo de los machos para señalizar sus atributos (Collias & Collias, 1984; Borgia & Gore, 1986). En este caso, las plumas serían llevadas exclusivamente por ellos durante la construcción del nido y antes del periodo de puesta. También cabría esperar que los machos realizasen intensas demandas de cópula al traer las plumas al nido. Además, el transporte de plumas será más frecuente cuando las hembras vayan a iniciar un nuevo periodo fértil. Si el transporte de plumas es un indicador de la capacidad de aportar cuidados parentales del macho, cabría esperar que aquéllos que transporten más plumas y de mayor tamaño inviertan más en defensa del nido, en el tiempo empleado dentro del nido incubando o empollando, y realicen mayor número de cebas; además, ya que las hembras pueden invertir en reproducción de forma diferencial en función del atractivo de sus machos (Thornhill, 1983, 1984; Bluhm, 1985; Hughes & Hughes, 1985; Simmons, 1987; Yamamoto et al., 1989; Petrie & Williams, 1993; Sheldon, 2000), las hembras de esos machos darían lugar a puestas de mayor tamaño (Manuscrito IV).

Material y Métodos

Poblaciones de estudio

Población en condiciones de cautividad

En los años 1998 y 2003 se capturaron individuos de gorrión común de varias poblaciones naturales de Granada (Padul, Atarfe, jardín de la Facultad de Ciencias). Estos individuos se mantuvieron en cautividad dentro de un aviario de 45 m3 en la Facultad de Ciencias de la Universidad de Granada hasta el año 2007. El tamaño de la población se mantuvo más o menos constante (media 75 ± SD = 10 individuos) durante los años de estudio con una razón de sexos entorno a 1:1. El aviario estuvo provisto de 40 cajas nido, de las cuales alrededor del 50 % fueron ocupadas para nidificar en cada estación de cría. Todos los individuos se marcaron con anillas de colores para su reconocimiento. La población estuvo provista ad libitum de agua, mezcla de diversas semillas, larvas de mosca, vitaminas, calcio y otras sales minerales, manzana, lechuga y pasta de cría (más detalles en Moreno-Rueda & Soler, 2002). Para la construcción de los nidos se introducía en el aviario algodón y otros materiales vegetales cada dos días a lo largo de las temporadas de cría. La iluminación era artificial y estuvo regulada por un temporizador que mantenía a la población bajo el mismo fotoperiodo que existía en el exterior.

Población en condiciones naturales

La población natural estuvo localizada en Dassen Island (33◦25’S, 18◦05’E), Sudáfrica, país por donde esta especie se dispersó a partir de su introducción artificial a finales del s. XIX (Summers-Smith, 1988; Brooke, 1997). La isla de Dassen es una reserva natural de 222 ha y se encuentra a 9 km. de la costa oeste de Sudáfrica. Está permanentemente habitada tan sólo por cuatro personas que ocupan las escasas construcciones humanas existentes. Toda la isla está cubierta por vegetación arbustiva con la excepción de unos pocos árboles introducidos y localizados alrededor de las construcciones humanas. Como son escasos los huecos que quedan en dichas construcciones y la mayoría están ocupados por otras especies más agresiva que el gorrión común (Ryan, 2004), los gorriones nidifican casi exclusivamente en las ramas de estos árboles. Durante los años de estudio (2004 y 2005), se encontraron 40 nidos activos en esta población.

Coloración de los huevos

En la población de gorrión común mantenida en cautividad, se fotografiaron 206 puestas completas procedentes de 33 hembras diferentes. Del total de hembras, 9 eran de primer año de edad y 25 tenían más de un año de edad. La edad de las hembras que nacieron en cautividad pudo ser bien determinada; en el caso de aquéllas que procedían de poblaciones naturales y que se reprodujeron en el mismo año de captura, se consideró que tenían al menos un año. Las puestas de 19 hembras fueron fotografiadas durante un solo año. A 16 de estas hembras se les fotografiaron al menos dos puestas consecutivas. Obtuvimos fotografías de las puestas durante dos o más años de 14 hembras.

Para realizar las fotografías, los huevos se depositaron según su orden de puesta sobre una cartulina gris neutro que incluía una carta de color y una regla. En esta cartulina también se incluyó información sobre la identidad de la hembra y/o la caja en la que estaba nidificando, el número de puesta y la fecha (Figura 1). Las fotografías se tomaron con una cámara digital Minolta Dimage 7.

Figura 1. *Puesta de una hembra de la población en cautividad. Con objeto de homogeneizar la obtención de datos relativos al patrón de coloración de los huevos, las fotografías de esta y el resto de puestas analizadas fueron tomadas sobre una cartulina gris neutro y junto a una carta de color y una regla.*

Se analizaron las fotografías de cada puesta para determinar los parámetros del patrón de motas de los huevos (intensidad de coloración, distribución y tamaño), según la metodología seguida por Gosler (1993). En ella se utilizan diversas categorías para valorar la intensidad de coloración de las motas: (1) todas las motas de muy baja intensidad de color, (2) todas las motas de mediana intensidad de color, (3) algunas motas con color intenso y (4) todas las motas de color intenso; la distribución de las motas (proporción de motas que se encuentran en la mitad roma del huevo: 1) > 80%, 2) 71-80%, 3) 61-70%, 4) 51-60%, 5) 50%), y el tamaño de las motas: (1) pequeño, (2) medio, (3) grande. El color de fondo de los huevos se clasificó en cuatro tonalidades: (1) blanco, (2) blanco/marrón, (3) blanco/azulado, (4) azulados. De cada puesta analizada se tenía información sobre el orden de puesta, el número de puesta, el tamaño de puesta, y la edad de las hembras a las que pertenecían (Manuscrito I).

Reconocimiento y rechazo de huevos

Un huevo conespecífico se introdujo en diferentes puestas (N = 21) de 8 hembras de la población en cautividad durante las temporadas de cría de los años 2003, 2004 y 2005, para determinar si el tamaño de los huevos influía sobre el rechazo de huevos extraños. El huevo experimental fue fotografiado con el resto de la puesta completa de los hospedadores sobre una cartulina gris neutro en la que se incluyó una regla para medir el tamaño de los huevos tanto de los hospedadores como del huevo experimental (ver más detalles en Manuscrito II).

Con el fin de determinar cuáles de las características de coloración de los huevos pueden influenciar en mayor medida el rechazo de huevos extraños, a 21 hembras de esta población se les modificó el color de un huevo propio, en la siguiente puesta el tamaño de las motas, y luego la densidad de motas. Para determinar si la modificación de más de una característica de los huevos genera mayor frecuencia de rechazo que la modificación de una sola, en las puestas sucesivas se modificó conjuntamente el color del huevo y el tamaño de las motas, y posteriormente el tamaño y la densidad de las motas. Estas características se modificaron con pintura plástica (Titanlux © marrón-tabaco nº 544), diluida en el caso de la

modificación del color de fondo para que se siguiese observando el patrón de las motas y no afectase a la eclosión de los huevos. Las respuestas frente a los huevos experimentales fueron la aceptación, expulsión, enterramiento del huevo con material de nido y el abandono de la puesta.

La metodología seguida en la modificación de las características de los huevos y las respuestas frente a los huevos experimentales se especifican con mayor detalle en los Manuscritos II y III.

Defensa del nido

En la población natural de gorrión común de Dassen Island, tras comprobar el mantenimiento de la capacidad de rechazo de huevos extraños de la población (Manuscrito III), se realizó un experimento para determinar si la relación entre la frecuencia de rechazo de huevos y la defensa de los nidos era aditiva o antagonista. En este experimento se introdujo un huevo natural conespecífico en los nidos. Al introducir los huevos, se colocó un modelo disecado de hembra de gorrión común a unos 50 cm. de cada nido en el grupo experimental. En un grupo control se colocó un modelo disecado de hembra de estornino pinto, y en un segundo grupo control se introdujo el huevo sin colocar ningún modelo disecado. Se utilizó el modelo de estornino porque es una especie muy común en la isla, y porque su morfología difiere suficientemente de la de los gorriones comunes, de forma que nos permitiría diferenciar entre la defensa del nido frente al riesgo de parasitismo o una defensa más generalizada (Grim, 2005). Tras la introducción de los huevos y la colocación de los modelos disecados, se realizaron 15 minutos de observación de los nidos a partir de la llegada de algún miembro de la pareja hospedadora. Durante las observaciones se anotaron diversas variables que describieron el grado de defensa de los nidos (p.ej. intervalo de tiempo desde que comienza la observación hasta que llega algún miembro de la pareja, tiempo que tarda en llegar cada miembro de la pareja, número de gritos de alarma, tiempo dentro del nido, número de aproximaciones a los modelos y la distancia media de cada aproximación). Más detalles sobre la metodología seguida pueden consultarse en el Manuscrito III. Se realizaron revisiones diarias de los nidos para anotar las respuestas de las parejas frente a los huevos experimentales.

Ocultamiento de la puesta

Para determinar el patrón de ocultamiento a lo largo de un día, durante la secuencia de puesta, y a lo largo de la temporada de cría, 39 nidos de la población natural de Dassen Island fueron visitados en el año 2004 al amanecer, a media mañana, a media tarde y al atardecer. En esas visitas se anotó si los huevos o pollos estaban o no cubiertos por plumas, la eficacia del ocultamiento (el número de huevos o pollos cubiertos por plumas respecto del tamaño de puesta o nidada), y la cantidad de plumas que formaban parte del nido, tanto en su interior (la taza) como en el exterior. Debido a la dificultad de contar todas las plumas, esta medida se obtuvo mediante un rango de 0 (no existen plumas formando el nido) a 5 (tanto el interior como el exterior del nido está cubierto por plumas).

Para determinar la posible influencia del riesgo de ser parasitado sobre el ocultamiento de la puesta (**Hipótesis 1**), se cuantificó la eficacia de ocultamiento de huevos y el número de plumas que cubrían los huevos (i) antes de realizar el experimento de la defensa del nido vs rechazo de huevos, (ii) tras realizar las observaciones y (iii) al haber transcurrido una hora.

La influencia de las condiciones meteorológicas sobre el ocultamiento (**Hipótesis 2**) se comprobó gracias a las variables obtenidas por el personal encargado del faro de la isla

(temperatura, humedad, intensidad del viento, nubosidad, lluvia y niebla). Estas variables se recogían al amanecer, a media mañana y al atardecer durante toda la temporada de cría, y se relacionaron con los valores de ocultamiento recogidos en las visitas diarias descritos anteriormente.

En el caso de la influencia del riesgo de depredación sobre el ocultamiento de la puesta (**Hipótesis 3**), se realizó un experimento que incluyó un tratamiento experimental y uno control en los mismos nidos. El tratamiento experimental consistió en colocar un modelo disecado de culebra bastarda (Malpolon monspessulanus) a 50 cm. de cada nido, mientras que en el tratamiento control se colocó un palo de madera con la misma forma que el modelo de culebra. Tras la colocación de los modelos se realizaron observaciones de 15 minutos desde la llegada de algún miembro de la pareja al nido. Durante las observaciones se anotaron diversas variables que determinaron si los modelos se detectaron como posibles depredadores, así como el grado de defensa de los nidos. La eficacia de ocultamiento y el número de plumas que cubrían los huevos se registraron (i) antes de cada tratamiento, (ii) tras finalizar la observación y (iii) al transcurrir una hora.

Para analizar si el cubrimiento de los huevos puede reducir la asincronía de eclosión (**Hipótesis 4**) relacionamos la media de la frecuencia de ocultamiento y de su eficacia (porcentaje de huevos/pollos cubiertos respecto al total) con la proporción de pollos (respecto al tamaño de puesta) que emergen en el primer día de eclosión.

El patrón del ocultamiento de la puesta en función de la fase del evento reproductor y la agresividad de las hembras frente a los machos durante el periodo de puesta nos indicarían si este comportamiento tiene la función de ocultar información a los machos acerca de su periodo fértil (**Hipótesis 5**).

Para determinar si el transporte de plumas forma parte del cortejo a las hembras, y si muestra la inversión en cuidados parentales que están dispuestos a hacer los machos, se realizó un experimento en el que se manipuló la cantidad de plumas que formaban parte de los nidos. Este experimento consistió en dos tratamientos experimentales y un tratamiento control realizados a los mismos nidos. Antes de cada tratamiento se comprobó si los huevos o pollos estaban cubiertos por plumas, la eficacia de cubrimiento y la cantidad de plumas que había dentro y fuera del nido. En uno de los tratamientos experimentales se eliminaron la mitad de las plumas que formaban parte del nido sin dañar su estructura. En el segundo tratamiento experimental se añadieron la mitad de plumas respecto a las que tenía cada nido; y en el tratamiento control se removieron las plumas sin eliminar ni añadir. Tras cada tratamiento se realizaron observaciones de una hora donde se recogieron variables para cada miembro de la pareja como: el número de viajes al nido con plumas, el tamaño y número de esas plumas, el tiempo enseñando las plumas al otro miembro, el número de peticiones de cópulas, dónde eran depositadas las plumas (taza o estructura externa), tiempo defendiendo el nido o dentro incubando o empollando, y el número de cebas en los nidos con pollos. Posteriormente, se relacionaron el número de plumas que formaban parte del nido antes del tratamiento, el número de viajes de los machos con plumas y el número de plumas traídas en cada viaje con el tamaño de puesta, para determinar si existe una inversión diferencial en reproducción por parte de las hembras en función de la cantidad de plumas y esfuerzo de los machos (ver más detalles metodológicos en Manuscrito IV).

Resultados y Discusión

Coloración de los huevos (Manuscrito I)

Influencia de la identidad de las hembras sobre la coloración de huevos

La identidad de la hembra influye, según nuestros resultados, sobre la coloración de huevos en el gorrión común (Tabla 1). En esta especie, la varianza del patrón de coloración explicada por la identidad de la hembra se encontró entre el 5 % y el 10 % para el color de fondo de los huevos y la intensidad de color y el tamaño de las motas; no obstante, fue de un 40,5 % para la distribución de las motas. La intensidad de color y el tamaño de las motas se encontraron influenciados por el orden de puesta, el número de puesta y la edad de las hembras (Tabla 1), existiendo además covarianza significativa entre ambas (Figura 2). Sin embargo, la distribución de las motas sólo se encontró influenciada por el orden de puesta y el tamaño de puesta (Tabla 1), y no existió una relación significativa con la intensidad ni el tamaño de motas. El color de fondo fue explicado de forma significativa por todas las variables tenidas en cuenta (Tabla 1). Estos resultados mostrarían que el color de fondo, la intensidad de color y el tamaño de las motas tienen un componente ambiental más importante que la distribución de las motas.

Variable dependiente	Variables explicativas	Tipo de variable	Estimador	gl	F/Z	p
Intensidad de color en motas	Hembra	R			2.32	0.012
	Orden de puesta	C	-0.14	1,558	26.16	<0.001
	Número de puesta	C	0.18	1,558	7.27	0.007
	Edad	F		2,90.6	10.00	<0.001
Tamaño de motas	Hembra	R			2.93	0.002
	Orden de puesta	C	-0.16	1,586	6.61	0.013
	Número de puesta	C	0.13	1,586	3.87	0.051
	Edad	F		2,7.4	15.79	0.002
Distribución de motas	Hembra	R			3.32	<0.001
	Orden de puesta	C	-0.24	1,788	67.85	<0.001
	Tamaño de puesta	C	0.21	1,788	18.97	<0.001
Color de fondo	Hembra	R			2.65	0.004
	Orden de puesta	C	-0.23	1,515	10.24	0.001
	Número de puesta	C	-0.28	1,535	11.64	< 0.001
	Tamaño de puesta	C	0.29	1,536	7.49	0.006
	Edad	F		2,36.4	5.96	0.018

Tabla 1. *Resultados de los modelos GLMM y GLIMMIX con las variables que explican de forma significativa la intensidad de color, tamaño y distribución de las motas y el color de fondo. La columna "Tipo de variable" indica si la variable se ha incluido en el análisis como covariable, factor fijo o factor aleatorio. Se dan también los grados de libertad (gl). Los valores de F se dan para las covariables y factores fijos, y los Z para los factores aleatorios. El signo de los estimadores muestra la relación positiva o negativa entre las covariables y la variable dependiente.*

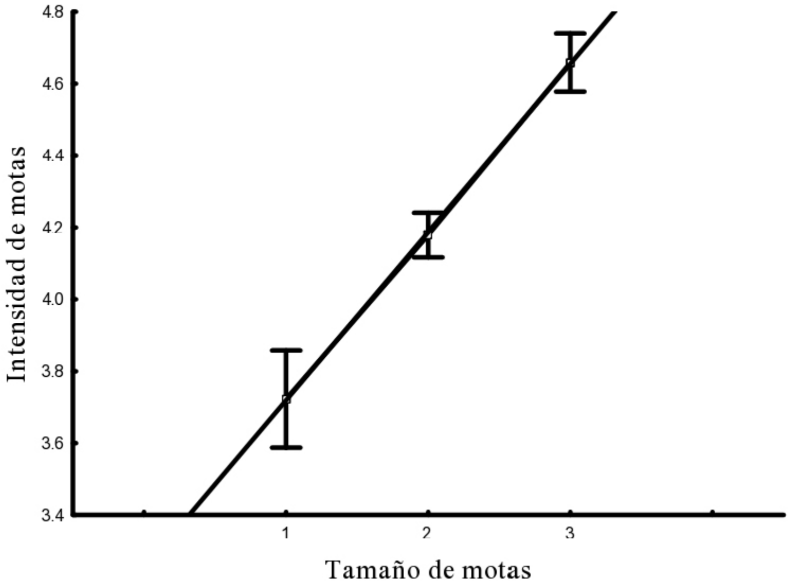

Figura 2. *Relación positiva entre la intensidad de color y el tamaño de las motas. Los datos representados son las medias con la desviación estándar.*

Limitación de pigmentos

Las primeras puestas de una temporada de cría tuvieron mayor proporción de huevos azulados que las últimas puestas (Tabla 1). Además, dentro de una puesta, los últimos huevos suelen ser mayoritariamente blancos (Tabla 1). Estos resultados sugieren que existe un posible coste para mantener la misma inversión de pigmento en el color de fondo a lo largo de una puesta y de una temporada de cría. Respecto a las motas, el valor de las tres variables relacionadas con ellas disminuyó en la secuencia de puesta. Los últimos huevos tuvieron menor número de motas, más pequeñas y de color menos intenso (Tabla 1). Esto sugiere que, al menos a corto plazo, también puede existir una limitación en la inversión de protoporfirina en la cáscara de los huevos. No obstante, con el avance de la temporada de cría aumentaron tanto la intensidad de color como el tamaño de las motas (Tabla 1), lo que indicaría que no existe tal limitación a largo plazo (al menos en condiciones de cautividad).

Por lo tanto, nuestros resultados sugieren que, para las hembras de gorrión común, mantener la cantidad de biliverdina es costoso tanto a corto como a largo plazo (Moreno et al., 2005; Krist & Grim, 2007), y mantener la cantidad de protoporfirina es costoso al menos a corto plazo (Moreno & Osorno, 2003).

Variables reproductivas y patrón de coloración de huevos

Tanto el tamaño de puesta como la edad de las hembras se correlacionaron significativamente con el color de fondo de los huevos. Las hembras con puestas más grandes tuvieron mayor proporción de huevos azulados, y las hembras de mayor edad pusieron mayor proporción de huevos blancos (Tabla 1). Estos resultados concuerdan con otros estudios que encontraron que la edad de las hembras y/o su condición física influyen sobre la inversión de biliverdina en la cáscara de huevos (Moreno et al., 2005; Siefferman et al., 2006; Krist & Grim, 2007). Por tanto, en el gorrión común los huevos azulados podrían indicar la calidad de las hembras, ya que sólo hembras en buena condición serían capaces de traslocar a la cáscara de los huevos importantes cantidades de este pigmento con propiedades anti-oxidantes en lugar de emplearlas para eliminar los radicales libres (Moreno & Osorno, 2003).

Otro de los resultados mostró que las puestas de mayor tamaño tuvieron huevos con mayor número de motas y de color más intenso. Por lo que, dado que normalmente las hembras con puestas mayores son las que se encuentran en mejor condición en el momento de la puesta (revisión en Martin, 1987; Christians, 2002), este resultado daría soporte a la hipótesis de que sólo las hembras que tengan mejor condición pueden poner huevos más pigmentados con protoporfirina (Moreno & Osorno, 2003). En este contexto, nuestro estudio mostró que la intensidad de color y el tamaño de las motas disminuyen con la edad de las hembras (Tabla 1; Figura 3). Las hembras de primer año pusieron huevos similares en intensidad de color y tamaño de motas que las hembras de edad intermedia, aunque las hembras de mayor edad pusieron huevos significativamente con motas de color menos intenso y más pequeñas. Esto podría deberse a senescencia, de manera que las hembras más viejas tienen menos capacidad de invertir pigmentos en la cáscara de los huevos.

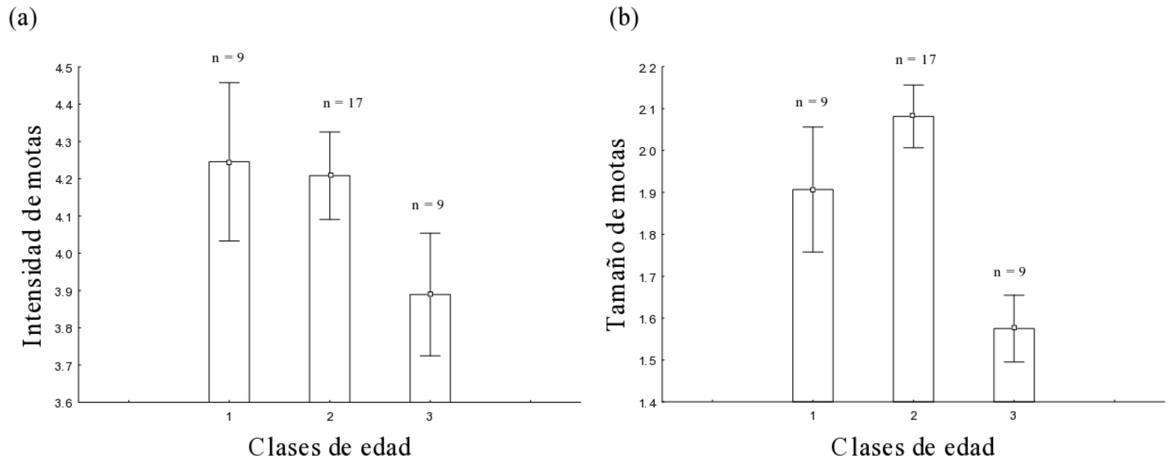

Figura 3. *Diferencia en (a) intensidad de color de las motas y (b) tamaño de las motas entre las tres clases de edad (1 = hembras de primer año, 2 edad intermedia = 2-3 años, 3 edad avanzada = ≥ 4 años).*

Sin embargo, el tamaño y la intensidad de color de las motas aumentaron con el número de puesta, lo que puede deberse al coste reproductivo de las puestas anteriores (las hembras se encontrarían en peor condición física). Este resultado apoyaría la hipótesis alternativa de que las hembras en peor condición física ponen huevos más moteados, ya que altos niveles de protoporfirina producen estrés fisiológico que se reflejaría en la condición física de las hembras o en su respuesta fisiológica (Martínez-de la Puente et al., 2007).

Reconocimiento y rechazo de huevos (Manuscrito II)

El tamaño de los huevos es muy repetible para cada hembra de gorrión común, y existen diferencias significativas entre hembras (Anderson, 2006). Esto podría favorecer el rechazo ante la presencia de un huevo parásito que difiera en tamaño respecto a los de la puesta de la hospedadora. Sin embargo, se encontró que el tamaño de los huevos tiene poca o ninguna influencia sobre el reconocimiento y rechazo de huevos extraños. Sólo el trabajo realizado por Marchetti (2000) encuentra un efecto de esta característica sobre el reconocimiento y rechazo de huevos parásitos conespecíficos en el mosquitero de Hume (*Phylloscopus humei*). Este estudio demostró, contrariamente a nuestros resultados, que la "decisión" de rechazar se basaba en el tamaño relativo de la puesta hospedadora y que los individuos aceptaban los huevos que eran de un tamaño similar a los suyos.

El estudio detallado en el Manuscrito I mostró que las características de coloración de los huevos son muy semejantes para una misma hembra y difieren significativamente entre ellas. Estas características se mantuvieron en un rango de variación, y es la distribución de motas la que estuvo más determinada por la identidad de las hembras y mostró menos variabilidad entre puestas de una misma hembra. Por lo tanto, cabría esperar que la diferencia entre huevos propios y parásitos en la/s característica/s con menos variabilidad facilitase el rechazo de huevos (Victoria, 1972; Rothstein, 1982; Moksnes et al., 1993; Stokke et al., 2002, 2004).

Los experimentos realizados sobre el efecto de las características de coloración de los huevos sobre el comportamiento de rechazo, mostraron que la modificación del patrón de motas (tamaño y densidad), y no la modificación del color, dio lugar a una mayor tasa de rechazo (Figura 4). Por otro lado, no se produjo una “suma de estímulos” en el caso del gorrión común, ya que ninguno de los experimentos en los que se modificaron dos características generó mayor frecuencia de rechazo que aquellos en los que sólo se modificó una sola (Figura 4). En otras especies, el patrón de motas es el máximo responsable del reconocimiento y rechazo de huevos parásitos y tampoco se produjo el llamado “suma de estímulos” (Underwood & Sealy, 2006; Hauber et al. 2006; Polaciková et al. 2007; Moskat et al. 2008).

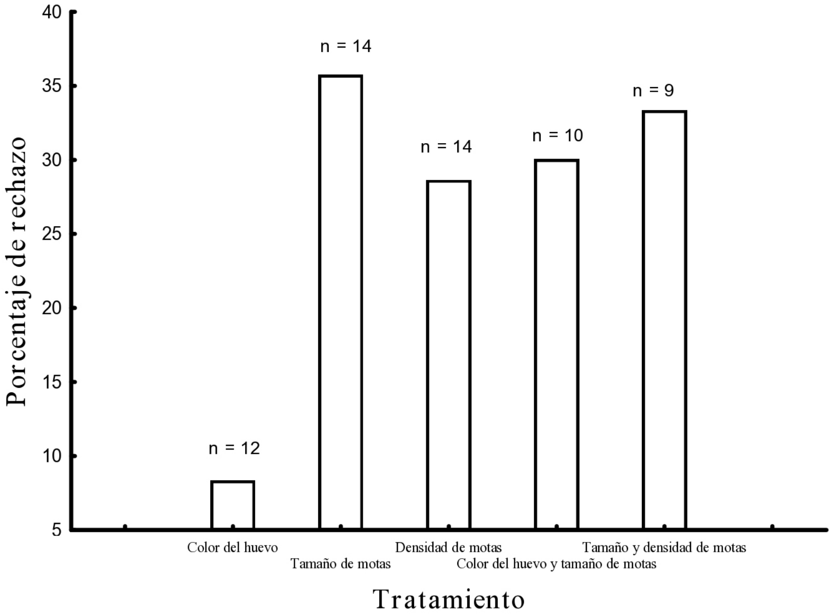

Figura 4. *Porcentajes de rechazo generados por el experimento de modificación de las características de coloración y patrón de motas de los huevos en el gorrión común.*

La mayoría de las aves que nidifican en nidos cerrados o cavidades tienden a poner huevos sin motas (Kilner, 2006). Además de otras hipótesis que intentan explicar la presencia de motas en algunas de estas especies (p.ej. indicador de la calidad de la hembra, o compensar la falta de calcio en el ambiente para reducir la pérdida de agua durante la incubación; Moreno & Osorno, 2003; Gosler et al., 2005; Higham & Gosler, 2006; Martínez-de la Puente et al., 2007), algunos estudios indican que el parasitismo de cría explica la presencia de motas para facilitar el reconocimiento y rechazo de huevos (Stokke, et al., 1999, 2002; Davies, 2000; Soler et al., 2000; Lahti, 2005, 2006; Underwood & Sealy, 2006; Hauber et al. 2006; Polaciková et al. 2007; Moskat et al. 2008). Los resultados de esta tesis (Manuscritos I y II) muestran que la coloración de los huevos en el gorrión común es más variable dentro de una misma hembra y que tiene poca o ninguna influencia sobre el rechazo

de huevos extraños. Sin embargo, el patrón de motas, que sí influye en el rechazo de huevos extraños, es menos variables dentro de cada hembra, y su varianza está explicada en un 40,5 % por la identidad de las hembras. Debido a estos resultados y a que el gorrión común es una especie que nidifica en nidos cerrados o cavidades, donde la luminosidad es escasa, se sugiere que el mantenimiento de este patrón de motas podría deberse al PCC. De esta forma, el contraste de claros y oscuros en la cáscara de huevos determinado por el patrón de motas sobre el fondo de los huevos sería la característica que facilita el reconocimiento y rechazo de huevos parásitos.

Defensa del nido (Manuscrito III)

El porcentaje de rechazo del huevo experimental no difirió estadísticamente entre los tratamientos. Este resultado indica que la presencia de una hembra conespecífica cerca del nido no incrementa la probabilidad de rechazo de un huevo extraño. Esto coincide con lo encontrado por Moksnes & Elbertø (2006), quienes mostraron que en el estornino pinto tampoco se produce una relación positiva entre la presencia de una hembra intrusa y el rechazo de huevos conespecíficos. Un posible motivo por el que no se ha encontrado una relación positiva entre la presencia de una posible hembra parásita y el rechazo de huevos es que el gorrión común es una especie colonial, existiendo varios nidos en los árboles de la zona de estudio, los cuales se encuentran muy cerca unos de otros, de modo que la presencia de varias hembras en un mismo árbol es habitual.

Estudios anteriores realizados en el marco del parasitismo de cría interespecífico mostraron una relación antagónica entre la defensa del nido y el rechazo de huevos extraños (Neudorf & Sealy, 1992; Soler et al., 1999). Soler et al. (1999) sugirieron que dado que cada estrategia lleva asociada una serie de costes, sería más rentable para los hospedadores especializarse en un solo tipo de estrategia de defensa frente al parasitismo de cría (defensa del nido o rechazo de huevos). Una situación similar podría aplicarse al PCC, aunque los resultados mostraron que la probabilidad de rechazo de huevos no depende del grado de defensa del nido, al menos en el gorrión común. Las variables que tuvimos en cuenta como indicadoras de la defensa de los nidos no difirieron significativamente entre las parejas que aceptaron o rechazaron los huevos experimentales en el tratamiento en el que se colocó el modelo disecado de hembra de gorrión común. Esto indicaría que el comportamiento de reconocimiento y rechazo de huevos en el gorrión común no depende de la probabilidad de ser parasitados o de la incapacidad de asumir los costes asociados a ambos tipos de estrategias (costes de defensa del nido *vs* costes de rechazo de huevos).

Por otro lado, se encontró que los gritos de alarma fueron más numerosos en los nidos en los que se colocó alguno de los modelos disecados, y que el tiempo de llegada de los machos fue menor en estos grupos, siendo aún menor en el grupo al que se le presentó el modelo de estornino. Esto último podría deberse a que la presencia de estorninos es poco común en los árboles donde nidifican los gorriones en la zona de estudio, lo contrario que la presencia de varias hembras conespecíficas. Por tanto, se sugiere que el gorrión común podría presentar una defensa generalizada del nido (Grim, 2005), en lugar de un reconocimiento específico de una posible hembra parásita.

Ocultamiento de la puesta (Manuscrito IV)

Hipótesis 1- Evitar el parasitismo de cría (Clark & Robertson, 1981; Briskie & Sealy, 1988): en los experimentos realizados para determinar si el ocultamiento de huevos podría tener la función de evitar el parasitismo de cría en esta especie se encontró que, a pesar de que los modelos de aves disecadas fueron detectados como posibles intrusos (mayor número de gritos de alarma en comparación con el grupo en que no se presentó un modelo disecado), el ocultamiento de huevos no se incrementó al aumentar el riesgo de ser parasitados. Este resultado puede deberse a que la presencia de una hembra conespecífica cerca de los nidos no parece indicar un mayor riesgo de parasitismo en esta especie (ver más arriba y Manuscrito III).

Hipótesis 2 - Termorregulación del nido (Bochenski, 1961; Caldwell & Cornwell, 1975; Haftorn, 1978): no se encontró un patrón específico de ocultamiento o cubrimiento de huevos a lo largo del periodo de puesta, y no obtuvimos ninguna relación entre este comportamiento con la variabilidad de las condiciones meteorológicas. Estos resultados rechazarían, en el gorrión común, esta hipótesis de termorregulación del nido, pero sólo en función de las condiciones externas, igual que ocurre en la mayoría de las especies de páridos (Parus spp., Haftorn & Slagsvold, 1995) o el pájaro moscón (Remiz pendulinus, Valera et al., 1997). Sin embargo, la cantidad de plumas que se encuentran formando parte del nido (dentro y fuera), varió entre las diferentes fases del evento reproductor, siendo significativamente mayor durante la incubación y con pollos recién eclosionados, los momentos en que más requerimientos hay de termorregulación (Figura 5). Esto podría indicar que la cantidad de plumas que forman parte del nido sirve para incrementar el aislamiento del nido (termorregulación dentro del nido), disminuyendo la pérdida de calor (Haftorn, 1978; Skutch, 1983; Hansell, 1995, 2000). La frecuencia con la que se alterna la incubación con otras actividades refleja un compromiso entre la energía que necesitan los adultos, y la necesaria para que se produzca un buen desarrollo embrionario (Nice, 1937; Davis, 1960; Drent et al., 1985; Bryan & Bryant, 1999). Por lo tanto, un nido que se encuentre bien aislado reduciría el tiempo que los padres dedican a la incubación, relajando tal compromiso (Collias & Collias, 1984; Kern et al., 1993; Conway & Martin, 2000a, b). Por otro lado, los pollos recién eclosionados pierden calor rápidamente y no tienen capacidad de termorregulación (Sturkie, 1976; Rovee-Collier et al., 1991). El mayor problema para los padres que están cuidando de pollos recién eclosionados es su simultánea necesidad de regular la temperatura corporal de los pollos y aportar el alimento necesario para su crecimiento (Rovee-Collier et al., 1997).

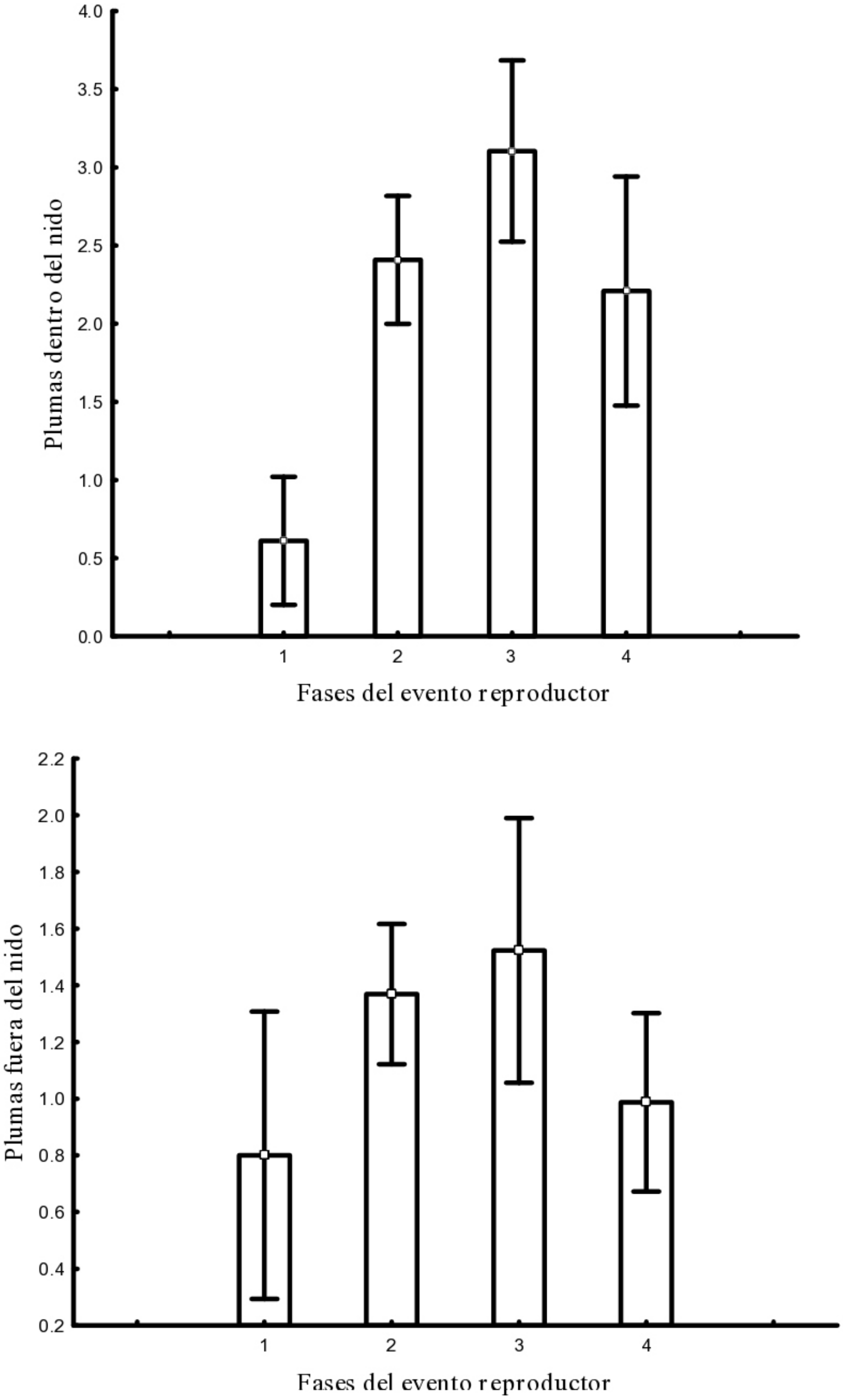

Figura 5. *Cantidad de plumas dentro y fuera de los nidos (N = 50) en las diferentes fases del evento reproductor (1 = antes de la incubación, 2 = durante la incubación, 3 = pollos recién eclosionados y 4 = pollos con 5 o más días de edad).*

Los resultados de esta tesis sugieren que las plumas que forman el nido en el gorrión común podrían reducir la pérdida de calor, con lo que se reduciría el compromiso existente entre la energía que necesitan los huevos para el desarrollo embrionario, y los pollos recién eclosionados para el crecimiento, y la energía que necesitan los adultos para sobrevivir. Es decir, las plumas compensarían la ausencia temporal de los padres de modo que, cuantas más plumas se acumulen en el nido, mayor sería el tiempo en que los padres pueden ausentarse.

Hipótesis 3 - Protección contra depredadores (Broeckhuysen & Frost, 1968; Perrins, 1979): según esta hipótesis, el cubrimiento de los huevos ocultaría la puesta a los depredadores para protegerla. Si fuese así, cabría esperar que cuanto mayor fuese el valor de la puesta (tamaño de puesta), mayor sería la frecuencia y eficacia del ocultamiento (Broekhuysen & Frost, 1968; Keller, 1989). Sin embargo, los resultados obtenidos muestran que el tamaño de puesta no influye sobre el ocultamiento o su eficacia. En el experimento realizado sobre la influencia del aumento del riesgo de depredación sobre el ocultamiento de los huevos, a pesar de que en el tratamiento experimental se produjeron mayor número de gritos de alarma que en el tratamiento control, la eficacia de ocultamiento y el número de plumas que cubrían los huevos fueron menores tras realizar las observaciones y al transcurrir una hora desde que se hacía el experimento. Por tanto, no parece que el cubrimiento de la puesta con plumas tenga una función antidepredadora en la población estudiada.

Hipótesis 4 - El cubrimiento de la puesta reduciría la asincronía de eclosión (Stenning, 1995): los resultados obtenidos no apoyan esta hipótesis, ya que el número de pollos que eclosionaron el primer día no dependió de la frecuencia de cubrimiento de la puesta o de su eficacia.

Hipótesis 5 - El cubrimiento de la puesta tiene la función de ocultar información sobre el periodo fértil de las hembras (hipótesis del engaño; Valera et al., 1997): en las especies en las que se cumple esta hipótesis, las hembras suelen tener algunas ventajas que incrementan su eficacia biológica, como son la obtención de cópulas fuera de la pareja o la posibilidad de ser poliándricas (Valera et al., 1997). En estas especies, el ocultamiento de huevos está relacionado con los posteriores cuidados parentales, ya que éstos se llevan a cabo por un solo miembro de la pareja (Schönfeld, 1994), debido al abandono del otro miembro (Persson & Öhrström, 1989; Hoi et al., 1994, 1996). Por lo tanto, las hembras podrían ocultar información de la puesta de los huevos a sus machos cubriéndolos, y así ser ellas las primeras que abandonen la puesta y que sean los machos los que la saquen a delante, mientras ellas podrían emparejarse con otra pareja (Valera et al., 1997). En estos casos, el ocultamiento de los huevos se realiza sólo durante el periodo de puesta (Valera et al., 1997). Los resultados de este estudio mostraron que el cubrimiento se produce en las diferentes fases del evento reproductor, sobretodo durante la incubación y con pollos recién eclosionados, lo cual no coincide con las predicciones de la hipótesis del engaño (Valera et al., 1997). Además, en el gorrión común existen pocos casos de poliandria, siendo mayoritariamente monógamos (Veiga, 1992). Por otro lado, tanto hembras como machos entran en el nido en las diferentes fases del evento reproductor (Summers-Smith, 1963; North, 1980), ambos se encargan de los cuidados parentales (revisión en Anderson, 2006), y no es habitual el abandono de alguno de los miembros durante la reproducción (Summers-Smith, 1958). Tanto por las características de la especie como por los resultados encontrados, se sugiere que el ocultamiento de la puesta no se produce para ocultar información sobre el periodo fértil de las hembras.

Las observaciones realizadas durante el experimento de manipulación de la cantidad de plumas que forman parte de los nidos mostraron que los machos son los máximos responsables de llevar las plumas, especialmente durante la incubación. Al llevarlas, los machos llaman a las hembras y se las muestran durante unos minutos, aunque habitualmente no se produce petición de cópula. Esto podría deberse a que las hembras no se encontraran en el periodo fértil. Por otro lado, la mayoría de las veces las plumas fueron depositadas dentro o en la entrada del nido. En el tratamiento en el que se quitaron las plumas los machos realizaron un mayor número de viajes con plumas que en los otros dos tratamientos (Figura 6).

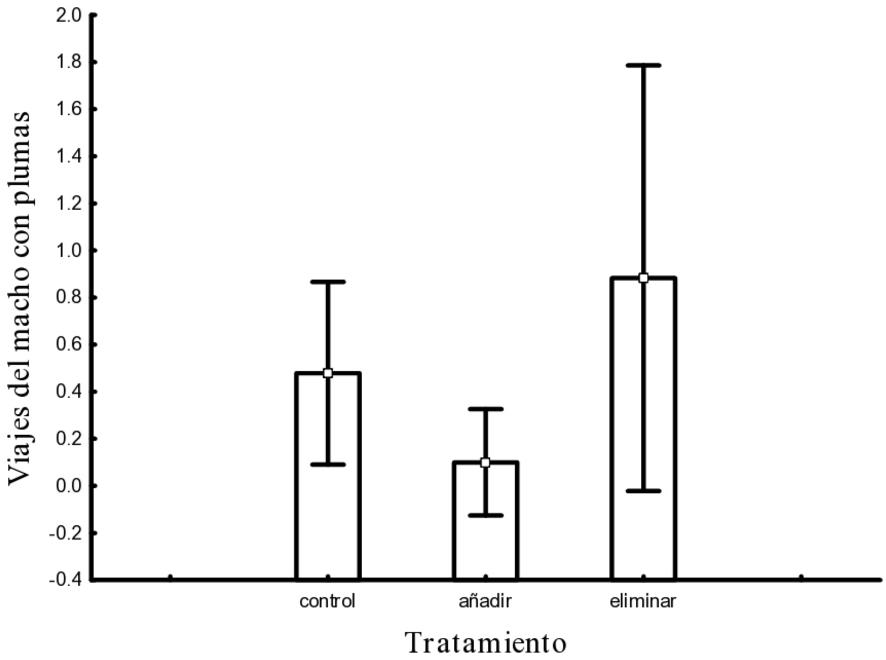

Figura 6. *Número de viajes que realiza el macho con plumas en cada tratamiento del experimento de manipulación de cantidad de plumas del nido (N = 50).*

Por su parte, la cantidad de plumas que forman el nido no estuvo relacionada con el resto de las variables que se tuvieron en cuenta para determinar la capacidad de cuidados parentales de los machos (p.ej. tiempo de incubación, tiempo empollando, tasa de cebas). Sin embargo, sí existió una relación positiva y significativa entre la cantidad de plumas que existen formando parte de la cuenca y parte interna de la cúpula del nido y el tamaño de puesta (Figura 7). Además, en el tratamiento en el que se quitaron las plumas de los nidos que se encontraban en el periodo de puesta, el tamaño de puesta estuvo relacionado positivamente y de forma significativa con el número de viajes con plumas que realizó el macho, y el número de plumas que trajo. Debido a que las hembras de gorrión común son capaces de ajustar su tamaño de puesta en función de diversos condicionantes (revisión en Anderson, 2006), estos resultados sugieren una inversión reproductiva diferencial de las hembras dependiendo de la capacidad de llevar plumas al nido de los machos como ocurre en otras especies con los materiales de los nidos (p.ej. collalba negra Oenanthe leucura, Soler et al., 1996).

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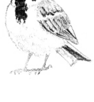

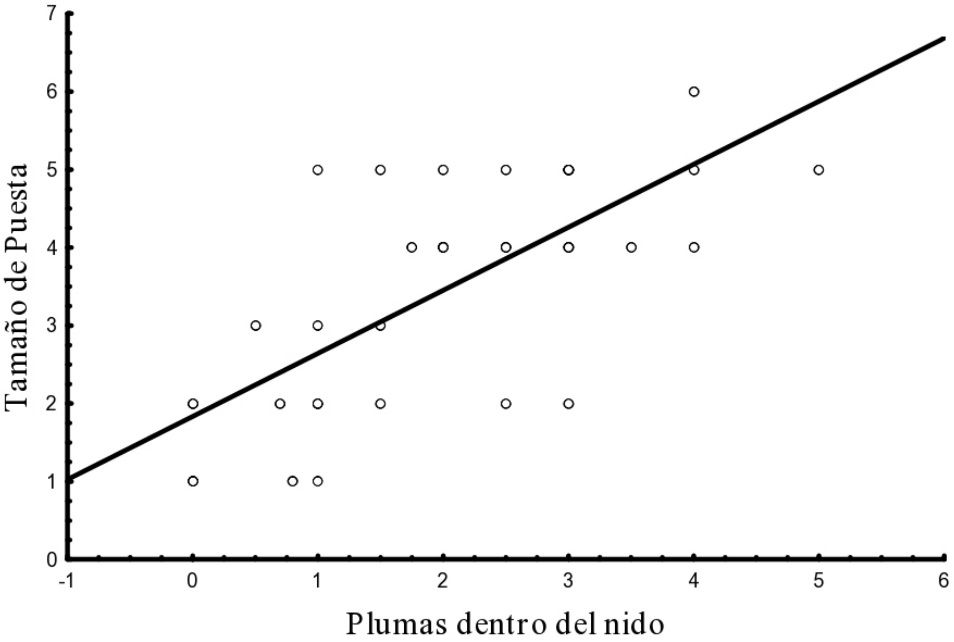

Figura 7. *Relación entre el número de plumas dentro del nido y el tamaño de puesta.*

Cabe esperar que el tiempo y la energía utilizados para encontrar y transportar plumas se reste de otras actividades vitales como la búsqueda de alimento. En el estornino negro (Sturnus unicolor), el transporte de materiales especiales al nido aparentemente no está relacionado con la inversión de los machos en la alimentación de sus pollos, y los machos que transportan más cantidad de estos materiales prácticamente no alimenta a su descendencia (Veiga et al., 2002). En este caso, el transporte de plumas en el gorrión común podría indicar la calidad de los machos y, al mismo tiempo, ser en sí mismo un tipo de cuidado parental, que aumente el aislamiento del nido evitando la pérdida de calor, y permitiendo que ambos miembros de la pareja puedan pasar más tiempo fuera del nido realizando otras actividades. Además, si los machos son eficaces trayendo plumas al nido, lo que aumentaría el aislamiento del nido, las hembras podrían aumentar el tamaño de puesta, dado que los huevos o pollos pequeños necesitarían menos cuidados en el nido (suministro de calor) por estar mejor aislado.

Conclusiones

1. En el gorrión común, la distribución de las motas fue la característica de coloración del huevo que sufrió menos variación dentro de cada hembra.
2. Tanto el número, tamaño e intensidad de color de las motas como la intensidad del color de fondo del huevo disminuyeron con el orden de puesta, lo que sugiere que la deposición de pigmentos sobre los huevos está limitada en cada evento reproductor.
3. Las hembras con puestas de mayor tamaño, y que no eran de edad avanzada, pusieron huevos con mayor número de motas, mayor intensidad de coloración y mayor tamaño, además de una mayor proporción de huevos azulados. La deposición de pigmentos en la cáscara de los huevos en el gorrión común parece estar, por tanto, relacionada con la calidad de las hembras.
4. El rechazo de huevos parásitos en el gorrión común no estuvo determinado por las diferencias de tamaño y color entre los huevos del hospedador y los huevos parásitos, pero sí por el patrón de distribución de las motas. En consecuencia, el PCC podría actuar como presión selectiva favoreciendo el mantenimiento de las motas en los huevos de esta especie.
5. Ni el riesgo de parasitismo (medido a partir de la presencia de una hembra conespecífica cerca del nido) ni el nivel de defensa del nido alteraron la probabilidad de rechazo de huevos parásitos. Por tanto, en la población natural estudiada el gorrión común mostró una defensa generalizada del nido con ausencia de estrategias particulares contra el PCC.
6. En el gorrión común, el cubrimiento de los huevos no parece estar relacionado con el parasitismo de cría, las variables ambientales externas o la depredación. Tampoco parece que su función sea disminuir la asincronía de eclosión u ocultar información sobre el periodo fértil de las hembras. Sin embargo, la cantidad de plumas que forman el nido sí parece estar relacionado con su termorregulación interna.
7. Las plumas que forman parte de los nidos fueron transportadas principalmente por los machos. Este transporte podría ser en sí mismo un tipo de cuidado parental que podría indicar la calidad del macho.
8. El transporte de plumas al nido por los machos de gorrión común podría ser un rasgo seleccionado sexualmente, ya que las hembras incrementaron su inversión reproductiva (tamaño de puesta) en respuesta a un mayor transporte de plumas.

Conclusions

1. The distribution of spots was the shell characteristic showing less variation within females.
2. Number, size and colour intensity of spots, as well as ground colour, in egg shells diminished with laying order, suggesting that shell pigments are limited in each reproductive event.
3. Females with larger clutches, and not advanced age, laid eggs with more spots, which showed more intense colour and were larger. Moreover, these females laid a higher proportion of bluish eggs. This suggests that the pigmentation of both spots and ground may be related to female quality in the house sparrow.
4. Egg rejection in the house sparrow was not affected by the diference in size or colour between host’s and parasitic eggs, but it was determined by the variation in spots pattern. Accordingly, the PCC could be a selective pressure favouring the maintenance of spots in house sparrow eggs.
5. The presence of a conspecific female near to the nest did not increase the probability of rejection of an alien egg, and neither nest vigilance nor defence was related to the probability of egg rejection. Therefore, the house sparrow shows a general defence of the nest with no particular strategies against PCC.
6. Egg covering in the house sparrow was not related to the risk of conspecific brood parasitism, external environmental variables, or to the risk of predation. It neither prevents the hatching asynchrony, nor hides information about female fertile period. Nevertheless, the amount of nest feathers appears to be related to nest internal thermoregulation.
7. Feathers are brought to the nest primarily males, and this transportation could be a kind of parental care than could indicate male quality.
8. Feathers transport to the nest by male sparrows could be a sexually selected trait, as females enlarged their reproductive investment (clutch size) in response to increased transport of feathers.

Perspectivas

Los resultados obtenidos en esta tesis doctoral sugieren la existencia de una base genética que mantiene las características de los huevos (coloración y tamaño) dentro de un rango de variación en cada hembra. No obstante, sería interesante realizar futuros estudios que muestren la repetibilidad y heredabilidad de las características de coloración (Collias, 1993; Gosler et al., 2000). Con estos nuevos estudios se podría determinar si existe realmente un control genético, con lo que nos ayudaría a comprender mejor qué presiones selectivas han favorecido la presencia de pigmentos en los huevos del gorrión común, y cuál es su función.

Por otro lado, en el trabajo realizado sobre la posible relación existente entre la cantidad de pigmentos depositados en la cáscara de los huevos y la condición de las hembras de gorrión común, se utilizó una población en cautividad y medidas indirectas de condición (tamaño de puesta y edad). Por lo tanto, sería necesario tomar medidas que indiquen directamente la condición de las hembras en poblaciones naturales de gorrión común y relacionarlas con el patrón de coloración de los huevos. De este modo, nos aseguraríamos de que la deposición de pigmentos, tanto biliverdina como protoporfirina, son buenos indicadores de tal condición en esta especie. Además, serían necesarios estudios que relacionen la cantidad de pigmentos con los cuidados parentales de los machos y comprobar si la cantidad de pigmentos invertida en la cáscara de huevos se produce como una señal seleccionada sexualmente para indicar a los machos la condición de las hembras, con lo que se incrementarían sus cuidados parentales (Moreno & Osorno, 2003). Así mismo, sería interesante comprobar otras hipótesis funcionales que intentan explicar la presencia de motas en los huevos (p.ej. estructural, Gosler et al., 2005).

Respecto a la función del transporte de plumas a los nidos, serían necesarios nuevos estudios que encuentren este comportamiento en otras poblaciones de gorrión común (p.ej., que sufran mayor frecuencia de PCC o tasas de depredación), y comprobar que se produce por los mismos motivos encontrados en esta tesis doctoral. Además, se deben tomar variables que relacionen alguna medida concreta de calidad de los machos (p.ej., capacidad de forrajeo) con la cantidad de plumas que forman parte del nido para comprobar que este comportamiento podría indicar a las hembras dicha calidad. Relacionar la cantidad de plumas con el tiempo que pasa cada miembro de la pareja fuera del nido, la limitación de alimento, la supervivencia de los adultos y de los pollos, también sería de gran interés para determinar si las plumas que forman el nido sirven para mantener mejor el calor y permitir que éstos pasen más tiempo fuera del nido realizando otras funciones, tal y como sugieren nuestros resultados.

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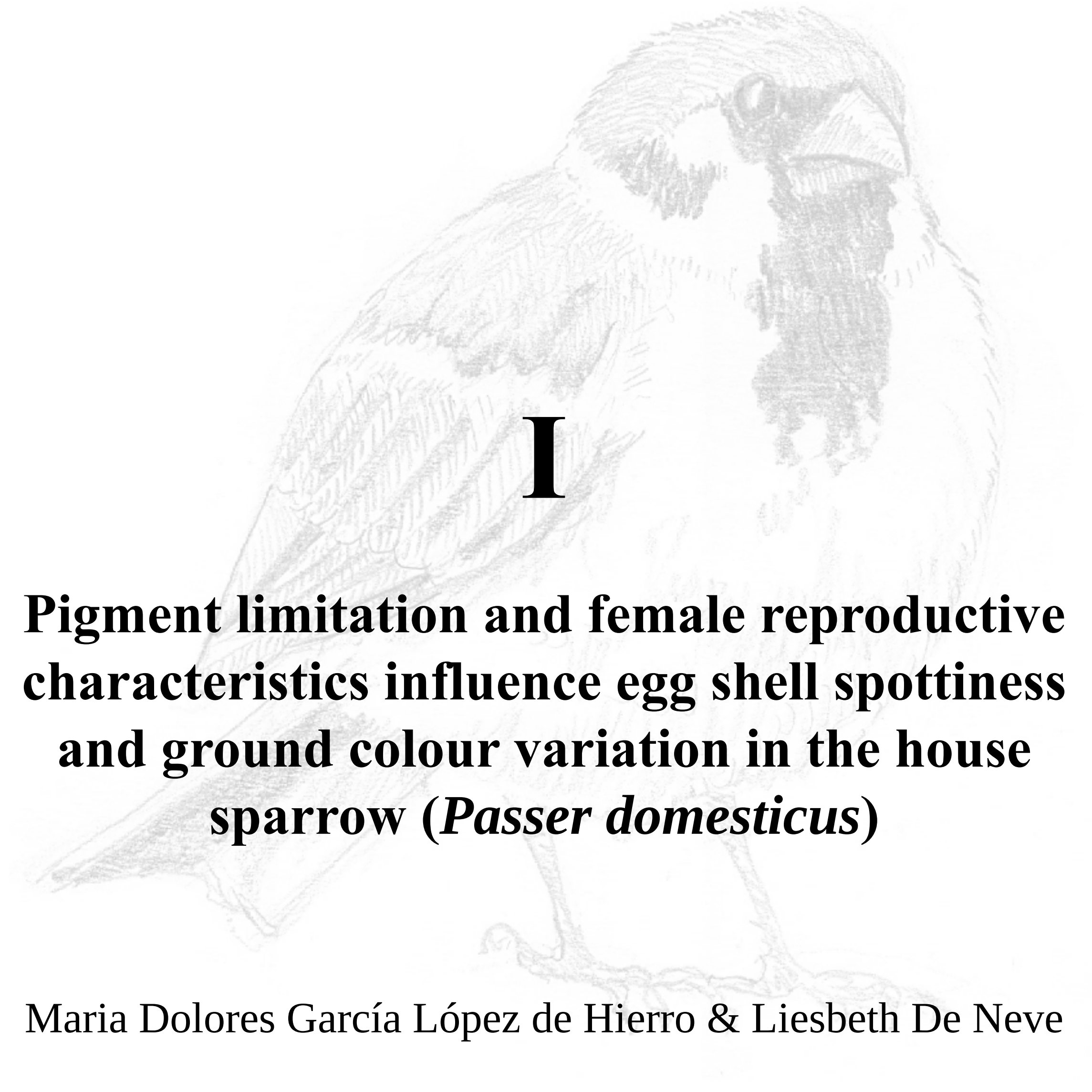

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Pigment limitation and female reproductive characteristics influence egg shell spottiness and ground colour variation in the house sparrow (*Passer domesticus*)

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Pigment limitation and female reproductive characteristics influence egg shell spottiness and ground colour variation in the house sparrow (*Passer domesticus*)

Summary

In the present study we investigated the egg colour patterns of the same females over several consecutive years in a captive population of house sparrows (Passer domesticus). The objectives were (1) to estimate the importance of genetic influences, (2) to study if pigment deposition may be limited for laying females and (3) to explore if indicators of female quality (i.e. clutch size, age) affected egg colour patterns. Our results showed the existence of a genetic basis which determines the egg patterns of a given female. Furthermore, egg ground colour and the intensity and size of spots diminished according to the position in the laying sequence, indicating a limited capacity to deposit these pigments for each reproductive event. Moreover, young females and females with larger clutches laid more densely spotted eggs with more intense and larger spots, as well as a larger proportion of eggs with a bluish ground colour, suggesting that both pigmentations may be related to female physical condition. Our results also indicate that the distribution of spots is the egg characteristic which seems to be less influenced by environmental factors.

Keywords: Biliverdin; Protoporphyrin; *Passer domesticus*; Egg colour; Egg shell spottiness

Introduction

The great variation in egg colour in different bird species has always received much attention from evolutionary biologists and numerous hypotheses on the subject have been proposed in recent decades (reviewed in Underwood and Sealy 2002; Kilner 2006). For different bird taxa, this variation has been explained in the context of egg mimicry to face predation risk (e.g. Bakken et al. 1978; Lloyd et al. 2000; Blanco and Bortellotti 2002), to permit egg recognition in the case of brood parasitism (Stokke et al. 1999, 2002; Davies 2000; Soler et al. 2000; Lathi 2005, 2006), or in the context of sexual selection where egg colour may signal the female's physical condition (Moreno and Osorno 2003, Moreno et al. 2006; Soler et al. 2005; Siefferman et al. 2006). Nevertheless, as with any other phenotypic characteristic, the variation in egg colour between females is due to a combination of genetic, environmental and maternal influences. All the proposed functions for egg colour are the outcome of evolutionary processes, thus indicating a genetic basis. It is therefore important to understand the source of variation in order to be able to test the various hypotheses advanced to explain egg colour variation. However, very few studies have analysed the variation in egg colour and spot patterns in this context (Collias 1993; Gosler et al. 2000).

The extensive between-female variation in egg coloration, compared with the low within-clutch colour variation found in numerous studies, suggests that in general egg colour has an important genetic component. The best-studied species in this respect are perhaps the brood parasites. For example, the common cuckoo (Cuculus canorus) uses some ten species as hosts (Moksnes and Roskaft 1995). The interspecific variation in egg patterning of the different hosts has favoured the emergence of distinct lines of female cuckoos, called gentes, which mimic the egg patterns of each of the different host species (Moksnes and Roskaft 1995; Davies 2000). This indicates that genes for egg pattern are located on chromosome W (found only in females) and thus that patterns are inherited exclusively via the maternal line in some species (Punnett 1933; Jensen 1966; Gibbs et al. 2000, but see Mahler et al. 2008). In support of this idea, Gosler et al. (2000) found that in a natural population of the great tit (Parus major) there was strong evidence that egg pattern was under genetic control, explaining over 80% of the variation in all the studied egg colour characteristics, and that the heritability of patterns was linked to the female sex in this species. Collias (1993) concluded that the presence or absence of egg spots in the village weaver (Ploceus cucullatus) is controlled by more than one pair of autosomic alleles but, given the large variation in spot abundance, distribution and type, it is probable that spot pattern is under polygenic control in this species. In the same way, Mahler et al (2008), found no associations between eggshell spotting and mtDNA haplotypes, which suggests that eggshell spotting is not maternally inherited in shiny cowbird (Molothrus bonariensis). Nevertheless, no other studies of natural populations have investigated egg spot patterns to reveal this genetic component.

It is also important to distinguish between spot patterns and eggshell ground colour. In poultry, at least, it is well known that ground colour is under polygenic control (Wei et al. 1992) and is inherited in a Mendelian fashion, through both female and male lines (Hutt 1949; Collias 1993). Thus the mechanisms determining eggshell ground colour and spot patterns are not the same and the genetic variation in these two eggshell characters may be independent of each other.

Genetic influences apart, egg colour is probably also affected by environmental conditions and/or female physical condition. Biliverdin (an antioxidant, responsible for blues and greens) and protoporphyrins (a pro-oxidant, responsible for reds and browns) are the principal pigments responsible for egg colour in birds (Kennedy and Vevers 1976; Miksik et al. 1996; Underwood and Sealy 2002). The results of poultry studies show how the quantity

of protoporphyrins, which gives rise to different ground colour shades in these species, may vary according to diet (Joseph et al. 1999). Recently, Gosler et al. (2005) have proposed that protoporphyrins are used to compensate for localised shell thinness arising from a lack of calcium in the environment , thereby reducing the permeability and water loss during incubation (Higham and Gosler 2006). Jagannath et al. (2008), corroborate the relationship previously reported between shell thinning and DDE contamination (Ratcliffe 1970). However, this relationship was found to be significant only in those eggs in which internalized protoporphyrin spotting was found, reinforcing the view that protoporphyrin pigmentation is related to eggshell thickness. Also in the case of biliverdin, evidence has emerged of the importance of the environment (rainfall and temperature) on the blue/green ground colour of common cuckoo eggs and one of its most important hosts, the reed warbler (*Acrocephalus scirpaceus*) (Avilés et al. 2007). With regard to the hypothesis that egg colouration may signal female physical condition (Moreno and Osorno 2003), a growing number of studies provided support to the hypothesis that the deposition of the antioxidant pigment biliverdin in the eggshell may depend on the higher antioxidant capacity of laying females, and thereby be indicative of female quality (Moreno et al. 2006; Krist and Grim 2007; Soler et al. 2008). In fact, a positive relationship has been detected between eggshell ground colour intensity and the immune system in female pied flycatchers (*Ficedula hypoleuca*; Moreno et al. 2005) or the eurasian sparrowhawk (*Accipiter nisus*; Jagannath et al. 2008), and with physical condition in female eastern bluebirds (*Sialia sialis*; Siefferman et al. 2006), collared flycatchers (*Ficedula albicollis*, Krist and Grim 2007). This positive relationship with female physical condition has recently also experimentally been manifested in pied flycatchers (Moreno et al. 2006) and spotless starlings (Soler et al. 2008).

Nonetheless, a possible relation between egg spots due to porphyrins and female physical condition or reproductive parameters has only received very little attention up till now (Miksik et al. 1994, 1996; Martinez-de la Puente et al. 2007). Protoporphyrins are synthesized in the blood as an intermediate metabolite of haemoglobulin, and are transferred via epithelial cells to the shell gland during egg formation (Baird et al. 1975). Due to the pro-oxidant properties of protoporphyrins (Afonso et al. 1999, Shan et al. 2000), it has been proposed that they could either signal female quality because increased pigmentation would indicate oxidative tolerance (Moreno and Osorno 2003) or, alternatively, be an indicator of poor condition, since high levels of protoporphyrins produce physiological stress that may be reflected in females' physiological response and condition (Martínez-de la Puente et al. 2007). Martínez-de la Puente et al. (2007) found support for the latter hypothesis, since blue tit (*Cyanistes caeruleus*) females that laid more spotted eggs showed poorer body condition, higher cellular concentration of the stress protein HSP70 and marginally lower total immunoglobulin levels in blood plasma.

In the present study, we collected data over a four-year period from various clutches laid by the same females in a captive house sparrow (*Passer domesticus*) population, which was kept under the same environmental conditions: food and water being freely available. This species lays eggs which vary both in ground colour and in the distribution of brownish-red spots (Seel 1968; Lowther 1988). We estimated the underlying genetic influence on maintenance of egg colour pattern (i.e. the extent to which particular females repeatedly lay very similar-looking clutches and to which these differ from those laid by other females). Furthermore, we analysed variation in spot patterns and ground colour according to egg laying order and according to the number of clutches laid. Finally, we determined the influence on variation in egg ground colour and spot patterns of clutch size and female age, two reproductive parameters indicating female quality (i.e. Martin 1987; Christians 2002; Garamszegi et al. 2004; Martínez-de la Puente et al. 2007).

Methods

The study species

The house sparrow nests in cavities or builds enclosed nests on tree branches and performs between one and seven reproductive attempts during each breeding season in Europe (Cramp and Perrins 1994). The species is chiefly monogamous and has a low frequency of extra-pair copulations (Veiga and Boto 2000). The ground colour of house sparrow eggs varies from pure white to bluish and the eggs are covered with spots of diverse size and pigmentation. The distribution of spots varies considerably, from a large patch at the blunt end to a uniform spot pattern across the entire eggshell and the last-laid egg in a clutch tends to be very different from the others (Seel 1968; Yom-Tov 1980; Lowther 1988).

Characteristics of the study population

The study population has been kept in a 45m3 aviary in the Faculty of Science of Granada University since 2003. Due to significant mortality, especially of fledged juveniles in the post-breeding period, the population size was more or less constant (mean 75 ± SE 10 individuals) throughout the study years, with a mean sex ratio of 1:1. The aviary provided 40 nestboxes, of which about 50% were occupied each breeding season. All the sparrows were individually colour-ringed. The birds were provided *ad libitum* with water, seed mix, fly maggots, vitamins, powdered calcium, mineral salts, apple, lettuce and nestling food. They were also provided with a sand tray for their habitual dust-baths. Cotton wool and plant material was provided for nest construction during the breeding season. The artificial illumination was regulated by a timer which kept the birds at the same photoperiod as the external environment.

General methods

The study was carried out during the breeding seasons of 2003-2006 inclusive. Daily observations were done from the start of each breeding season to identify pair members and their nest boxes as well as possible changes in pair-composition or of nest box use. The nest boxes were examined daily to obtain information on the process of nest building, clutch size, laying order and the number of clutch. Throughout the study there were no instances of two eggs being laid in the same day in any of the nest boxes, so there is practically no chance that any of the eggs in the studied- clutches was deposited by another female (Petrie and Møller 1991; Jackson 1992).

Female age (between one and at least five years) was also included in the analyses. Birds were captured from the wild in the winter of 2002/03, thus the ages of females which were not born in captivity were taken to be at least the number of years they spent in captivity, plus one year.

All nestlings were colour-ringed at 12 days of age with two rings of the same colour on the left leg to indicate birth-year, and with a colour combination of two rings on the right leg distinguishing individuals. We were thus able to know the ages of breeding birds and to identify the female descendants of each breeding female in successive years.

Evaluation of egg characteristics

During the course of the study 206 complete clutches, laid by 33 different females, were photographed against a neutral grey card, incorporating a colour chart, using a Minolta Dimage 7 digital camera.

Assessments of egg characteristics were carried out for each egg from the photographs (n = 830 eggs). Clutches of 19 females were photographed in only one year, either because the birds died during the next winter or because they laid their first clutch in 2006, the final year of study. However, for these females, except for three, we had information on at least two consecutive clutches during the same breeding season. Information from two or more years was available for 14 females. With respect to first-time breeders, we obtained photos of clutches of two females in 2005 and seven in 2006. Clutches laid by first-time breeders in 2004 were used in a parallel experiment which did not permit complete clutches to be photographed and so these were not used to contribute first-time breeder data to the present study. Thus, in total we obtained data from 9 first-time breeders and 25 adults females, from which one of the first-time breeders past to adult in the following breading season.

The same observer assessed the photos of each clutch against the following parameters, following the criteria and methodology of Gosler (1993): Principal classes: A) Spot Intensity: (1) feint, (2) pale, (3) medium, (4) some intense spots , (5) all spots intense; B) Spot Distribution, approximate percentage spots covering the egg-shell in one-half, typically the blunt end: (1) > 81%, (2) 71-80%, (3) 61-70%, (4) 51-60%, (5) 50%; in this variable, the class 1 indicate that most of the spots are in the blunt end of the egg (i.e. low distribution of spots) and in the rest of the classes the spot distribution increases to class 5 which indicates that the spots are distributed among the whole egg-shell. C) Spot Size: (1) small, (2) medium, (3) large. And finally, shell ground colour: white, brownish-white, bluish-white, or bluish. Unspotted eggs received a 0-quote for all the spot-parameters.

Repeatability of the observer’s assessments was estimated by evaluating the characteristics of 280 eggs from the 63 clutches of 16 females in 2003 twice (Lessells and Boag 1987). The second evaluation took place 15 days after the first. Repeatability of the observer’s assessments was highly significant for all variables ($P < 0.0001$ in all cases). Thus, clutches were evaluated once only in the following years and the data from the first assessment of 2003 were used.

Statistical analyses

A General Linear Mixed Model (GLMM) was used to determine the variables which best explained variation in intensity, distribution and size of spots.

Given the very low percentage of eggs with a brownish-white and bluish-white ground colour (see Results), these eggs were not included in the analysis to determine which reproductive parameters best explained variation in eggshell ground colour, to avoid a possible dilution of the effects of the explanatory variables. In this case a Generalized Linear Mixed Model (GLIMMIX) was used in which the dependent variable (ground colour) had a binomial distribution (0 = white ground colour, 1 = bluish ground colour, logit link function).

In all analyses laying order, clutch size and the number of clutch were considered as covariables in all analyses. Also, to determine whether there are differences in egg colour pattern according to age, we included in the analysis a variable to distinguish between age classes (1 = first-time breeders, 2 = middle age, two and three years old and 3 = advanced age, ≥ four years old) as a fixed factor using Bonferroni adjustment. The variables female identity and year were included as random factors to determine whether differences existed in egg colour patterns between females, and to take into account possible random variation

due to study year and in this way avoid pseudo-replication. From these analyses we obtained the variance of ground colour, intensity, distribution and size of spots explained by female identity.

The model residuals followed a normal distribution (Kolmogorov-Smirnov: $p > 0.2$), justifying the validity of the models. Since the explanatory variables may be correlated, a forward and backward stepwise procedure was used to test the significance of each variable one by one, adding (forward) or eliminating (backward) only those variables which resulted in the largest increase of fit in the model. This procedure results in the model which most adequately explains the variation of the dependent variable. We used the Akaike criterion to decide the best fit model (AIC, Akaike 1973).

The random factors were never excluded from the models, even when they did not have a significant effect, to take random variation due these factors into account.

The degrees of freedom of the GLMM and GLIMMIX models were calculated using the Satterthwaite method (Fai and Cornelius 1996).

The GLMM and GLIMMIX procedures were performed using the SAS program (SAS 1989-96 Institute Inc., Cary, NC, USA; Littell et al. 1996).

Results

Female identity had a significant effect on all egg colour pattern characteristics but the year had no significant effect on any of them (Tables 1 and 2).

The spot intensity was significantly influenced by the clutch number, egg laying order and female age (Table 1). Spot intensity increased with clutch number, i.e. the last clutches laid by a given female had more intense spots than the first ones. Also, the first eggs within a given clutch were more intensely spotted than the final ones (Table 1). Spot intensity also tended towards a positive correlation with clutch size, although this was not significant (Table 1). Finally, older females had the less intense spots (Table 1, Fig.1a), existing no significant difference between first time breeders and middle-age (GLMM Bonferroni corrected: $P = 0.315$, Fig.1a) but yes between first time breeders and older females (GLMM Bonferroni corrected: $P = 0.003$, Fig.1a) and middle-age and older females (GLMM Bonferroni corrected: $P < 0.001$, Fig.1a).

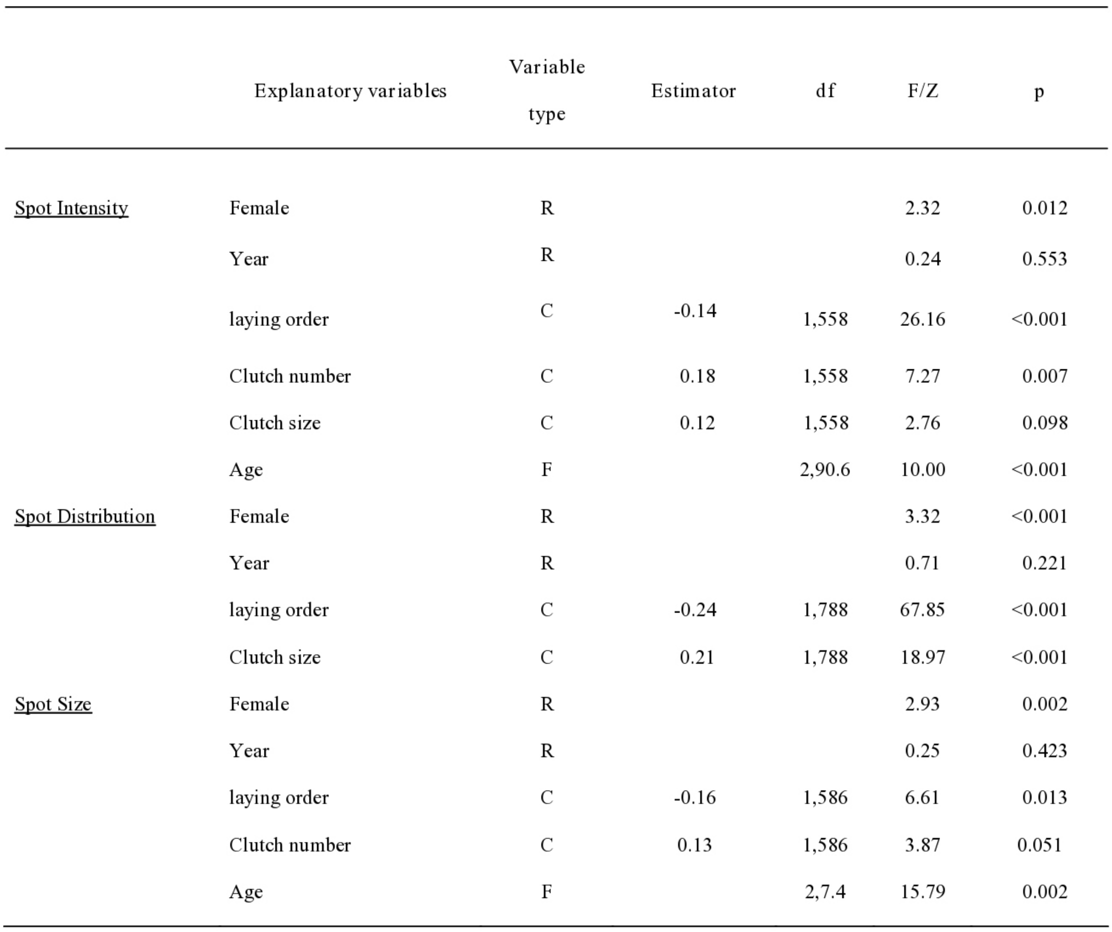
Spot distribution diminished significantly according to an egg’s position in the laying sequence, but increased with clutch size (Table 1).

Spot size increased significantly with clutch number but showed a significant negative correlation egg laying order (Table 1). Also female age affected significantly spot size (Table 1). Spot size was very similar between first time breeders and middle-age breeders (GLMM Bonferroni corrected: $P = 0.82$, Fig.1b), but older females had smaller spots compared to both first time breeders (GLMM Bonferroni corrected: $P = 0.01$, Fig.1b) and middle-age breeders (GLMM Bonferroni corrected: $P = 0.01$, Fig.1b).

On the other hand, the variance attributable to female identity in spot patterns was higher for spot distribution (40.5%) than for spot intensity and size (7.4% and 10% respectively). Also, spot intensity and size covaried significantly between them but not with spot distribution (Intensity/Size: F1,32 = 100.7; $P < 0.001$; Intensity/Distribution: F1,32 = 1.5; $P = 0.2$; Distribution/Size: F1,32 = 3.4; $P = 0.1$).

With respect to ground colour, within the study sample of 830 eggs, 69.6 % were white, 1.4 % were brownish-white, 3.8 % bluish-white, and 25.1 % were bluish. Ground colour (white vs bluish) was significantly influenced by clutch number, clutch size, laying

order and female age (Table 2). The last clutches of the season had more white eggs than the earlier ones and eggs from small clutches were mainly white. Within a clutch, the last-laid eggs were mainly white ones and older females laid a higher proportion of white eggs (first time breeders = 67.9 %, middle-age = 64.8 %, older females = 85.0 %). Only 5 % of the ground colour variance was attributable to female identity.



	Explanatory variables	Variable type	Estimator	df	F/Z	p
Spot Intensity	Female	R			2.32	0.012
	Year	R			0.24	0.553
	laying order	C	-0.14	1,558	26.16	<0.001
	Clutch number	C	0.18	1,558	7.27	0.007
	Clutch size	C	0.12	1,558	2.76	0.098
	Age	F		2,90.6	10.00	<0.001
Spot Distribution	Female	R			3.32	<0.001
	Year	R			0.71	0.221
	laying order	C	-0.24	1,788	67.85	<0.001
	Clutch size	C	0.21	1,788	18.97	<0.001
Spot Size	Female	R			2.93	0.002
	Year	R			0.25	0.423
	laying order	C	-0.16	1,586	6.61	0.013
	Clutch number	C	0.13	1,586	3.87	0.051
	Age	F		2,7.4	15.79	0.002

Table 1. *GLMM models which best explained variation in Intensity, Distribution and Size of spots . The “Variable Type” column indicates whether a variable was regarded as a covariable (C), fixed factor (F) or random factor (R). F values are given for covariables and fixed factors and Z values for random factors. The sign of the estimator indicates a positive or negative relation between covariables and the dependent variable.*

	Explanatory variables	Variable type	Estimator	df	F/Z	P
Ground colour	Female	R			2.65	0.004
	Year	R			1.03	0.151
	laying order	C	-0.23	1,515	10.24	0.001
	Clutch number	C	-0.28	1,535	11.64	< 0.001
	Clutch size	C	0.29	1,536	7.49	0.006
	Age	F		2,36.4	5.96	0.018

Table 2. *GLIMMIX model which best explained variation in egg ground colour (binomial distribution variable, logit link function). The "Variable type" column indicates whether a variable was regarded as a covariable (C), fixed factor (F) or random factor (R). F values are given for covariables and fixed factors and Z values for random factors. The sign of the estimator indicates a positive or negative relation relation between covariables and the dependent variable.*

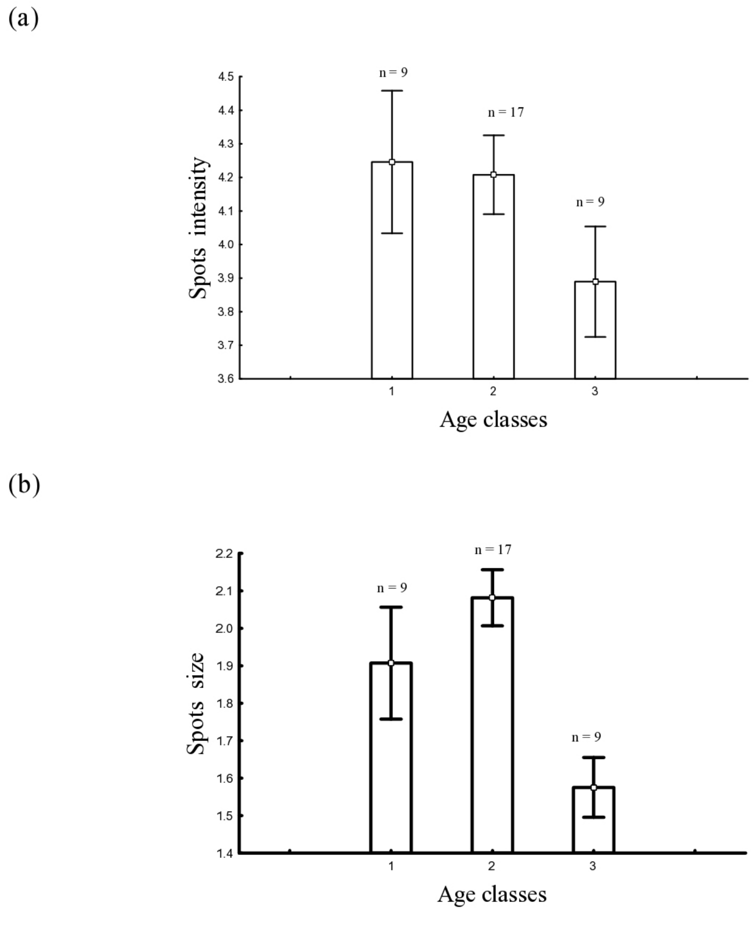


Figure 1. *The difference in* ***(a)*** *spot intensity and* ***(b)*** *spot size between the three age classes (1 = first-time breeders, 2 middle age = two and three years old, 3 advanced age = ≥four years old).*

Discussion

The genetic component of egg coloration

According to our results, house sparrow egg colour was significantly determined by female identity. This may indicate the existence of an important genetic component which maintains egg colour pattern in this species within a relatively narrow range of environmental variation. Our results are in accordance with studies of the village weaver, where both ground colour and spot patterns were found to be genetically determined (Collias 1993), or of the great tit, where the spot pattern of eggs laid by a particular female was repeatedly similar and where female identity explained over 80 % of the variation in all egg parameters (Gosler et al. 2000).

In house sparrows, the amount of colour pattern variance explained by female identity was between 5 % and 10 % for ground color, spot intensity and size, and 40.5% for spot distribution. Ground colour was significantly explained by all studied environmental variables (Table 2). Spot intensity and size were influenced by the same environmental variables (laying order, clutch number and female age) and there existed a significant covariance between both. Spot distribution, on the other hand, was affected only by laying order and clutch size and was not significantly related to the intensity or size of spots. These results suggest that the ground colour, intensity and size of spots may have a larger environmental component than spot distribution.

Pigment limitation

The first clutches within a given breeding season had a higher proportion of bluish eggs compared to final clutches. In addition, the last laid eggs within the clutch were more likely to be white than bluish. This is in accordance with previous findings on free-living populations of pied flycatchers and collared flycatchers where the proportion of blue eggs was larger among first laid eggs within the clutch (Moreno et al. 2005; Krist and Grim 2007). Our results then indicate the possible cost of maintaining the same level of investment in ground colour throughout the clutch and throughout the breeding season, even when food is freely available.

All three variables related to red-brown spottiness of eggs diminished according to egg laying order, last laid eggs in the laying sequence were less spotted and showed smaller and less intense spots than first laid eggs. This suggests that, at least at short term, the deposition of protoporphyrin would be limited for females. The increasing intensity and size of spots across the breeding season could show no limitation in the deposition of protoporphyrin at long term.

Reproductive variables and egg shell patterns

Both clutch size and female age affected significantly the proportion of bluish eggs. Female house sparrows laying larger clutches had a higher proportion of bluish eggs and, furthermore, the proportion of bluish eggs declined with female age. Our results are in accordance with recent findings in pied flycatchers (Moreno et al. 2005), eastern bluebirds (Siefferman et al. 2006) or collared flycatchers (Krist and Grim 2007) relating female age and/or physical condition to investment in bluish ground colour, thereby further supporting the hypothesis that also in house sparrows blue eggs may signal female quality (Moreno and Osorno 2003).

Our results show that pigmentation (spot intensity and size) increased with the number of clutches. It can be expected that, in general, female condition would diminish according to the course of the breeding season (review in Christians 2002). Even though food was freely available in our captive population, females most likely suffered the reproduction cost of raising previous clutches near the end of the season. So if spottiness were an indicator of females' condition (Miksik et al. 1994, 1996; Martínez-de la Puente et al. 2007), less pigmented eggs within the same female are expected in clutches laid at the end of the breeding season. However, our results show a contrary tendency and, then, rather supporting the hypothesis that females in worse condition laid more pigmented clutches (Martínez-de la Puente et al. 2007) or that the course of the breeding season was not costly for the deposition of brownish pigments at long term in house sparrows in captivity conditions.

On the other hand, larger clutches had more densely spotted eggs with more intense spots compared to small clutches. Since clutch size is a reliable indicator of female quality (review in Martin 1987; Christians 2002), these results could support the hypothesis that only females of better quality were able to lay more pigmented eggs (Moreno and Osorno 2003). In this context, our study rather supports the hypothesis that red-brownish pigmentation of eggs could indicate the higher capacity to withstand the pro-oxidant protoporphyrin or remove it more efficiently to the eggshell, thereby indicating female quality (Moreno and Osorno 2003). Furthermore, spottiness showed also a relationship with females' age. The intensity and size of spots diminished with age; young females laying more pigmented eggs. In addition, eggs of first-time breeders had similar spot intensity and size than middle-age breeders, but older females had significantly less intensity and smaller spots. It is known that first-time breeding females tend to have less reproductive success due to their inexperience (Parsons 1975; Hatchwell 1991; Brinkhof et al. 1993), and/or their lower quality (e.g. less capacity to defend a good territory; lower social dominance; see e.g. Forslund and Pärt 1995). However, findings on a linear relationship between female condition and age are rather trivial, there are evidences of females increasing condition with age (review in Christians 2002; Martínez-de la Puente et al. 2007; Krist and Grim 2007), but on the other hand, there is also evidence that elderly females may display a poorer physical condition than those of intermediate age (Clutton-Brock 1988; Newton 1989; Stearns 1992; Robertson and Rendell 2001; Moreno et al. 2005). In fact, the difference in reproductive parametres between the most extreme age classes has been found to be generally very small (Gratto et al. 1983; Lequette and Weimerskirch 1990; Wiggins 1990; Weimerskirch 1990; Robertson et al. 1994; Flint and Grand 1996; Viñuela 1997). So, old females, laying less pigmented eggs, probably experience worse physical condition than females at intermediate age. Our results, then, are not in agreement with the positive relation found between blue tit female age, condition and egg pigmentation (Martínez-de la Puente et al. 2007). They found that females laying less spotted eggs with less reddish spots were in better condition, which in turn was positively related with age. However, only two age classes where distinguished (yearlings and adults (two or more years old)). Then the possible effect of a lower condition at older age on egg pigmentation could not be taken in account in that study.

Conclusions

Our captive population of house sparrow showed the existence of a genetic basis which determines the egg patterns of a given female. The distribution of spots is the shell characteristic which tended to be less influenced by environmental factors. Furthermore, both spots and ground colour deposited in the egg shells diminished according to the position of each egg in the laying order, indicating a limited ability of depositing pigments for each reproductive event. Moreover, females with larger clutches and no advanced age laid more densely spotted eggs with more intense and larger spots, as well as a larger

proportion of eggs with a blue ground colour, suggesting that both pigmentations may be related to female quality.

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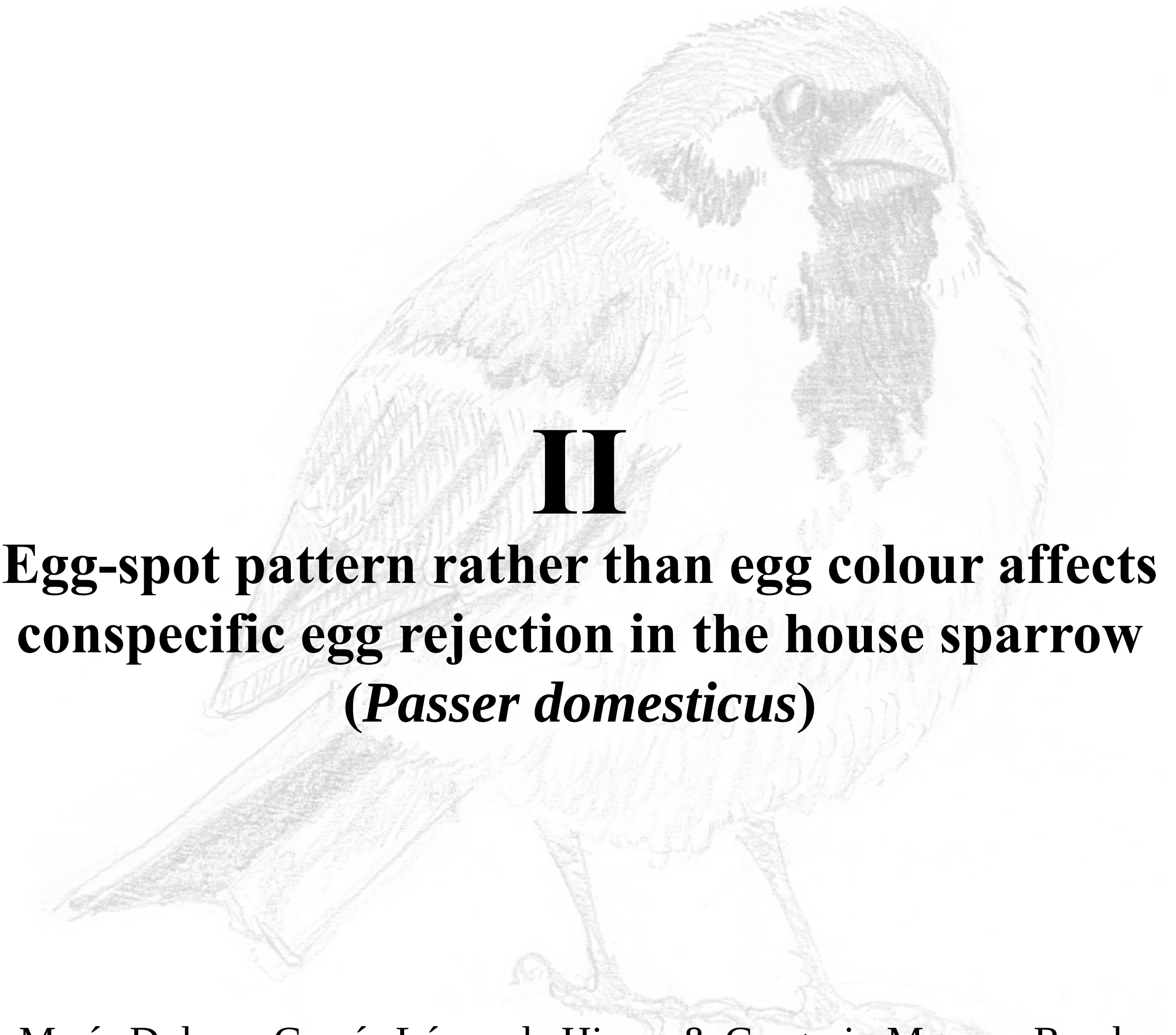

II

Egg-spot pattern rather than egg colour affects conspecific egg rejection in the house sparrow (*Passer domesticus*)

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Aceptado en Behavioral Ecology and Sociobiology

Egg-spot pattern rather than egg colour affects conspecific egg rejection in the house sparrow (*Passer domesticus*)

Abstract

Brood parasitism could be a selective pressure on each female to have a type of egg that permits recognition. House sparrow (*Passer domesticus*) undergoes conspecific brood parasitism and can recognize parasitic eggs. In this study, we analyse the effect of relative size in experimental parasitic eggs compared to the host eggs. We modify egg colour and the spot pattern to determine the influence of these characteristics on egg rejection. Furthermore, we examine whether egg rejection increases with "stimulus summation". Our results show that egg rejection is not affected by relative egg size. However, the change in the spot pattern proved to exert the highest influence on egg rejection (32.4% of trials), significantly higher than when only egg colour is changed (3.8%). Therefore, our results suggest that parasitism may be a pressure favouring the maintenance of spotted eggs in house sparrow.

Keywords: Egg rejection, Conspecific brood parasitism, House sparrow, *Passer domesticus*.

Introduction

Bird eggs vary considerably among females within a species in terms of size, colour, and spot patterns, and various hypotheses attempt to explain this variability (reviewed in Underwood and Sealy 2002; Kilner 2006). A function of variability in egg colour and spot pattern may be to facilitate egg recognition of foreign eggs in species with interspecific or conspecific brood parasitism (Victoria 1972; Freeman 1988; Davies and Brooke 1989a, b). Sexual selection has been also invoked to explain intraspecific variation in egg colour (Moreno and Osorno 2003; Soler et al. 2005). Spotted eggs have been related to crypsis against depredation in open nests, with eggs from hole-nesting birds being frequently spotless (Kilner 2006). Independently of functional hypotheses, egg colour and spot patterns are also affected by environmental and female conditions (Gosler et al. 2005; Avilés et al. 2007; Martinez-de la Puente et al. 2007). Egg size, although highly repeatable within females, also varies among females of the same species (reviews in Williams 1994; Christians 2002).

Conspecific Brood Parasitism (CBP) is a reproductive tactic by which a female lays eggs in nests of conspecific individuals, which then care for the eggs and young (Yom-Tov 1980; Andersson 1984; Rohwer and Freeman 1989; Petrie and Møller 1991). CBP imposes costs to hosts such as reduced incubation efficiency, increased mortality of own young, or increased investment in parental care (Møller 1987; Evans 1988; Hepp et al. 1990). For this reason, hosts are selected to develop antiparasitic defences such as the recognition and rejection of parasitic eggs (Petrie and Møller 1991). Therefore, CBP would favour each female to have an egg type that reduces the intraclutch egg variability and increases the difference among females in a population (Victoria 1972; Collias 1984; Freeman 1988). In fact, colour and spots pattern have a genetic component (Wei et al. 1992; Collias 1993; Gosler et al. 2000). This would facilitate the learning of the egg characteristics (Rothstein 1974, 1975, 1978; Lotem et al. 1995; Hauber and Sherman 2001; Petrie et al. 2009), and egg characteristics kept to a lesser variation within the clutch would serve to recognize the presence of parasite eggs (Stokke et al. 1999; Davies 2000; Soler et al. 2000).

The influence that only one feature of the eggs exerts on recognition and rejection may be less important than the summation of several egg features, due to the effect of a "stimulus summation" (Rothstein 1982). Among the characteristics of the eggs that could generate the recognition and rejection of foreign eggs, are egg size, ground colour, and the colour, size and density of spots. In the village weaver, Ploceus cucullatus, which is host to other species as well as conspecifics, each female lays one type of egg different from the others throughout their lives, with different ground colours, both spotted as well as unspotted (Victoria 1972; Collias 1984). Females reject eggs that differ from their own in the ground colour, and when the ground colour of parasite eggs is within the range of host clutch, the presence or absence of spots determines the rejection (Victoria 1972). Parasitic cuckoos lay relatively small eggs for its body size presumably to match the host eggs in size and increase the chance of acceptance (Payne 1974). Recent experiments have confirmed that some hosts can discriminate against foreign eggs based on its size (Marchetti 2000).

The house sparrow, Passer domesticus, despite nesting in holes, lays spotted eggs, which vary both in ground colour and in the density of brownish-red spots (Seel 1968; Lowther 1988; Harrison 1991). House sparrow egg colour is determined by female identity, but variability between and within clutches of the same female remains (López de Hierro and De Neve unpublished data). House sparrows suffer CBP at a rate of 0–12% (Manwell and Baker 1975; Kendra et al. 1988; Cordero et al. 1999; Veiga and Boto 2000; López de Hierro and Ryan 2008), and have the ability to recognise and reject eggs at a rate around of 32-35% (Kendra et al. 1988; Moreno-Rueda and Soler 2001; López de Hierro and Ryan

2008). Egg rejection is costly in house sparrow, which lose 44.4% of their eggs, the abandonment of the clutch being usual (Moreno-Rueda and Soler 2001).

The goal of the present study is (1) to analyse the effect of egg characteristics (egg size, colour, and spot patterns) on egg rejection; (2) to determine which egg characteristics most influence the egg rejection in the house sparrow; and (3) to examine whether the rejection of experimental eggs increases owing to the "stimulus summation," when more than one egg characteristic is modified. For this, we collected data over a four-year period from various clutches laid by the same house sparrow females.

Materials and Methods

The study species

House sparrows nest in cavities or build closed nests among tree branches (Cramp and Perrins 1994) and are chiefly monogamous, with a low rate of extra-pair copulations (Veiga and Boto 2000). Egg size is highly repeatable for a particular female (Anderson 2006), and it does not seem to be affected by the advance of the breeding season (Veiga 1990; Anderson 1998; although see Lowther 1990), or the clutch size (Lowther 1990; Veiga 1990; Marcos and Monrós 1994). Nevertheless, egg size of the last egg frequently varies within a clutch (Lowther 1990; Marcos and Monrós 1994). The ground colour of house sparrow eggs varies from pure white to bluish and there are a small percentage of brownish eggs (in our females, 1.4 %, n = 830 eggs; López de Hierro, unpublished data); the eggs have spots of varying size and brown tones, and the density of spots varies considerably, from a large patch at the blunt end to a uniform spot pattern throughout the entire eggshell (Summers-Smith 1963; Dawson 1964; Harrison 1991; Figure 1, column 1). The last-laid egg in a clutch tends to be strikingly different from the others in colour features and size (Seel 1968; Lowther 1988; Anderson 2006).

Characteristics of the study captive nesters

The individuals used in the study had been kept in a 45 m3 indoor aviary in the Science Faculty of the University of Granada since 1999. The number of individuals was more or less constant (mean 75 ± SD = 10 individuals) throughout the study years, with a sex ratio around 1:1. The aviary provided 40 nest boxes, about 50% of which were occupied each season. All the sparrows were individually colour-ringed. The birds were provided ad libitum with water, seed mix, fly maggots, vitamins, powdered calcium, mineral salts, apple, lettuce and nestling food (more details in Moreno-Rueda and Soler 2002). They were also provided with a sand tray for their habitual dust-baths. Cotton wool and plant material were provided for nest construction during the breeding season. The artificial illumination was regulated by a timer which kept the birds at the same photoperiod as the external environment.

Previous studies of the same individuals revealed that egg rejection rate in experimentally parasitized nests was 23-30% (Moreno-Rueda and Soler 2001), a frequency not significantly different from rejection rates founded in natural populations (35 %, Kendra et al. 1988; 33 %, López de Hierro and Ryan 2008). Therefore, it seems that captive conditions do not affect the rejection behaviour in house sparrow.

General methods

The study was carried out during the breeding seasons of 2003-2006 inclusive. Daily observations were made from the start of each breeding season to identify pair members and their nest boxes as well as possible changes in pair-composition or of nest box use. The nest boxes were examined daily to gather information on the nest-building process, laying date, laying order, clutch size, clutch number per season, and instances of CBP. We inferred brood parasitism if two new eggs were laid on the same day (Yom-Tov, 1980), given that this species lays one egg every 24 h (Cramp and Perrins 1994), but throughout the study, there were no instances of two eggs being laid on the same day.

Experimental design

Egg size

A conspecific egg was placed in different clutches (n = 21) of 8 females during 2003, 2004 and 2005 breeding season to determine whether egg size influences parasitic-egg rejection (there is no significant difference in egg rejection among clutches and years; Moreno-Rueda and Soler 2001, and unpublished data). The experimental egg was added to the host's nest when the second or third host egg was laid and before the onset of incubation. Fresh natural eggs were used in our experiments since it has been shown that artificial eggs increase the costs of rejection and so may influence the decision to accept or reject the experimental egg (Martín-Vivaldi et al. 2002). All experimental eggs used in this study were supplied by other nests of the captive nesters who did not participate in this experiment. Eggs were collected the day they were laid and transferred to another nest, or kept fresh in a refrigerator for almost a day. The experimental eggs were photographed with the complete host clutch using a Minolta Dimage 7 digital camera. For each photo, we placed the eggs on a Kodak neutral-grey card that included a ruler to correct the egg-size measurements in order to examine differences in egg size among the female's own eggs and the foreign egg. Egg maximal length (L) and maximal width (W) were assessed for eggs from the photographs using the ruler tool of the Photoshop program. With the same tool, we evaluated the result measured for a centimetre in the ruler on the Kodak neutral-grey card. With the value obtained when measuring this real centimetre the egg measurements were corrected. Afterwards, the egg length and width were used in the volume formula ($V = 0.498 \times W2 \times L$; Spaw and Rohwer 1987).

Repeatability of the observer's assessments was estimated by measuring these characteristics twice in 81 eggs (Lessells and Boag 1987). The second measures took place 15 days after the first. Repeatability of the observer's assessments was highly significant for the all variables ($R = 0.9$, $P < 0.0001$). There was no significant differences when egg size was measured with calliper or with photos (Wilcoxon matched pairs: $Z = 1.26$, $P = 0.21$, $n = 20$).

Modification of egg features

For 21 females, we modified the colour and spot pattern of their own eggs features in successive clutches (n = 59) to determine whether such modifications influence egg rejection. The features modified were (a) egg colour (n = 12), (b) spot size (n = 14), (c) spot density (n = 14), and (d) a+b (n = 10), and (e) b+c (n = 9) to determine how the modification of more than one factor influenced egg rejection. All modifications were made to five females.

The egg features were modified with plastic paint (Titanlux © brown tobacco nº 544) as follows: (a) for the egg colour, the plastic paint was diluted so as not to hide the pattern of the spots and without affecting the hatching of the experimental eggs. The tone produced was darker than the original ground colour but similar to the original colour of the spots in order not to change this factor (see Fig. 1). (b) The size of ten spots chosen randomly was increased by 25% with a nº 7 brush. These spots were distributed throughout the egg so that the female could notice the change in the spots despite the constant rotation of eggs during incubation. The painting was consistent with the original colour of the spots (Fig. 1). (c) Spot density was increased painting 30 spots evenly distributed with the same colour and size as the rest of the spots on the egg (Fig. 1). (d) Change in egg colour and size of spots; and (e) size and density of spots on the same egg, were changed following the methods described above.

Figure 1. *Experimental modification of egg colour and spot pattern. On the right are real house sparrow eggs, and on the left, the modifications in egg colour (A), spot size (B), spot density (C), egg colour plus spot size (D), and spot size plus spot density (E). The real eggs are from the same clutch where the experimental eggs were modified.*

Egg rejection

The following responses to experimental eggs were noted during the daily inspections: (1) acceptance, the experimental egg remained in the nest until at least one egg hatched; (2) ejection, the experimental egg disappeared or was found crushed inside the nest; (3) egg-burial, when the experimental egg was found buried in the nest lining; (4) clutch desertion, the entire clutch was found cold after incubation began. Responses 2, 3, and 4 were considered egg rejection.

Statistical analyses

To determine whether the size of the experimental egg or the change in the characteristics of the egg influenced rejection, we used a Generalized Linear Mixed Model (GLIMMIX; Littell et al. 1996), in which the dependent variable (egg rejection) had a binomial distribution (0 = acceptance, 1 = egg rejection), associated to a logit function. To value the effect of egg size, the explanatory variables were the size of the female's own eggs, experimental egg size, and the difference between the mean size of the female's own eggs and the experimental egg size. In experiments on egg-feature modifications, the treatments were included as a fixed factor. To determine whether "stimulus summation" influences egg rejection, we performed an analysis with a variable to differentiate the treatment with one modification or two modifications as a fixed factor. Female and year variables were introduced as random factors in all GLIMMIX analyses. The inclusion of female identity in the analyses precluded pseudoreplication. In the study, we used non-related females and experienced breeders. Hosts may learn to recognise a foreign egg better after a successful rejection (Hauber et al. 2006). Nevertheless, this is not the case in the house sparrow, in which a successful rejection did not affect the future host responses (unpublished data).

After results for the GLIMMIX of egg-feature modification, and the large differences in percentages of egg rejection between treatments varying in colour (treatment a) and those varying spot pattern (treatments b, c, d and e), another analysis was performed (GLIMMIX), comparing the two major types of modification (0 = egg colour, 1 = spot pattern). In this analysis, we included data from an experiment varying egg colour, but not spot patterns, performed on 14 different females in 2001. In this experiment, we varied the egg colour with plastic blue paint (Titanlux © blue nº 347). We included these data to increase the sample size of egg-colour modification, because there was no difference in response between the two experiments (Chi-square test: $\chi 2$ Yates corrected = 0.01, P = 0.9). The GLIMMIX analysis was carried out in the same manner as the previous ones, including the two major types of modification (egg colour and spots patterns) as a fixed factor.

The models residuals adjusted to a normal distribution (Kolmogorov-Smirnov: $P > 0.2$; Siegel and Castellan 1988). To decide the best fit model of GLIMMIX, we used the Scale Disperse criterion (Scale Disperse > 0.98 in all analyses; Littell et al. 1996). The degrees of freedom of GLIMMIX models were calculated using the Satterthwaite method, and for this reason the degrees of freedom vary among analyses. This method is recommended for unequal group variances (Fai and Cornelius 1996). The GLIMMIX procedures were performed using the SAS program (SAS 1989-96 Institute Inc., Cary, NC, USA; Littell et al. 1996).

Results

The egg size differed more between females than within females (ANOVA: F1,13 = 206.3, P < 0.001). The experiment of a foreign-egg introduction generated 33.4% of egg rejection (n = 21). The female's own egg size did not influence egg rejection (GLIMMIX: F1, 3.3 = 0.1, P = 0.9), as well as the experimental egg size (F1,3 = 0.3, P = 0.6). Egg rejection was not affected by the difference between the female's own egg size and experimental egg size (F1,14 = 0.1, P = 0.8).

In experiments modifying the features of female's own egg, 27.1% of the modified eggs were rejected (n = 59), but there were no significant differences in the response to the treatments (GLIMMIX: F4,27 = 0.8, P = 0.5). Although the change in the colour generated the lowest percentage of rejection, and the size of spots resulted in the highest (Fig. 2). The change of more than one feature in the same egg did not influence the egg rejection more than in the treatments with only one modification (GLIMMIX: F1,48 = 0.2, P = 0.6; Fig. 2). However, significant differences were found in the response on egg colour vs. spot-pattern modification (GLIMMIX: F1, 37 = 6.0, P = 0.02), with egg-colour modification resulting in a lower egg rejection rate (3.8%, n = 26) than spot-pattern modification (32.4%, n = 37).

Frequencies of egg rejection in this study (27-33%) did not significantly differ from those found in previous studies in the same captive nesters (23-30%, Moreno-Rueda and Soler 2001) neither in wild populations (35%, Kendra et al. 1988; 33%, López-de-Hierro and Ryan 2008) (Fisher Exact Test, always P > 0.5). The frequency of egg rejection did not vary with own host spots colouration (r = 0.01, P = 0.96), spots distribution (r = 0.18, P = 0.63) or spots size (r = 0.16, P = 0.66, n = 20 in all cases).

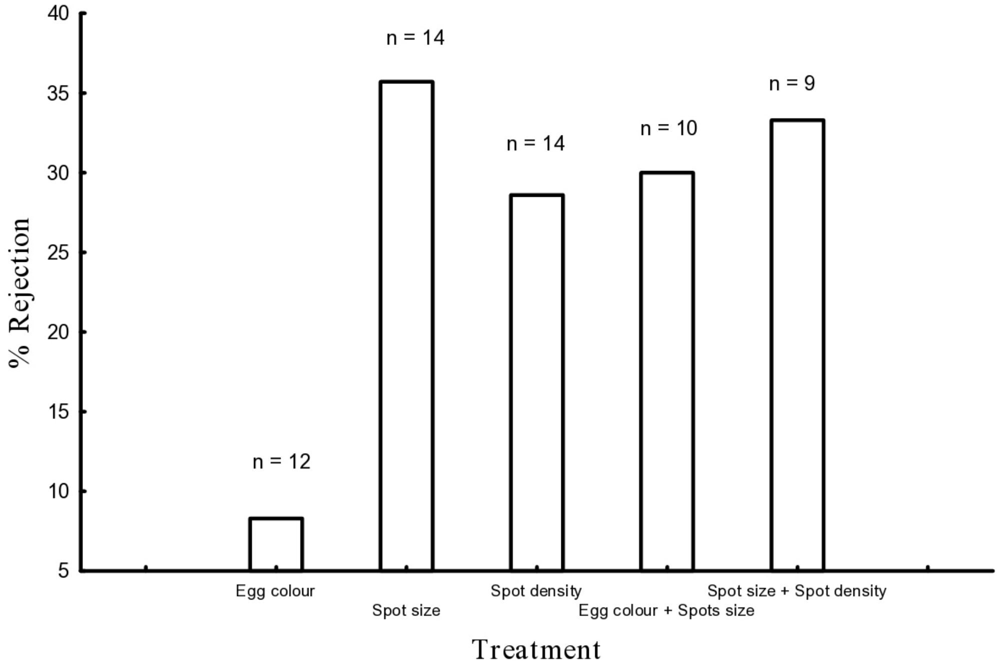

Figure 2. *Egg rejection percentages of modified eggs for colour and/or spot traits*

Discussion

Results show that egg rejection is not affected by host-egg size, experimental-egg size or the difference between the size of the female's own eggs and that of the experimental egg. Nevertheless, the modification of spots patterns generated significantly more egg rejection

when compared with egg-colour modification. That is, the results suggest that foreign egg rejection is caused by variation in spot patterning, but is not significantly influenced by egg size or egg colour.

Hosts may recognise foreign eggs on the grounds of discordance (a relatively crude rule by which the egg type in the minority is rejected) or by “true recognition” of their own eggs (Rothstein 1975; see also Hauber and Sherman 2001). True recognition may take the following two forms: hosts may learn to identify their own eggs by imprinting on them (Rothstein 1974; Lotem et al. 1995) and can thus reject from memory (Petrie et al. 2009). Alternatively, they could reject on the basis of direct comparison (Lahti and Lahti 2002).

In this study, we found no effect of egg size on rejection despite the high repeatability in egg size within females, and the significant difference between females (Anderson 2006; this study), which could facilitate foreign-egg rejection. Other studies that have considered this factor in egg recognition have concluded that egg size has little or no influence on the rejection of conspecific eggs because of the high variability among the eggs laid by an individual female (Victoria 1972), or because the egg size is very similar among females of the same species (Jackson 1998; Lahti and Lahti 2002). To our knowledge, only Marchetti (2000) found an effect exerted by the conspecific egg size on rejection, this being in the yellow-browed leaf warbler (Phylloscopus humei). That study demonstrated that rejection decisions are based on the relative size of eggs in the host clutch, with individuals accepting eggs of similar size as their own. By contrast, in the house sparrow, the difference between the female’s own eggs and foreign eggs did not influence the rejection decision.

According to López de Hierro and De Neve (unpublished data), house sparrow egg colour and spot pattern are significantly determined by female identity. This may indicate a genetic component that maintains egg-colour patterns in this species within a relatively narrow range of environmental variation. Because of this variability in egg characteristics (colour and spots pattern) between females and clutches in the house sparrow, we should expect the variation in any of them to facilitate the recognition and rejection of foreign egg (e.g. Victoria 1972; Rothstein 1982; Moksnes et al. 1993; Stokke et al. 2002, 2004; Moskat et al. 2008a). However, only the spot pattern, but not egg colour, significantly affected egg rejection in the present study. Moreover, none of the treatments that changed two features in a single egg presented a greater effect on egg rejection, suggesting that there is no “stimulus summation” in the rejection of foreign eggs in the house sparrow. Even in the treatment of modifying colour and spot size in the same egg, the percentage of rejection was very similar to that caused by changing only the spots size, and much higher than that from altering only the egg colour (Fig. 2). The probability of rejection in the blackcap (Sylvia atricapilla) is significantly influenced by the colouration of the blunt egg part, egg rejection being more probable when darker is the blunt egg part of the host clutch (Polaciková et al. 2007). This may be connected with the spot concentration in the blackcap’s eggshell. Similarly to our results, the warbling vireo (Vireo gilvus) hosts reject brown-headed cowbird’s eggs only based on eggshell spot pattern (Underwood and Sealy 2006). In the great reed warbler (Acrocephalus arundinaceus), egg rejection increases gradually with the increase in spot density (Hauber et al. 2006; Moskat et al. 2008a).

Intraclutch variation affects egg rejection in other species (Avilés et al. 2004; Cherry et al. 2007; Moskat et al. 2008b). However, in the house sparrow, intraclutch variability does not affect egg rejection (López de Hierro and Soler 2006). On the other hand, more spotted eggs could indicate lower quality (Martínez-de la Puente et al. 2007), and egg rejection could be more probable in low-quality clutches, given the high costs of egg rejection in this species (Moreno-Rueda and Soler 2001). However, spotting characteristics of own eggs did not affected the probability to egg rejection in this study.

Long ago, it was noticed that birds nesting in cavities tended to lay white eggs,

whereas spotted eggs were related to open nests, as confirmed by recent comparative analyses (Kilner 2006). About 80% of birds that build nests in exposed sites lay eggs that have red or brown spots (Lack 1958), which is interpreted as an adaptation for concealment from predators (Tinbergen et al. 1962; Solís and de Lope 1995; Lloyd et al. 2000; Sanchez et al. 2004; Kilner 2006). The question arises why the house sparrow, a hole-nesting bird, has eggs that are conspicuously spotted. Cavity nester species which presently lay spotted eggs might have changed their nesting habit from open nesting to cavity nesting, and retained spottiness from their open-nesting time. However, the primitive nest type in the house sparrow is a more or less spherical structure (Kulczycki & Mazur-Gierasinsk, 1968; Heij, 1986), therefore, being a closed nest.

Protoporphyrins are the principal pigments responsible for egg-spot patterns in birds (Kennedy and Vevers 1976; Miksik et al. 1996). Due to the pro-oxidant properties of protoporphyrins (Afonso et al. 1999; Shan et al. 2000), it has been proposed that they could either signal female quality because increased pigmentation would indicate oxidative tolerance (Moreno and Osorno 2003) or, alternatively, be an indicator of poor condition, since high levels of protoporphyrins produce physiological stress that may be reflected in females' physiological condition (Martínez-de la Puente et al. 2007). Protoporphyrins may also be used to compensate for localised shell thinness arising from a lack of calcium in the environment (Gosler et al. 2005), thereby reducing permeability and water loss during incubation (Higham and Gosler 2006).

Besides these explanations, brood parasitism explains the presence of spot patterns as a means of facilitating egg recognition (Swynnerton 1918; Stokke, et al. 1999, 2002; Davies 2000; Soler et al. 2000; Lahti 2005, 2006; but see Moskat et al. 2008a). In another study (López de Hierro and De Neve unpublished data), egg-colour variance explained by female identity was very low (5% - 10%), while the spot pattern was the feature that presented the least variability and its variation was explained in a 40.5 % by the female identity. This implies that spot pattern, least variant within females, is better than egg colour to egg rejection. In addition, in hole-nesting birds, low light in the nest could hamper the reliable recognition of colours but allow recognition of contrasts in light and dark, i.e. spot patterns. In summary, our results suggest that spot patterns in the house sparrow may be maintained for the recognition and rejection of foreign eggs, an explanation that does not exclude other functions (signalling or structural).

Ethical Note

The capture and retention of sparrows was authorized by the Andalusian government (Consejería de Medio Ambiente). This research adhered to the legal requirements of Spain and all institutional guidelines. The paint used in the egg features modifications (Titanlux © brown tobacco nº 544 and Titanlux © blue nº 347) is not toxic for animals nor the environment, which follows the Directive 1999/45/EC (RD.255/2003). The manipulation did not have adverse effects on the embryos, as experimental eggs were accepted (N = 43) 25 eggs hatched successfully (58.14 %). This hatching success did not differ significantly (Chi-square test: χ21,253= 0.11, P = 0.7) with the hatching rate of non-manipulated clutches in this captive nesters in 2000 (58.4%, n = 206 eggs, Moreno-Rueda and Soler, 2002).

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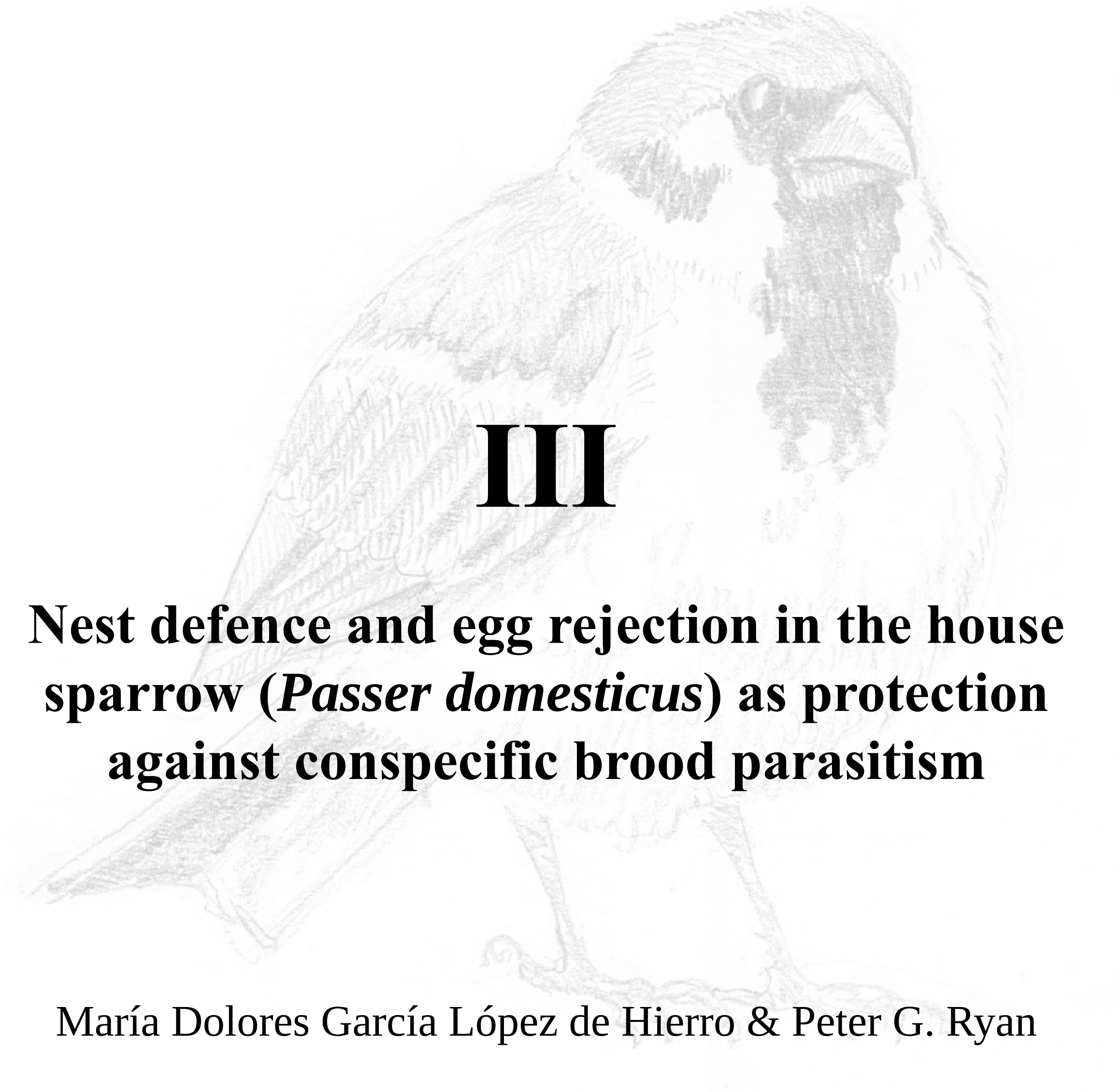

III

Nest defence and egg rejection in the house sparrow (*Passer domesticus*) as protection against conspecific brood parasitism

María Dolores García López de Hierro & Peter G. Ryan

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Nest defence and egg rejection in the house sparrow (*Passer domesticus*) as protection against conspecific brood parasitism

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Summary

Nest site availability is a factor associated with conspecific brood parasitism (CBP) in birds. The house sparrow (*Passer domesticus*) population on Dassen Island, South Africa, suffers from limited nesting space availability. We estimated the incidence of CBP in this population and determined experimentally whether sparrows retain the capacity to recognise and reject parasitic eggs. Other strategies that have evolved to thwart brood parasitism include nest guarding and nest defence. The presence of an intruding female near a nest may result in antagonistic behaviour as well as increasing the rejection of parasitic eggs (i.e., additive stimulus). This study tests if the presence of an intruding conspecific female generates an additive stimulus or whether nest guarding/defence and egg rejection are antagonistic responses, which has been studied principally in cases of interspecific brood parasitism (IBP). Despite space limitations, CBP was not detected in this population, and one third of foreign eggs were rejected. However, nest guarding/defence was not related to egg recognition and rejection. Egg rejection in this population does not appear to depend on the probability of nests being parasitised or on an inability to assume the costs associated with nest guarding/defence and with egg rejection.

Keywords: house sparrow, *Passer domesticus*, conspecific brood parasitism, nest defence, additive stimulus, antagonistic defences.

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Introduction

Females of some bird species avoid providing any parental care by laying eggs in the nests of other females of the same species (conspecific brood parasitism CBP; e.g., Yom-Tov, 1980a; Rohwer & Freeman, 1989). Three forms of this alternative reproductive strategy occur: (1) parasitic females that attempted to breed normally but have lost their nest, due to inclement weather or predators, (2) females that did not undertake any breeding attempt, because their physical condition was inadequate to take on the costs associated with reproduction and (3) parasitic individuals that breed themselves, but lay additional eggs in other nests (Yom-Tov, 1980a; Davies, 2000). CBP increases the reproductive costs of host pairs, which have to care for the parasitic eggs (Rohwer & Freeman, 1989; Petrie & Møller, 1991). The principal cost is investment in offspring to which the parents are genetically unrelated, to the detriment of their own offspring. The increased brood size reduces chick growth rates and the probability of offspring survival after fledging (Martin, 1987; Magrath, 1991) and, thus, parental fitness (review in Yom-Tov, 1980a; Rohwer & Freeman, 1989; Petrie & Møller, 1991).

Hosts have evolved several defences to reduce the costs of parasitism (review in Davies, 2000), including defending their nests against parasitic females (Petrie & Møller, 1991), and the recognition and rejection of parasitic eggs (e.g., Victoria, 1972; Rothstein, 1975, 1982). Both nest defence and the recognition and rejection of parasitic eggs are costly strategies for the hosts, because time invested in guarding and defending the nest is lost to other biological functions, such as foraging. Moreover, the process of recognising and rejecting parasite eggs may lead to rejection costs, in which a host may inadvertently expel one of its own eggs during the course of rejecting parasitic ones (Davies et al., 1996; Lotem & Nakamura, 1998; Røskaft & Moksnes, 1998). These costs of parasitism are principally the same for species that suffer interspecific brood parasitism (IBP: parasitism by a parasitic species on hosts of another species), and have been studied and received much attention predominantly in the context of the coevolutionary arms-race between obligate brood parasites and their hosts (e.g., Soler et al., 1999, 2000; Davies, 2000). In some of these host species, nest defence and egg rejection are positively correlated (Moksnes et al., 1990), but in others they are antagonistic responses due the costs involved (Neudorf & Sealy, 1992; Hochberg, 1997; Soler et al., 1999).

The presence of the parasite near the host's nest, suggesting the possibility of being parasitized, may increase the rate of egg rejection (e.g., Davies & Brooke, 1988; Moksnes & Røskaft, 1989; Moksnes et al., 1993, 2000). Bartol et al. (2002) conclude that the sight of the cuckoo at the nest may increase rejection rate by stimulus summation in great reed warblers (*Acrocephalus arundinaceus*). They observed more aggressiveness in pairs who reject experimental eggs. However, Moksnes & Røskaft (1989) failed to observe any relationship between the degree of host aggression and the tendency to desert the nest in Norwegian meadow pipits (*Anthus praetnsis*). The only experimental test of whether there is a 'conditional stimulus' in the rejection behaviour towards conspecific additional eggs did not find any support for the hypothesis among common starlings (*Sturnus vulgaris*), because the hosts never removed any eggs, even when they responded aggressively towards a stuffed conspecific female at their nest (Moksnes & Elbertø, 2006).

The costs of anti-parasite defences may influence the strategy followed by species capable of egg recognition (Soler et al., 1999). When nest defence is sufficient to ensure an individual host's efficiency against brood parasitism, natural selection could favour a decline in egg recognition and parasite egg rejection, to reduce the total cost of anti-parasite defence (antagonistic defences: Soler et al., 1999). Thus, hosts subjected to IBP could avoid being parasitised by exhibiting high levels of defence against parasite individuals during the laying period, when brood parasitism chiefly occurs (Folkers & Lowther, 1985; Neudorf & Sealy, 1992). A high level of nest defence reassures a host that it has not been parasitised, so that it would invest less time in checking its clutch and egg ejection errors would decline (Davies & Brooke, 1988; Honza et al., 2004).

The house sparrow (*Passer domesticus*) is a well-studied species in which CBP and egg recognition/rejection behaviour are known to occur (Manwell & Baker, 1975; Kendra et al., 1988; Moreno-Rueda & Soler, 2001). Our study (1) determines the incidence of CBP and the capacity for egg recognition/rejection in a house sparrow population with limited nest-site availability and (2) reports the relationship between the frequency of egg recognition/rejection and nest guarding/defence. We hypothesise that if the presence both of an intruder female and an experimentally parasitic egg act as an additive stimulus, those pairs which defend their nests most vigorously will also be those which display the highest rates of egg rejection. Conversely, if there is an antagonistic relationship between both types of anti-parasitic defence,

then those pairs which show greatest nest guarding/defence should exhibit the lowest rates of egg rejection. Such relationships have only previously been investigated in instances of interspecific brood parasitism.

Materials and methods

Study species

House sparrows nest in cavities and build closed nests among tree branches (Cramp & Perrins, 1994) and are chiefly monogamous, with a low rate of extra-pair copulations (Veiga & Boto, 2000). They suffer CBP at a rate of 0–10% (Manwell & Baker, 1975; Kendra et al., 1988; Cordero et al., 1999), and have the ability to recognise and reject eggs (Kendra et al., 1988; Moreno-Rueda & Soler, 2001). The species was introduced to South Africa in the late 19th century and spread throughout the country (Summers-Smith, 1988; Brooke, 1997). The study population was located on Dassen Island (33°25′S, 18°05′E), a 222 ha nature reserve lying 9 km from the west coast of South Africa. Sparrows of this population usually lay more than one clutch per breeding season with a mean clutch size of 3.6 ± 1.1 eggs ($N = 21$; Ryan, 2004). The vegetation is chiefly shrubby, with a few alien trees (*Myoporum serratum* and *Amsinckia menziesii*) around the few buildings on the island. A high proportion of house sparrow nests are on tree branches, because there is a lack of available cavities in the few buildings, and they are mostly occupied by the European starlings (hereafter referred to as starlings), which are more aggressive than sparrows when it comes to nest site competition (P.G.R., personal observation). Thus, the population finds itself with limited nest-site availability, which could lead to an increase in CBP (Møller, 1987).

Data collection

The study took place in 2004 and 2005. Each nest was visited early each morning and afternoon during the breeding season, beginning before eggs were laid. All eggs were marked with an indelible marker when they were first laid, and we recorded clutch size, start of incubation, the number of young which hatched and fledged, as well as any instances of CBP. Brood parasitism was inferred if two new eggs were laid on the same day (e.g., Harms et al., 1991; Jackson, 1992; Lyon, 2003), given that most species lay

one egg every 24 h (Cramp & Perrins, 1994). Other studies have inferred parasitism from eggs appearing outside the laying sequence, unusually large clutches (e.g., Yom-Tov, 1980a; Petrie & Møller, 1991) or the presence of eggs which are very different from the remainder of the clutch in size and/or colour (e.g., Colwell, 1986; Calvo et al., 2000). However, genetic determination of maternity shows that size and colour differences are insufficient to confirm a parasitic origin (McRae, 1997; Carriello et al., 2004; Grønstøl et al., 2006). Genetic confirmation of maternity provides the most accurate method to detect CBP, but our method was adequate, because nests were revised twice per day starting during nest construction. Alien eggs could be overlooked if rejection occurs shortly after laying. However, other experimental studies that we carried out on the house sparrow suggest that this would not be a problem, since the rejection response of house sparrows typically only commences on the second day after egg addition (López de Hierro & Soler, unpublished data).

Experimental design

Two types of experiments were carried out during the 2004 breeding season to determine whether this population had the capacity to recognise and reject eggs: (1) introducing an additional egg laid by another female sparrow and (2) exchanging a randomly selected host egg with a foreign conspecific egg. The introduction and exchange experiments were carried out when the second or third egg was laid before the onset of incubation in alternating nests within each nest tree, to ensure a homogeneous distribution of both experiments. The eggs were added because in CBP it is unusual that a host egg gets broken during parasitic egg laying and we aimed that the CBP was done as real as possible. Natural eggs were used in our experiments since it has been shown that artificial eggs increase the costs of rejection and so may influence the decision to accept or reject the experimental egg (Martín-Vivaldi et al., 2002). All experimental eggs used in this study were supplied by a captive population held at the Science Faculty of the University of Granada (Spain). Eggs were collected the day they were laid and kept fresh in a refrigerator. However, only few eggs could be brought from Spain and, therefore, we performed simultaneously the egg-exchange experiments in order to increase sample size (egg introduction: $N = 13$; egg exchange: $N = 14$). A previous

study on the captive population in Granada did not find significant differences between the two experimental types on anti-parasite responses, within the same female (Moreno-Rueda & Soler, 2001).

To determine whether an antagonistic or a additive relationship exists between nest defence and egg rejection, during the 2005 breeding season we added an egg to one experimental group and two control groups. The egg was added on the third day after incubation commenced to ensure that a member of the host pair would soon be present. Egg rejection rates may be influenced by the breeding stage at which the parasitic egg is added, with most eggs being accepted if they are added once incubation of the host clutch is well advanced (Emlen & Wrege, 1986). However, incubation in house sparrows generally begins with the penultimate egg and lasts 12 days (Cramp & Perrins, 1994), so that incubation cannot be regarded as advanced before the sixth day. Adding an egg on the third day of incubation should not increase its chances of acceptance and would not affect the results. Moskát (2005) found that eggs added to nests of great reed warblers suffered the highest rejection rate on the third day of incubation.

In the experimental group ($N = 9$ nests), a mounted specimen of a female house sparrow was set up 50 cm. from each nest. For one of the control groups ($N = 9$ nests) we used a mounted female starling instead of a sparrow. The starling was chosen because it is common on the island but sufficiently different from a house sparrow not to be taken for a conspecific. We could, thus, differentiate between nest defence directed against possible parasitism and more generalised nest defence (Grim, 2005). Both the sparrow and starling models were positioned with their heads pointing towards the experimental nests, since posture increases the chance of being identified as an intruder (Knight & Temple, 1986; Sealy et al., 1998). The second control group ($N = 10$ nests) received an experimental egg without the presence of a mounted specimen.

After an egg was added, the nest was watched for 15 min following the arrival of either member of the pair. If neither parent appeared after 30 min the observation period was ended. The observer hid in vegetation 15 m from the nests so as not to influence normal behaviour.

The following variables were recorded to determine the degree of nest guarding and defence: (i) the time the nest was unattended (the interval between the start of observation and the arrival of a pair member) that implies time period during which an intruder female could introduce an egg without

any hosts nest defence, (ii) the interval before each of the nest owners arrived (latency of each pair member), this variable is used to detect a possible differential investment in nest guarding between sex, (iii) the number of alarm calls per minute by each pair member and the total number of alarm calls per minute by each pair, (iv) the number of times each pair member entered its nest and the total number of such entries by each pair, (v) the number of approaches to mounted specimens by each pair member and the total number of approaches by each pair and (vi) the estimated closest distance of each approach by either pair member (0–0.5 m, 0.5–1 m, 1–1.5 m, 1.5–2 m, 2–2.5 m, 2.5–3 m), and the pair closest approach distance (the minimum separation between one of pair member and mounted specimens). The median value of closest distance range was used in the analyses.

The comparison of alarm calling between groups exposed or not exposed to mounted specimens allowed us to be certain that the defensive response was directed at the specimens and was not provoked by other factors. If mounts were attacked during the observation period, aggressive responses were noted as maximum, the mount was removed and the experiment ended. The following responses to egg insertions were noted during the daily inspections: (1) acceptance: the experimental egg remained in the nest until at least one egg hatched, (2) expulsion: when either the experimental egg alone or it and any other egg disappeared or was found smashed inside the nest, (3) burial: when either the experimental egg alone or it and any other eggs were found buried in the nest lining, (4) clutch abandonment: when a full clutch was found cold after incubation began and (5) error: the expulsion or interment of an egg other than the experimental egg presumably due to an error of recognition. Responses 2, 3, 4 and 5 were considered positives responses to the experiment (i.e., egg recognition).

Statistical analyses

Results are presented as means ± S.D. or as percentages. A General Linear Model (GLM) was used to estimate differences in the degree of nest guarding and defence between the three treatments. The GLM was employed for each sex given the possible intersexual differences in intensity of nest guarding and defence. The explanatory variables were the treatment and presence/absence of the pair as fixed factors, and the degree of advancement of the breeding season as a covariable. With this last variable we refer to

laying date of the clutch where we performed the experimental parasitizing. The experiment was performed only once in every breeding pair, but it was done randomly in their 1st to 4rd clutch. Therefore, laying date is related to the number of clutch, i.e advancement of the breeding season. The pair present/absent variable was not used in the GLM for males since the female was always present on all but one occasion. Since some variables were not normally distributed, we tested the normality of the model residuals which did not differ from a normal distribution (Kolmogorov–Smirnov $p > 0.2$), thus validating the use of GLMs.

A non-parametric paired analysis (Wilcoxon Matched Pairs Test; after Siegel & Castellan, 1988) was used to estimate the degree of difference in nest defence between sexes. This analysis did not differentiate between treatments given the small sample size. Where the dependent variable (rejection) was of a binomial nature, analyses were carried by means of Logistic Regressions, following Quinn & Keough (2005). All analyses employed the STATISTICA 6.0 programme.

Results

We never found more eggs than the habitual clutch size, no eggs appeared outside the laying sequence and only one egg was laid on a given day. There were two occasions when an egg which was very different in size and colour from the rest of the clutch was found besides the usual different final egg.

Following the egg introduction/exchange experiments, the experimental eggs were rejected in 9 of 27 (33%) of nests. The exchanged eggs were rejected in three occasions (21.4%, $N = 14$) and the introduced eggs were rejected in six occasions (46.2%, $N = 13$). In all of these instances, rejection comprised egg expulsion; there were no cases of egg burial and nest abandonment. The process of expulsion led to the loss of eggs laid by the nest owner in four of the nine nests where expulsion occurred. Thus, expulsion proved costly in 44% of nests. In total, nine host eggs were lost, representing a loss of 24% of all the eggs laid by the females involved.

The egg rejection rate in the experiments involving ‘intruder’ females near host nests was lower in the experimental group with a conspecific sparrow mount (22%, $N = 9$) than in the control group with a control starling mount (38%, $N = 8$) or the control group with no mount (44%, $N = 9$). However, the differences between the experimental group and each of the control

groups were not significant (Fisher exact test: sparrow/starling mounts, $p = 0.6$, $N = 17$; sparrow mount/no mount, $p = 0.6$, $N = 18$) (an experimental egg was broken accidentally during our daily checks in each of the control nest groups so the two nests involved were excluded from the analysis).

In the nest defence experiments, a total of two females and five males, including both members of one pair, never appeared during the observation period. With respect to the effects of an intruder female (conspecific sparrow, starling or no intruder) on the degree of nest guarding/defence, we found no significant differences between female nest owners in response latency, number of entries to the nest, approaches to the mounts and closest distances from mounts (Table 1). However, there were significant differences between treatments in the number of alarm calls, which were also influenced by the presence or absence of the males in the nests (Table 1). Females gave more alarm calls per minute when presented with 'intruder' mounts (sparrow $= 3.3 \pm 1.0$, $N = 9$; starling $= 9.1 \pm 1.4$, $N = 8$; no mount $= 0.4 \pm 1.4$, $N = 7$; Table 1), and more when they were alone (male present $= 1.9 \pm 0.6$, $N = 20$; male absent $= 6.7 \pm 1.4$, $N = 4$). There was also a marginally significant tendency that females approached the model less frequently as the breeding season advanced (Table 1, Figure 1). Since the interaction between experiment and laying date was not signnificant (experiment $*$ laying date $F_{1,13} = 0.6$, $p = 0.4$), we analyzed the effect of laying date on the female approaches to the both type of mounts (Figure 1).

In the case of males, alarm calling, entry to nests approaches to the mounts and closest distances to mounts showed no significant differences between experimental treatments or as the season advanced (GLM, all $p > 0.2$). Nevertheless, latency periods in response to 'intruder' mounts showed a non-significant tendency to be shorter than in the absence of mounts (GLM $F_{2,17} = 3.4$, $p = 0.06$; sparrow $= 5.8 \pm 2.2$ min, $N = 7$; starling $= 4.7 \pm 2.1$ min, $N = 7$; no mount $= 12.1 \pm 2.6$ min, $N = 7$). There were no significant differences between males and females in the degree of nest guarding and defence (Wilcoxon Matched Pairs Test: latency, $Z = 1.2$, $p = 0.2$, $N = 20$; alarm calls/min, $Z = 0.6$, $p = 0.5$, $N = 20$; frequency of entering in the nest, $Z = 0.9$, $p = 0.4$, $N = 20$; the number of approaches to the mount, $Z = 0.2$, $p = 0.9$, $N = 14$; closest approaches distance to the mount, $Z = 0.2$, $p = 0.9$, $N = 12$). These analyses could not differentiate between treatments given the small sample size.

Table 1. Results of GLM that analysed the effect of explanatory variables on female nest defence behaviour.

	Explanatory variable	F	p
Latency	Treatment	0.5	0.6
	Presence/absence	0.9	0.4
	Laying date	0.2	0.7
Alarm calls/min	Treatment	10.7	<0.001*
	Presence/absence	10.0	0.005*
	Laying date	0.1	0.8
N entering	Treatment	2.6	0.1
	Presence/absence	1.0	0.3
	Laying date	2.0	0.2
N approaches	Treatment	0.1	0.8
	Presence/absence	0.9	0.3
	Laying date	3.9	0.07
Distance	Treatment	0.1	0.8
	Presence/absence	0.1	0.7
	Laying date	0.0	0.9

Explanatory variables were 'Treatment' (mounted specimen next to the nest: female house sparrow, female starling or without a mount), 'the presence/absence of the male' and 'laying date' (advance of breading season). Dependent variables were: (1) Latency to get to the nest (min), (2) Alarm calls/min, (3) *N* entering (the frequency of entering in the nest), (4) *N* approaches (the number of approaches to the mount) and (5) Distance (the closest approaching distance to the mount). Significant results ($p < 0.05$) are marked with an asterisk.

Considering only the group with the sparrow mount, we analysed whether rejection behaviour was determined by the degree of nest guarding/defence (mean per nest). The length of time that a nest was left unguarded did not affect the probability of rejection of foreign eggs (Logistic Regression: $\chi_1^2 = 0.3$, $p = 0.8$, $N = 9$). The different variables related to nest defence were also not associated with egg rejection rate (Logistic Regression: all $p > 0.2$, $N = 9$).

Discussion

Instances of CBP are expected in a population where nesting sites are limited (Møller, 1987), yet we found no clear evidence of CBP during the two

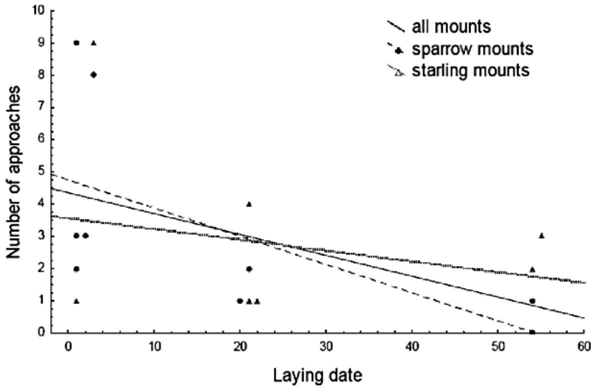

Figure 1. The negative relation between laying date (advance of the breeding season) and the number of approaches by house sparrow females to the female house sparrow mounts and starling mounts.

breeding seasons studied in the house sparrow population on Dassen Island, but we twice found an egg that was very different in size and colour from the others in the clutch in addition to the final egg of the clutch. These dissimilar eggs could be parasitic eggs, or their different appearance may be due to the natural variation in egg appearance within clutches being existent in house sparrows (Øien et al., 1995). In addition last laid eggs tend to be very different in this species (Seel, 1968; Yom-Tov, 1980b; Lowther, 1988). Several studies based on genetic maternity tests emphasize that eggs size and colour differences are insufficient to confirm whether they have been laid by a parasitic female (McRae, 1997; Carriello et al., 2004; Grønstøl et al., 2006). Since our finding of two possible CBP eggs is only based on visible field observations, we conclude that we did not find any definitive instance of CBP during the course of our study.

The failure to detect CBP may be because (1) the incidence of brood parasitism can vary between years within a population (e.g., Møller, 1987; Pinxten et al., 1991); (2) there was no space limitation for nests, despite the apparent scarcity of nesting holes on the island; or (3) the population has developed efficient anti-parasite defences, given that efficacy in nest guarding/defence reduces the frequency of brood parasitism (e.g., Petrie & Møller, 1991; Davies, 2000).

The presence of an 'intruder' female near a nest had an effect opposite to that expected, given that the percentage of egg rejection in the control groups (starling mount, no mount) was double (although not significant) that

of the experimental group (sparrow mount). Anyhow, it is, thus, clear that the presence of a conspecific near the nest does not increase the probability of rejection of an alien egg. Hence, our results suggest that there is no enhanced effect on egg rejection rates produced by seeing a possible parasitic female near a nest in the house sparrow. This is consistent with Moksnes & Elbertø (2006) who also found no conditional response ('additive stimulus') in the rejection rate towards CBP in the common starling.

Studies of the effect of the presence of a parasite on the probability of alien egg rejection have involved cases of IBP (e.g., Davies & Brooke, 1988; Moksnes & Røskaft, 1989; Moksnes et al., 2000). Bártol et al. (2002) placed a mounted specimen of a common cuckoo (*Cuculus canorus*) near the nest of a great reed warbler parasitised experimentally with mimetic cuckoo eggs and with conspecific eggs. They found that the rejection rate of cuckoo eggs increased by 20%, but that there was no increase in the rejection rate of alien warbler eggs. They consider that this is due to great reed warblers suffering both IBP and CBP. Hence the cuckoo mount has an additive stimulatory effect on rejection of mimetic cuckoo eggs because selection pressures for defence against cuckoos are greater, since this cuckoo species destroys the hosts' entire brood. Also the degree of difference between an alien egg and those of the host clutch is the most important factor in recognising parasitic eggs: alien conspecific eggs are harder to detect and their rejection involves more recognition errors. Nevertheless, a study in a captive population of house sparrow did not find any evidence that the degree of contrast between the introduced conspecific egg and the rest of the clutch affected egg rejection behaviour (López de Hierro & Soler, data not shown).

Also, the failure in the present study to find an effect on egg rejection of the presence of a conspecific female near the nest may be because this species is loosely colonial, with multiple nests in each tree, and adjacent trees are close together on Dassen Island, so that the presence of several females in a tree is normal. This could be a possible explanation why the sparrow mount had no effect on egg rejection.

Previous IBP studies have suggested that the interaction between nest defence and egg rejection may show a negative relationship due to the costs associated with anti-parasite defence (Neudorf & Sealy, 1992; Hochberg, 1997; Soler et al., 1999). Soler et al. (1999) found that magpies (*Pica pica*) which reject great spotted cuckoo (*Clamator glandarius*) eggs show less vigorous nest defence when presented with a parasite individual near the nest.

They suggest that hosts may specialise in one anti-parasite defence strategy (nest defence or egg rejection), so that they mainly display one of these behaviours. A similar situation could apply in cases of CBP, but our results indicate that the probability of egg rejection did not depend on the degree of nest vigilance, at least in house sparrow. Within the group presented with a mounted sparrow, nest defence did not differ between pairs which accepted or rejected the experimental egg. This implies that egg recognition and rejection behaviour in house sparrows do not depend on the probability of having been parasitized or on an inability to assume both types of associated costs (nest guarding/defence and egg rejection costs).

Furthermore, female nest defence (in terms of alarm calls) was almost absent when no mount was near the nest, increased when a female sparrow mount was presented, and was most intense when directed against a starling mount. Males tended to come back sooner to the nest when a moult was presented compared to the control situation, but this was also somewhat faster when the moult was a starling than when it was a sparrow. This tendency in both sexes for a higher nest defence against starlings is odd and unexpected since starlings are common on the island and do not form threat as potential predators for sparrows. However, starlings do not frequent the trees where sparrows breed (personal observation) and a starling presented at the nest probably called more the attention of the breeding pair than the presentation of a conspecific female, which is commonly nearby. One possibility could be that sparrows exhibited a generalised nest defence rather than specific recognition of a potential parasitic female.

In conclusion, we did not find clear intances of CBP in the population of house sparrows on Dassen Island. House sparrows rejected conspecific parasitic eggs in 33% of the cases, and expulsion resulted costly in terms of the loss of proper eggs in almost half of them. The presence of a conspecific female near the nest did not increase the probability of rejection of an alien egg and neither nest vigilance nor defence was related to the probability of egg rejection. House sparrows on Dassen Island exhibited a generalized nest defence, since defence was higher towards the sparrow and starling mounts compared to the control group (no mount).

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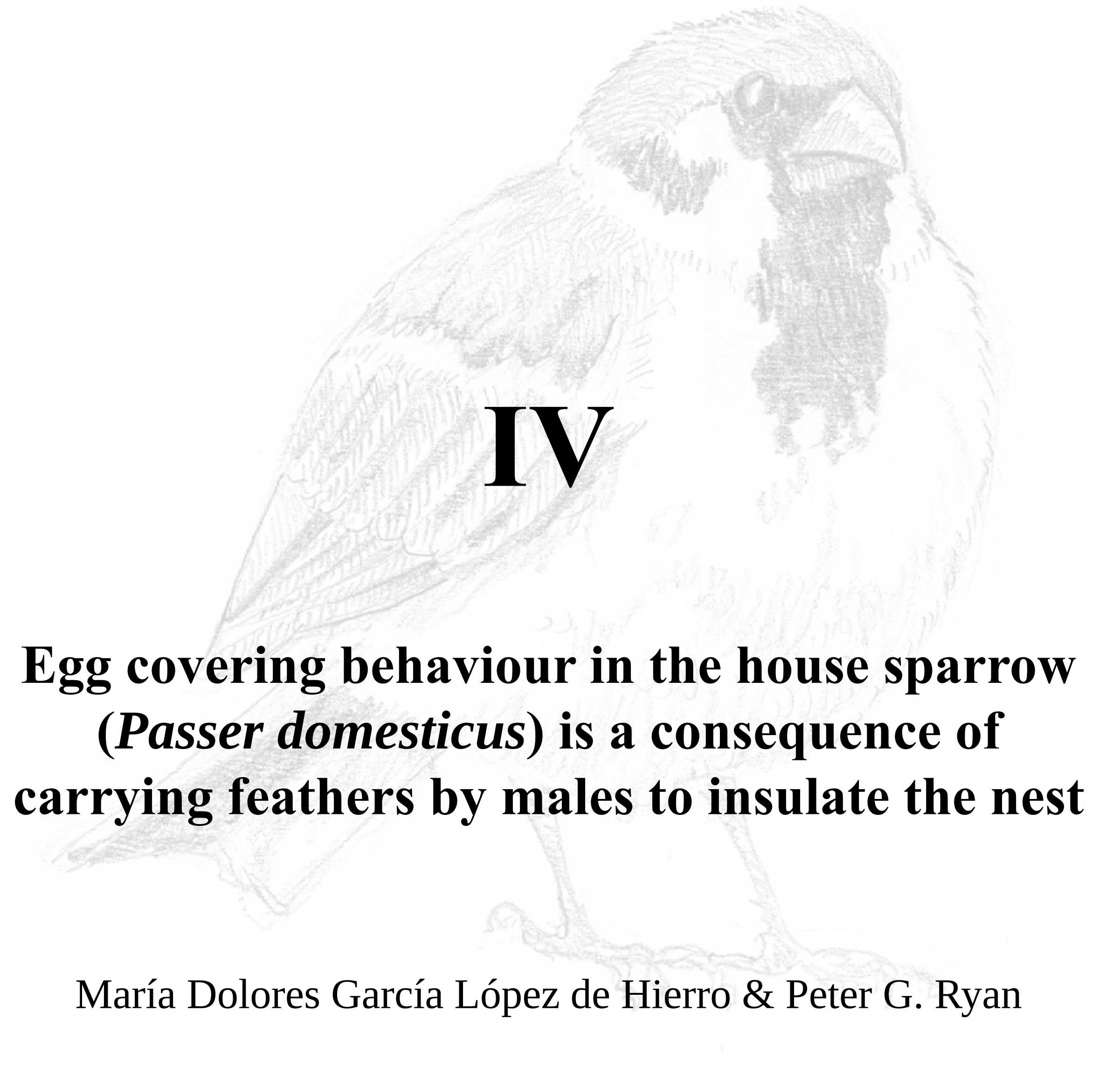

IV

Egg covering behaviour in the house sparrow (*Passer domesticus*) is a consequence of carrying feathers by males to insulate the nest

María Dolores García López de Hierro & Peter G. Ryan

En preparación

Egg covering behaviour in the house sparrow (*Passer domesticus*) is a consequence of carrying feathers by males to insulate the nest

Abstract

Several hypotheses have been proposed to explain egg covering in birds: improving nest insulation, reducing the risk of predation or brood parasitism, reducing hatching asynchrony, or concealing the female's fertile period. At the same time, males in several avian groups carry specialized materials as part of their courtship display or parental care. House sparrows (*Passer domesticus*) from a "natural" population that builds domed nests in trees on Dassen Island (South Africa) usually cover their eggs with feathers. By combining field observations and field experiments, we test the different hypotheses potentially explaining egg covering behaviour in this species. The number of feathers in the nest increased significantly during incubation and with newly hatched chicks. The carrying of feathers was largely the responsibility of males. Although the number of feathers in a nest did not correlate with parental care by the male, it positively influenced the investment in reproduction by females (i.e. clutch size). We suggest that carrying feathers enhances the insulative quality of the nest, allowing the male and female to spend more time away from the nest. Females appear to use feather carrying as a signal of male quality, responding by varying their reproductive investment.

Keywords: Egg cover, Carrying feathers, Nest isolation, House sparrow, *Passer doemsticus*.

Introduction

Egg covering behaviour is common in several bird species (reviewed in Champhell & Lack, 1985; Welty & Baptista, 1988). It behaviour have the cost of learning; it may take some time for a female to learn to cover the eggs properly, hence within a clutch there would be more covering late than early in the laying period (Haftorn & Slagsvold, 1995). Another cost is the time and energy spent covering the eggs, hence the rate of cover egg would be inversely related to the ambient temperature, and at incubation has begun, the eggs would be less cover than earlier (Haftorn & Slagsvold, 1995). The benefits of egg covering could include improved thermoregulation for the eggs, especially if neither parent is incubating (thermoregulation hypothesis; Bochenski, 1961; Caldwell & Cornwell, 1975; Haftorn, 1978; Haftorn & Slagsvold, 1995). Other authors have suggested that egg covering reduces predation risk by leading predators to believe that there are no eggs in the nest (avoidance of predation hypothesis; Broeckhuysen & Frost, 1968; Perrins, 1979; Götmark & Ahlund, 1984; Keller, 1989; Shimoda et al., 1994; Orizaola & Brana, 2003; Kreisinger & Albrecht, 2008) or makes it more dificult for an egg to be added to the nest in species that suffer brood parasitism (inter- or intraspecific) by concealing information about the nest contents (avoidance of brood parasitism hypothesis; Clark & Robertson, 1981; Briskie & Sealy, 1988). There may also be conflict between parents as to the degree of hatching asynchrony (Slagsvold & Lifjeld, 1989; Slagsvold et al., 1994), so females may cover the eggs during laying to delay the onset of incubation by males (avoidance of hatching asynchrony hypothesis; Stenning, 1995). Finally, in some species females may increase their fitness by concealing their fertile period to obtain more extra-pair copulations or to become polyandrous. Increasing aggression toward mates and covering the eggs during laying may result if females wish to conceal their fertile period (the deceptive hypothesis; Valera et al., 1997).

Sexual selection has been suggested to be a continuous process during different stages of the reproductive cycle with components arising from both pre- and post-mating selection (e.g. Thornhill, 1983, 1984; Møller, 1994; Eberhard, 1996). Females may vary their investment in reproduction in relation to the attractiveness of their mates (Thornhill, 1983, 1984; Bluhm, 1985; Hughes & Hughes, 1985; Simmons, 1987; Yamamoto et al., 1989; Petrie & Williams, 1993). Males in several avian groups carry specialized materials, like feathers (Hansell, 1995, 2000), that may be used as signals of mating status or genetic quality (Collias & Collias, 1984; Borgia & Gore, 1986; Moreno et al., 1994; Gwinner, 1997; Soler et al., 1998; Duffy & Gregory, 2002; Brouwer & Komdeur, 2004; see in case of females: Polo & Veiga, 2006). In some cases these materials are used as nest lining and may be used to cover the eggs (reviewed in Champhell & Lack, 1985; Welty & Baptista, 1988).

Here we explore the costs and causes of egg covering behavior in a population of house sparrows (*Passer domesticus*) on Dassen Island, South Africa. A high proportion of this population builds domed nests in the branches of trees. Such nests are thought to be the primitive nest type in this species (Kulczycki & Mazur-Gierasinsk, 1968; Heij, 1986). The house sparrow is a well-studied species in which conspecific brood parasitism (CBP) and egg recognition/rejection behaviour are known to occur (Manwell & Baker, 1975; Kendra et al., 1988; Moreno-Rueda & Soler, 2001; López de Hierro & Ryan, 2008). It is chiefly monogamous with a low rate of extra-pair copulations (Veiga & Boto, 2000).

To test the predictions of the various hypotheses developed to explain egg covering behaviour, we examined when egg covering occurred during the breeding cycle. (i) If egg covering is primarily for thermoregulation, we expect no specific pattern during egg-laying but an increase in covering during adverse weather (Haftorn & Slagsvold, 1995) and a general seasonal decline due to more predictable and generally good weather conditions later

in the breeding season (Valera et al., 1997). (ii) If egg cover is related to nest predation, we expect egg covering would be adjusted to the relative brood value; i.e. cover eggs more with increasing clutch size (Broekhuysen and Frost, 1968; Keller, 1989), and egg covering should increase as the risk of predation increases (Haftorn & Slagsvold, 1995). (iii) If egg covering is related to CBP, eggs should be covered more frequently during laying and early incubation, and egg covering should increase as the risk of CBP increases (Haftorn & Slagsvold, 1995). (iv) If egg covering reduces hatching asynchrony or hides information about the female’s fertile period, eggs should be covered from the start of laying for as long as the female can hide them, with no interruption in covering (Valera et al., 1997). (v) Finally, if carrying feathers is part of the male courtship display (Collias & Collias, 1984; Borgia & Gore, 1986) the feathers will be carried exclusively by males. If this is an indicator of the male quality, males carrying feathers to the nest are expected to make intensive demands for copulations at this time. Feather delivery should be more frequent when females start a new fertile period. If carrying feathers is an indicator of male parental care, males who bring more feathers should invest more in nest defence, incubation, brooding or feeding the chicks. In addition, females of males that bring more feathers should invest more in reproduction (i.e. have a larger clutch size), because females invest in reproduction in relation to the attractiveness of their mates (Thornhill, 1983, 1984; Bluhm, 1985; Hughes & Hughes, 1985; Simmons, 1987; Yamamoto et al., 1989; Petrie & Williams, 1993).

Materials and Methods

Study species

House sparrows were introduced to South Africa in the late 19th century and spread throughout the country (Summers-Smith, 1988; Brooke, 1997). The study population was located on Dassen Island (33◦25’S, 18◦05’E), a 222 ha nature reserve lying 9 km off the west coast of South Africa. Sparrows usually lay more than one clutch per breeding season (Summers-Smith, 1988) with a mean clutch size in this population of 3.6 ± 1.1 eggs (N = 21; Ryan, 2004). House sparrows suffer CBP at a rate of 0–10% (Manwell & Baker, 1975; Kendra et al., 1988; Cordero et al., 1999; López de Hierro & Ryan, 2008), and have the ability to recognise and reject around 32-35% of foreign eggs (Kendra et al., 1988; Moreno-Rueda & Soler, 2001; López de Hierro & Ryan, 2008). The typical tree nest on Dassen Island is a more or less spherical structure with a deep cup lined laregly with feathers, which could contribute to the insulative quality of the nest (Caldwell & Cornwell, 1975; Haftorn, 1978; Skutch, 1983). The feathers are also part of the basin where the eggs are deposited, and it is usual to find them covering the eggs (see results). Collecting of feathers is largely performed by males (see results), who call to the female and perform a dance around them or around the nest displaying the feather before it is added to the nest. During this display, females may stay near the nest observing the male, remain in the tree out of sight of the male, or depart from the nest tree.

Data collection

The study took place at 39 nests in 2004 and 40 nests in 2005. All eggs were marked with an indelible marker when they were first laid, and we recorded clutch size, start of incubation, and the number of young which hatched on the same day. To determine when egg covering occurs, nests were visited at sunrise, mid-morning, mid-afternoon, and before sunset in 2004. In order to reduce disturbance, we visited each nest twice a day, alternating sunrise and mid-afternoon on one day, and mid-morning and sunset the next day. In 2005, nests were

visited every day only in the morning. At each visit, we recordered whether the eggs or chicks were covered by feathers, and the proportion of the clutch or brood covered (i.e. extent of cover). We also scored the number of feathers inside and outside the nest. It wasn't practical to count all the feathers, so the same observer scored their abundance from 0 (no feathers) to 5 (whole nest-cup full of feathers). A subset of nests scored twice after looking at different nests suggests that repeatability of the measure was high (R> 0.90 in all cases; Lessells & Boag, 1987). Environment variables (air temperature, humidity, wind intensity, cloud cover, rain or fog) were recorderd daily at sunrise, mid-morning, and before sunset during the 2004 breeding season to determine if egg covering is related to local weather conditions.

Experimental design

Avoidance of predation hypothesis

To determine whether the risk of predation influences egg covering, we compared the reactions of birds exposed to a model snake with those when exposed to a control stick. The experiment, conducted during the 2005 breeding season, was made on seven nests. In the experimental treatment, a mounted montpellier snake (*Malpolon monspessulanus*) was set up 50 cm from the nest, while in the control treatment a stick of wood, similar in shape to the snake model, was deployed in the same position and posture. The snake's head was pointing towards the nest, because this posture increases the chance of being identified as an threatening predator (Knight & Temple, 1986; Sealy et al., 1998). After placing the mounts, the nest was watched for 15 min following the arrival of either member of the pair. If any parent did not appear after 30 min the observation period was ended. The observer hid in vegetation 15 m from the nests in order not to influence normal behaviour. The following variables were recorded: (i) the time the nest was unattended (the interval between after observer hid in vegetation and the arrival of a pair member), that implies time period during which nests could be predated, (ii) the number of alarm calls per minute by each pair member, (iii) the total number of alarm calls per minute (if we could not distinguish individuals), and (iv) the estimated closest distance of each approach by each pair member (0–0.5 m, 0.5–1 m, 1–1.5 m, 1.5–2 m, 2–2.5 m, 2.5–3 m). The median value of closest distance range was used in the analyses. If mounts were attacked during the observation period, aggressive responses were noted as maximum, the mount was removed and the experiment ended. We quantified the extent of egg cover and scored the number of feathers covering the eggs, before each manipulation, immediately after observation, and one hour later to determine if the increased risk of predation affected the egg covering.

Avoidance of CBP hypothesis

To measure the posible influence of CBP on the egg covering, we quantified the extent of egg covering in relation to an experiment to determine whether the relationship between nest defence and egg rejection is antagonistic or an additive (López de Hierro & Ryan, 2008). In this experiment, conducted during the 2005 breeding season, we added one egg to an experimental group and two control groups. In the experimental group (N = 9 nests), a mounted specimen of a female house sparrow was set up 50 cm from each nest. For one of the control groups (N = 9 nests) we used a mounted female common starling (*Sturnus vulgaris*) instead of a sparrow. The second control group (N = 10 nests) received an experimental egg without the presence of a mounted specimen (for more details see López de Hierro & Ryan, 2008). After an egg was added, we followed the same observational protocol and recorded the same variables as in the predation risk experiment described above.

Manipulation of the number of nest feathers

We experimentally manipulated the number of nest feathers in 50 nests during 2004 (N = 29 nests) and 2005 (N = 21) to determine whether carrying feathers is part of the male courtship display, designed to increase the chances of copulation, or an indicator of a male's investment in parental care. The experiment included two experimental and one control treatment on the same nests. Before each treatment we recordered if eggs or chicks were covered, the extent of such cover, and scored the number of feathers inside and outside the nest. In one of the experimental treatments half of the feathers from the dome, entrance and nest basin were removed without damaging its structure. In the second experimental treatment, the number of feathers were increased by roughly 50% in the dome, entrance and nest basin. The control treatment consisted on manipulating the feathers in the nest, but not removing or adding feathers. Each treatment was carried out in various stages of breeding: 1 = before incubation, 2 = during incubation, 3 = newly hatched chicks and 4 = chicks with 5 to 15 days old. At least one experimental and one control treatments was conducted on different days at each nest. After each treatment the observer hid in vegetation 15 m from the nest and observed activity by each pair member at the nest for one hour. The following variables were recorded: (i) the number of alarm calls per minute, (ii) the number of trips with feathers, (iii) the number and (iv) size of feathers in each visit (1 = smaller than the width of the chest, 2 = equal to the width of the chest, 3 = greater than the width of the chest), (v) the time showing feathers, (vi) the place where the feathers were deposited (1 = within the nest, 2 = at the entrance of the nest, 3 = feather discarded, 4 = departs with the feather), (vii) requests for copulation, (viii) obtaining copulation, and (ix) the location of the other member of the pair when its mate arrived with a feather. In addition, (x) the time of nest guarding, (xi) the time inside the nest with eggs or chicks (i.e. nest attentiveness), and, in the case of nests with chicks, (xii) the number of feeding events during the observation hour were recorded. After the observation period, the extent of covering of eggs or chicks was again recordered, and the number of feathers inside and outside the nest was scored. Following experimental treatments, feathers removed were returned and any added were removed to avoid any effect of the manipulation on the breeding attempt.

Statistical analyses

Cost of egg covering

To determine whether egg covering has associated costs (Haftorn & Slagsvold, 1995) a Generalized Linear Mixed Model (GLIMMIX) was used in which the dependent variable (egg covering) had a binomial distribution (0 = no cover, 1 = cover, logit link function). A General Linear Mixed Model (GLMM) was used to determine the variables which best explained the extent of egg cover (the proportion of eggs covered in respect to clutch size). To test whether there was any cost of learning to cover eggs (Haftorn & Slagsvold, 1995), the laying day secuence was considered as a covariable, while the time of day when egg cover and extent (1 = sunrise, 2 = mid-morning, 3 = mid-afternoon, 4 = sunset) were considered as fixed factors. The nest and the day in the breeding season were included as random factors to explore differences in egg cover and extent among nests, and to take into account possible random variation and in this way avoid pseudo-replication. To assess the cost of egg covering in terms of time and energy, the same analyses were made using the same model described above deleting laying date secuence as a covariable and including a fixed factor determining whether or not incubation had started.

Thermoregulation hypothesis

To determine whether environmental conditions influence egg covering behaviour and thus change nest insulation , we estimated the median frequency and extent of egg cover for all nests each day. These averages were compared with environmental variables recorded at the same periods (sunrise, mid-morning, and before sunset) using a General Linear Model (GLM) in which the median frequency of egg cover or the mean extent were the dependent variables. In these analyses, the day of the breeding season, and the temperature, humidity, wind speed, cloud cover and the presence of rain or fog were included as covariables. The variable indicating the time of day was included as a fixed factor.

Due to the potential importance of feathers (internal conditions) to improve the thermal insulation of the clutch (Caldwell & Cornwell, 1975), thus reducing the costs of incubation to parents (reviewed in Williams, 1996; Conway & Martin, 2000a) we determined when the number of feathers peaked inside and outside the nest. Average feather abundance scores were obtained for each stage of breeding using the scores estimated before the experimental manipulation of the number of nest feathers. We analyzed the possible difference in the number of feathers at different stages of breeding through a GLMM where the stage of breeding was a fixed factor, and nest and year were random factors.

Avoidancce of predation hypothesis

Because variables were not normally distributed and the mean extent of egg cover and the number of feathers covering the eggs were measured three times at each nest (see experimental design), we used an non-parametric analysis comparing two dependent samples, Wilcoxon matched pairs. This analysis estimated the difference in the extent of cover and the number of feathers covering the eggs among treatments, and also any differences in other behavioural variables. A Spearman rank correlation was used to determine if egg cover was adjusted to the relative brood value (clutch size) in all the nest used in 2004 (N = 39).

Avoidance of CBP hypothesis

For this experiment, we analyzed the differences in the extent of egg cover and the number of feathers covering the eggs among treatments using Kruscal-Wallis ANOVA, a non-parametric analysis comparing multiple independent variables, because each treatment was performed at different nests and variables were not normally distributed. The variables obtained during the observations were analyzed in Lopez de Hierro & Ryan (2008).

Hatching asynchrony hypothesis

Hatching asynchrony was measured as the number of chicks that hatched on the first day with respect to clutch size in both 2004 and 2005. Because only one date per nest was obtained, we analyzed how egg cover could favour hatching asynchrony through a multiple regression in which the year, the nest, the median frequency of egg cover and its mean extent during the laying period and incubation were included as independent variables.

Manipulation of the number of nest feathers

For the experimental manipulation of the number of nest feathers, we used a GLMM analysis to determine the possible differences in the number of alarm calls, the number of trips with feathers, the number of feathers, the average size of the feathers transported, and the average time displaying feathers between treatments and stage of breeding. This analysis included the stage of breading and treatment as fixed factors, and the year and nest as

random factors. The analyses were performed separately for each sex. To determine the possible differences between the sexes, we used a GLMM where we included a variable that differed between males and females as a fixed factor in addition to the stage of breeding and the treatment. The nest and year remained as random factors.

To assess whether the number of feathers found in a nest is related to parental care, we used a GLMM that included time of nest guarding, nest attentiveness, and the number of feedings (for nests with chicks) as covariables. We also included the stage of breeding and treatment as fixed factors, and the nest and year as random factors. The treatments were included because the variables were recorded during their observation.

We analyzed the possibility that the number of feathers in the nest influence a females's reproductive investment using a multiple regression with clutch size as the dependent variable. Independent variables included the number of trips with feathers made by males, the number of feathers brought on each trip, and the number of feathers inside and outside the nest. We included the breeding stage (laying period or incubation), laying date and the nest as predictor variables. To obtain explicit information of which of these variables could influence a females's reproductive investment, we used the nests where feathers were removed during the laying period and incubation.

Additional statistics

The models' residuals fitted a normal distribution (Kolmogorov-Smirnov: P > 0.2; Siegel & Castellan, 1988). In order to decide the best fit model of GLIMMIX, we used the Scale Disperse criterion (0.98 < Scale Disperse > 1 in all analyses; Littell et al., 1996). In GLMM analyses we used Akaike's information criterion (AIC) to decide the best fit model (Akaike, 1973). The degrees of freedom of GLIMMIX and GLMM models were calculated using the Satterthwaite method recommended for unequal group variances (Fai & Cornelius, 1996), and for this reason, degrees of freedom vary among analyses. The GLIMMIX and GLMM procedures were performed using SAS (SAS 1989-96 Institute Inc., Cary, NC, USA; Littell et al., 1996). Non-parametric analyses, multiple regressions and GLM were carried out with STATISTICA 6.0. (StatSoft, Inc., 2001).

Results

Cost of egg covering

Within a clutch to each nest there was no significant diference in egg covering (GLIMMIX: F1, 250 = 0.01, P = 0.984) or extent (GLMM: F1, 269 = 0.93, P = 0.334) during the laying sequence. In addition, egg covering (GLIMMIX: F4, 400 = 0.39, P = 0.532), and extent (GLMM: F1, 391 = 0.01, P = 0.986) was independent of the start of incubation. However, there were significant differences among nests during laying day secuence in egg covering (GLIMMIX: Z = 1.90, P = 0.028) and extent (GLMM: Z = 2.20, P = 0.013) as they depended on whether or not incubation begun (egg cover: GLIMMIX, Z = 1.87, P = 0.030; extent GLMM, Z = 2.17, P = 0.014).

Thermoregulation hypothesis

The number of feathers found inside and outside the nest increased during the incubation period and with newly hatched chicks, then decreased as chicks grew older (i.e. > 5 days old, Figure 1). These differences were significant (GLMM: feathers inside: F3,42 = 13.97, P <0.001; outside: F3,48.51 = 3.49, P = 0.022). However, egg covering did not change within a day (GLM: F2, 53 = 0.12, P = 0.888) or as the breeding season progressed (GLM: F1, 53 =

0.63, P = 0.428) when controlling for stage of breeding. There was also no change in the extent of egg covering (GLM: F1, 52 = 3.53, P = 0.078; F2, 52 = 2.03, P = 0.141 respectively). None of the environmental variables measured in this study significantly influenced egg covering behaviour (all variables P > 0.5).

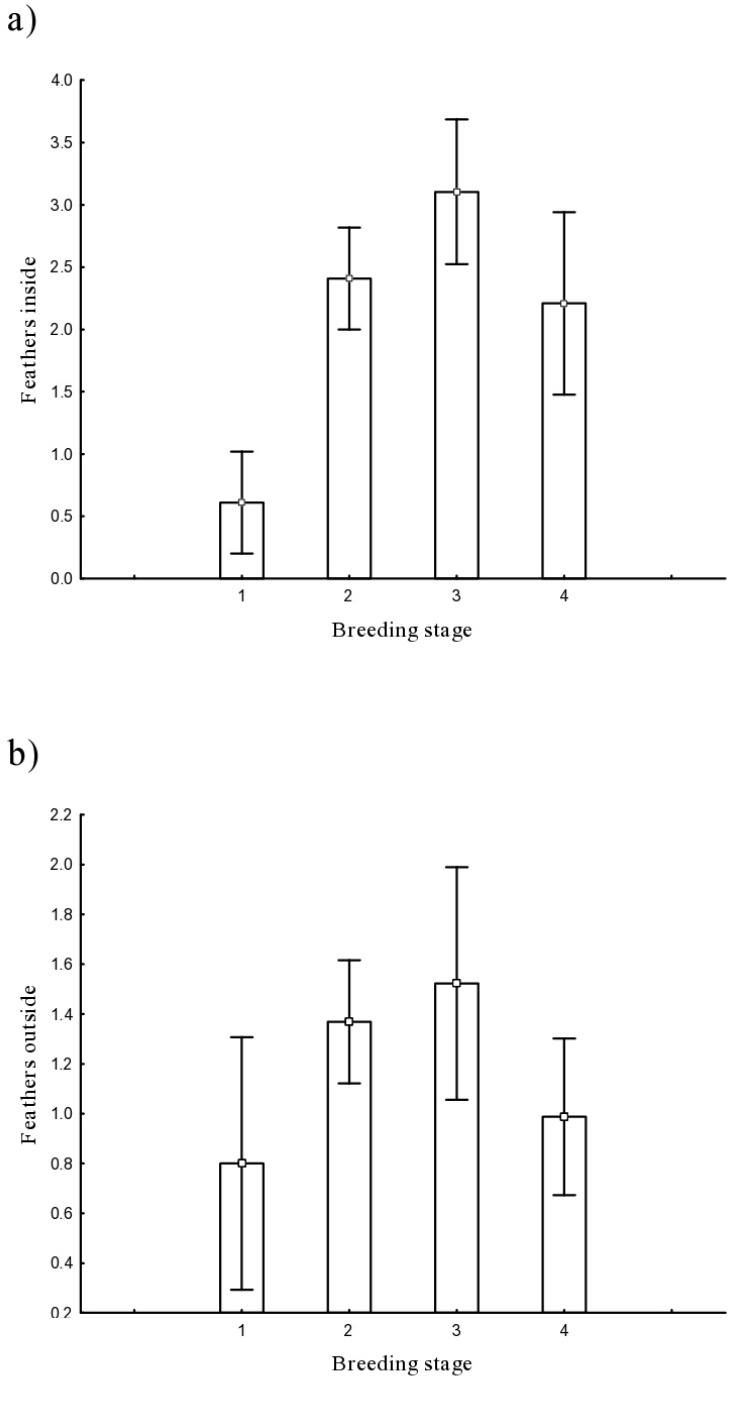

Figure 1. *Scores of the numbers of feathers inside (a) and outside (b) of house sparrow nests at diferent stages of the breeding cycle: 1 = before incubation, 2 = during incubation, 3 = newly hatched chicks, 4 = older chicks (n = 50 nests).*

Avoidance of predation hypothesis

The alarm calls per minute in the trees were marginally significant between treatments (Wilcoxon matched pair: Z = 1.83, P = 0.061, N = 7), with alarm calls being more frequent when confronted by the snake mount (sanke: 9.77 ± 9.48; control: 3.07 ± 4.24, N = 7). Nevertheless, the mean of the extent of egg covering decreased after the observation period and one hour later in the snake treatment (before treatment 0.64 ± 0.38, after treatment 0.43 ± 0.45, one hour later 0.07 ± 0.13, N = 7), and did not differ between treatments (Wilcoxon matched pair: after the observation period Z = 0.71, P = 0. 479; one hour later Z = 0.52, P = 0. 617, N = 7). Moreoveer, nor the other variables differed between treatments (Wilcoxon matched pair all variables: Z < 0.81, P > 0.500, N = 7). Relative brood value did not influence the median frequency of egg covering (Spearman correlation: rs = 0.23, P = 0.191, N = 39) or its mean extent (Spearman correlation: rs = -0.05, P = 0.789, N = 39).

Avoidance of CBP hypothesis

The effectiveness of egg cover increased after the observation period in all treatments (introduction only: before treatment 0.38 ± 0.49, after treatment 0.41 ± 0.42, N = 10; starling mount: before treatment 0.24 ± 0.38, after treatment 0.47 ± 0.48, N = 9; sparrow mount: before treatment 0.56 ± 0.45, after treatment 0.58 ± 0.43, N = 9). Nevertheless, it decreased one hour later (introduction only 0.18 ± 0.32, N = 10; starling mount 0.30 ± 0.35, N = 9; sparrow mount 0.36 ± 0.35, N = 9). Moreover, the number of feathers covering the eggs did not follow any pattern in any of the treatments, and there were no significant differences between treatments in the effectiveness of egg cover or the number of feathers covering the eggs (all variables P > 0.2).

Hatching asynchrony hypothesis

Most (92 %) of successful clutches in the 2004 and 2005 breeding seasons (N = 51) were asynchronous. From asynchronous clutches (N = 47), 33 (70%) hatched half the eggs on th first day, and of these only one egg did not hatch on the first day in 18 (55%) of nests. Nevertheless, the number of chicks hatched on the first day was not influenced by the median frequency or extent of egg covering (Multiple regression: median frequency of egg covering, R2 = 0.34, P = 0.576; mean extent, R2 = 0.43, P = 0.572).

Manipulation of the number of nest feathers

During nest observations, males brought 48 feathers on 41 occasions, significantly more than females (9 feathers on 8 occasions; GLMM: F1, 77 = 5.73, P = 0.019). The average delivery rate for males was 0.62 ± 1.92 trips per hour, compared to 0.11 ± 0.44 for females (N = 50; GLMM: F1, 73.6 = 5.00, P = 0.028). Males also brough larger feathers than females (male: 0.44 ± 0.90; females: 0.17 ± 0.61, N = 50; GLMM: F1, 92 = 4.43, P = 0.038). Excluding three feathers whose fate was not determined, most feathers delivered by males were deposited inside the nest (60%) or at the nest entrance (31%), with only 2% dropped onto the ground and 7% taken away from the nest again. By comparison, females only deposited 22% of feathers inside the nest; 67% were dropped onto the ground, and 11% were taken away. When males brought feathers, the female usually remained close to the nest (44%) or elsewhere in the nest tree (22%) watching the male. Sometimes (27%) she left the tree when the male arrived bearing a feather, but often returned subsequently to inspect the nest. On only 7% of occasions was the female absent when the male delivered a feather. By comparison, the male was apparently absent for 68% of deliveries by females. There was no significant difference in feather display time between the sexes (GLMM: F1, 126 = 1.91, P = 0.168). Males solicited copulations after 20% of feather deliveries, but no copulations were observed. Only one female solicitation was observed, and this was achieved.

There were significant differences between males in the number of trips with feathers (GLMM: Z = 3.27, P = 0.001) and number of feathers brought (GLMM: Z = 1.82, P = 0.034). The number of trips with feathers increased when feathers were removed from nests (0.88 ± 2.59 trips per hour compared to 0.10 ± 0.31 when feathers were added and 0.47 ± 0.89 for control nests, GLMM: Z2, 27.4 = 3.28, P = 0.049; N = 50). Other variables did not differ significantly between treatments (all variables P > 0.1). The number of trips with feathers (GLMM: Z3,24 = 4.26, P = 0.015), and number and size of feathers (GLMM: Z3,32.2 = 4.44, P = 0.010; Z3,57 = 5.36, P = 0.002, respectively) were greatest during incubation, whereas number of alarm calls increased from the pre-breeding period to incubation and then remained relatively uniform throughout the chick stage (GLMM: Z3,33 = 3.48, P = 0.026, Table 1).

	Before incubation	During incubation	Newly hatched chicks	Older chicks
Alarm call	12.00 ± 26.83	34.37 ± 80.96	32.44 ± 42.95	35.77 ± 478.22
Trips with feathers	0.56 ± 1.67	1.09 ± 2.54	0.07 ± 0.27	0.00 ± 0.00
Number of feathers	0.55 ± 1.66	0.79 ± 2.69	0.08 ± 0.27	0.00 ± 0.00
Feather size	0.26 ± 0.80	0.79 ± 1.11	0.08 ± 0.27	0.00 ± 0.00

Table 1. *Mean values of variables that differed significantly in males in different breeding stages during the experiment manipulating the number of nest feathers.*

There was no significant difference in the time males displayed feathers in relation to stage of the breeding cycle (GLMM: Z3,60.3 = 0.87, P = 0.464). In the case of females, there were no significant differences in the number or size of feathers carried between nests, treatments or different breeding stages (all variables P > 0.3).

The indicators of parental care did not influence the number of feathers inside or outside the nest ireespective of sex (all variables P > 0.3). Nevertheless, clutch size was positively and significantly related to the number of trips made by males with fetahers (multiple regression: R2 = 0.81, P = 0.02, N = 15), the number of feathers brought on each trip (R2 = 0.79, P = 0.03, N = 15), and the number of feathers inside the nest (R2 = 0.87, P = 0.01, N = 15)

Discussion

Cost of egg covering

Our results showed no significant diference in egg covering or extent during laying day sequence suggesting there is no cost of learning this behaviour (Haftorn & Slagsvold, 1995). However, it should be to noted that observations took place during the breeding season when some pairs had already laid one clutch, so pairs might have learned to cover the eggs in previous breeding attempts or seasons. In blue tits (Cyanistes caeruleus), more females covered the eggs when they left the nest in the middle of the laying period, fewer did so later during incubation and there was a tendency for females in good condition to cover and uncover the eggs more frequently than females in poor conditions (Haftorn & Slagsvold,

1995). In this work there was no diference in egg cover during the laying period and the condition of individuals was not measured, so we can not show that condition relationship. There was also no tendency for greater egg covering before incubation than during incubation, suggesting that the cost in terms of time and energy is limited (Haftorn & Slagsvold, 1995).

Thermoregulation hypothesis

We did not find that local weather conditions affected egg covering, with no increase in the behaviour during unfavorable weather. This mirrors findings for several species of tits (Parus spp., Haftorn & Slagsvold, 1995) and the penduline tit (Remiz pendulinus, Valera et al., 1997). However, despite the lack of a relationship between weather conditions and egg covering, the number of feathers in nests is significantly higher during incubation and when there are newly-hatched chicks, when there is most benefit to having a well-insulated nest (Haftorn, 1978; Skutch, 1983; Hansell, 1995, 2000). Having a well-insulated nest slows cooling of the eggs and newly-hatched chicks when parents leaves the nest, allowing them more time to devote to other activities including foraging (reviewed in Williams, 1996; Conway & Martin, 2000a, b). Previous studies have focused on proximate ecological factors (e.g. ambient temperature, time of day) that affect variation in incubation behaviour (e.g. Haftorn, 1984; Weathers & Sullivan, 1989; Conway & Martin, 2000a,b). The frequency with which parents alternate incubation with other activities reflect the trade-off between energy needs of adults and thermal needs of the developing embryos (Nice, 1937; Davis, 1960; Drent et al., 1985). Our results suggest that placing feathers in house sparrow nests could reduce the trade-off between the energy needs of eggs/newly hatched chicks, and the energy needs to adults. Nevertheless, additional studies are required to test this hypothesis.

Avoidance of predation hypothesis

Brood investment did not influence egg covering in house sparrows. Despite snake mount generated more alarms calls tha control treatment, the extent of egg covering did not differ between treatments after conducting the experiment and one hour later. In species where egg covering may serve to reduce predation (e.g., great crested grebes, Podiceps cristatus, black-necked grebes, Podiceps nigricollis; Broeckhuysen and Frost, 1968; Keller, 1989), egg covering also increase with risk predation and clutch size, which is not the case in house sparrows. For the initial findings it appears that egg cover has no role in avoiding predation in this species.

Avoidance of CBP hypothesis

In the experiment assessing the impact of an increased risk of parasitism, Lopez de Hierro & Ryan (2008) showed that house sparrows made significantly more alarm calls in treatments when a mounts was presented (sparrow and starling mounts), indicating that these were identified as potential intruders. We might thus expect egg covering to increase with a perceived threat of brood parasitism However, the results show that the increased risk of parasitism did not increase egg covering.

Hatching asynchrony hypothesis

House sparrow eggs hatch in the oreder in which they were laid (Veiga, 1990) and usually asynchronously (Seel, 1968; Anderson, 1994; Nhlane, 2000), although chicks typically hatch over two days (Weaver, 1943; Seel, 1968; Veiga, 1992; Anderson, 1994). Our results showed found a typical level of asynchronous hatching, but this was apparently not influenced by egg covering.

Deceptive hypothesis

Most cases where egg covering is to hide information about the female's fertile period, occurs in species with exclusive uniparental care where either sex can rear a brood (Schönfeld, 1994), and nest desertion occurs frequently (Hoi et al., 1994,1996; Persson & Öhrström, 1989). In these cases, females cover the eggs only during the laying period (Valera et al., 1997). This is contrary to our results for house sparrows, which continue to cover their eggs during incubation and small chick stages and the biparental care are common in this species (reviewed in Anderson, 2006). Although one member of a house sparrow pair may desert during a breeding attempt (Summers-Smith, 1958), the deceptive hypothesis fails to explain egg covering behaviour.

Manipulation of the number of nest feathers

Males bring most feathers to the nest, especially during incubation, and they brought more feathers after feathers were removed from the nest. These results suggest that carrying feathers could be part of the male courtship display. The failure of males to secure copulations during feather delivery has to be viewed with caution, because most observations were made during egg laying or after it, when females are less fertile. The number of feathers that was part of the nest was not related to other parental care variables considered in this study. However, the cost of nest construction can be substantial, particularly for species needing large amounts of specialised materials (Hansell, 2000). Feathers are important insulation material for the nests of many small birds (Collias & Collias, 1984; Møller, 1984), and the time and energy used to find and carry feathers is subtracted from other vital activities such as foraging. Therefore, collecting feathers could be a kind of parental care and an indicator of male quality. The amount of material carried by a male might function as an honest indicator of the genetic quality of the males like in starlings (Veiga et al., 2006), even though carrying specialised materials apparently does not indicate a male's willingness to invest in nestling feeding (Veiga et al. 2002). House sparrow nests with more feathers tend to have larger clutches, but whether this is a causal relationship is unknown. It may be that females are responding to other signals of male quality which happen to be correlated with feather delivery.

Conclusions

In this study we founded that the egg cover was not related to weather conditions, predation, CBP, hatching asynchrony or to hide infoormation about females fertil period. The amount of feathers increase during incubation and with newly-hatched chicks period. This could indicate that the amount of feathers that are part of the nest serves to increase the nest isolation to retaining the heat generated by the brooding parent reducing the trade-off existent between the energy needs to offspring and adults survival. The amount of feathers is responsability of males and influence females reproductive invest.

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