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TESIS DOCTORAL:

Relaciones sociales y formación de grupos con reproducción cooperativa en la Corneja negra (*Corvus corone corone*)

Social relationships and group formation in cooperatively breeding Carrion crows (*Corvus corone corone*)

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Resumen

Chiarati, E. 2011. Relaciones sociales y formación de grupos con reproducción cooperativa en la Corneja negra (*Corvus corone corone*)

La reproducción cooperativa se produce cuando además de la pareja de reproductores, otros individuos proveen cuidados a juveniles que no son sus descendientes directos. En las aves, los grupos cooperativos se forman principalmente por un retraso en la dispersión de los hijos, que ayudan a sus padres en la cría de nuevos pollos, posponiendo su propia reproducción. La explicación evolutiva de la reproducción cooperativa reside por lo tanto en identificar los factores subyacentes a la dispersión retrasada de los hijos y a su posterior decisión de ayudar en el nido. La hipótesis del "nepotismo" o "facilitación parental" propone que los hijos se quedan en el territorio natal por los beneficios que obtienen de la asociación prolongada con sus padres, como por ejemplo, un acceso preferencial a los recursos del territorio y la protección contra los depredadores. Respecto a la ayuda en el nido, la hipótesis del "pago de tributo" sugiere que la ayuda representa una 'renta' que los subordinados pagan a los reproductores dominantes para ser tolerados en el grupo. Esto implica que lo dominantes puedan 'castigar' los ayudantes que no contribuyen adecuadamente en la reproducción, o como se ha sugerido recientemente, que los mismos ayudantes puedan evitar el castigo mostrando comportamientos de sumisión. En esta tesis se evaluaron ambas hipótesis a partir del estudio de la dinámica social entre los miembros de grupos de corneja negra con reproducción cooperativa, durante el acceso a una fuente experimental de alimento. Los grupos incluyeron dos tipos de ayudantes de cría, hijos de la pareja de reproductores que retrasan su dispersión hasta 4 años e inmigrantes provenientes de otros territorios. Los resultados mostraron que el acceso al alimento en los grupos estuvo regulado por jerarquías de dominancia lineales y estables durante toda la época reproductora y a través de los años. Los machos reproductores ocuparon las posiciones más dominantes en los grupos, seguidos por los inmigrantes machos y los hijos machos no dispersados, que a su vez dominaron sobre todas las hembras. De acuerdo con la hipótesis del nepotismo, los machos reproductores dominantes proporcionaron a sus hijos un acceso preferencial a los recursos alimenticios del territorio, (1) asociándose preferentemente con ellos para compartir el alimento y (2) atacando a los inmigrantes machos con más frecuencia e intensidad, lo que permitió a los hijos no dispersados pasar más tiempo alimentándose que los inmigrantes a pesar de su inferior rango de dominancia. Además, los machos reproductores fueron siempre los primeros en alimentarse del cebo experimental novedoso para las cornejas, seguidos por los inmigrantes machos, mientras que los hijos no dispersados y las hembras reproductoras fueron los últimos en alimentarse. Los resultados mostraron que este orden de acceso al alimento no estuvo determinado por interferencia social, sino que reflejó los diferentes niveles individuales de neofobia. En grupos que fueron evaluados con dos cebos idénticos, los subordinados usaron únicamente el cebo que había sido anteriormente explotado por el macho reproductor dominante. Esto sugiere que el comportamiento exploratorio de los machos reproductores permite a los miembros subordinados del grupo superar su neofobia. De esta forma, los hijos no dispersados podrían beneficiarse de vivir con padres nepotistas obteniendo acceso a los recursos alimenticios del territorio sin incurrir en los riesgos de la exploración. Por último, no se encontraron evidencias que apoyen la hipótesis del pago de tributo en los grupos cooperativos. Contrariamente a las predicciones, ni el comportamiento agresivo de los reproductores dominantes ni el comportamiento de sumisión de los ayudantes se ajustaron a la contribución de los ayudantes en el nido. En cambio, al final de la temporada de cría, los machos reproductores redujeron su agresividad hacia los inmigrantes machos, que en consecuencia disminuyeron la frecuencia de comportamientos de sumisión e incrementaron el tiempo alimentándose junto con el macho dominante. La falta de 'pago de tributo' en los grupos cooperativos de corneja negra podría derivar de la importante función como fuerza de trabajo de reserva que los ayudantes 'perezosos' desempeñan en situaciones desfavorables, que permite prevenir una reducción del éxito reproductor del grupo.

Palabras clave: reproducción cooperativa, dispersión, comportamiento de ayuda, dominancia, nepotismo, neofobia, pago de tributo, Corneja negra, *Corvus corone*

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Abstract

Chiarati, E. 2011. Social Relationships and group formation in cooperatively breeding Carrion crows (*Corvus corone corone*)

Cooperatively breeding societies are characterized by individuals providing care to young that are not their offspring. Natal delayed dispersal is typically a prerequisite for cooperative behaviour in birds, because helpers are often offspring that remain in the natal territory past the age of independence and aid their parents in rearing new siblings. The evolutionary explanation of cooperative breeding therefore lies in identifying factors influencing offspring delayed dispersal and their subsequent decision to help at the nest. The hypothesis of "parental facilitation" or "nepotism" suggests that offspring delay dispersal because of the benefits obtained from the prolonged association with their parents through, for example, preferential access to the resources of the territory and/or defence against predators. Regarding helping behaviour, the "pay to stay" hypothesis proposes that it represents a 'rent' that subordinates pay to the dominants in order to be tolerated in their territory. This implies that dominant breeders should 'punish' helpers that do not provide sufficient help, or, as recently suggested, that 'lazy' helpers should prevent punishment by displaying submissive behaviours. This thesis analysed both hypotheses by studying the social dynamics in cooperatively breeding groups of carrion crow during the access to an experimental food source. Social groups comprised two types of helpers at the nest, namely offspring of the breeding pair, which can stay on the natal territory for up to four years and immigrants. Results showed that the access to food was regulated by linear dominance hierarchies that remained stable through the breeding season and over the years. Breeding males were always at the top of the hierarchy, followed by male immigrants and male offspring, which were dominant over all the females in their group. According to the hypothesis of nepotism, dominant breeding males provided their offspring with a preferential access to food resources of the territory by (1) attacking male immigrants with more frequency and intensity than offspring and (2) associating preferentially with their offspring on the feeding spot and sharing food with them. This parental facilitation allowed the offspring to spend more time feeding than higher-rank immigrants. Moreover, breeding males were fast approaching a novel food resource, followed by male immigrants, whereas retained offspring and breeding females were last. Results showed that this order, which matched the dominance ranks, was unlikely to be enforced through social interference but derived form differences in individual level of neophobia among group members. In groups that were simultaneously presented with two identical novel food sources that could not be monopolized by one individual, subordinates only used the one that was first explored by the dominant male. This indicates that the explorative behaviour of the dominant breeding male provided cues that helped subordinates to overcome their neophobia. Therefore, retained offspring may benefit from living in families with their nepotistic father by gaining access to food without incurring the risk of exploring. Finally, I found no evidences of ‘pay to stay’ in cooperative groups. Contrarily to predictions, neither the aggressive behaviour of the dominant breeding males nor the submissive behaviour of helpers (retained offspring / immigrants) correlated with the level of contribution at the nest of the latter. Instead, at the end of the breeding season, dominant breeding males reduced significantly their aggressions towards immigrant males, who reduced the frequency of submissive behaviours accordingly and increased the time spent eating together with the dominant male, whereas alpha male/offspring relationships did not change over time. I suggest that the seemingly lack of ‘pay to stay’ in crows arises because of the important insurance function of ‘lazy’ helpers, which can fully compensate for a sudden reduction in the provisioning effort of the group, avoiding a decrease in reproductive success during unfavourable circumstances.

Keywords: cooperative breeding, dispersal, helping behaviour, dominance, nepotism, neophobia, pay to stay, Carrion crow, *Corvus corone*

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Al piccolo Tobia

Lista de artículos

Esta tesis se basa en los siguientes cuatro artículos, a los que se refiere en el texto con sus números romanos correspondientes.

I. Chiarati, E., Canestrari, D., Vera, R., Marcos, J.M., Baglione, V. 2010. Linear and stable dominance hierarchies in cooperative carrion crows. *Ethology*, 116: 346-356. *doi:10.1111/j.1439-0310.2010.01741.x*

II. Chiarati, E., Canestrari, D., Vila, M., Vera, R., Baglione, V. 2011. Nepotistic access to food resources in cooperatively breeding carrion crows. *Behavioral Ecology and Sociobiology*, in press. *doi:10.1007/s00265-011-1187-1*

III. Chiarati, E., Canestrari, D., Vera, R., Baglione, V. 2011. Subordinates benefit from exploratory dominants: response to novel food in cooperatively breeding carrion crows. Submitted to *Animal Behaviour*.

IV. Chiarati, E., Canestrari, D., Vera, R., Baglione, V. 2011. Do subordinates pay to stay in cooperatively breeding carrion crows? Unpublished.

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INTRODUCCIÓN

La reproducción cooperativa

Los animales que viven en grupo a menudo muestran algún tipo de comportamiento cooperativo (Krause y Ruxton 2002). La cooperación, por ejemplo, se manifiesta en la caza, en la defensa de los recursos y del territorio, y en algunas especies incluso en la reproducción. La reproducción cooperativa se produce cuando en un grupo social, además de la pareja de reproductores, otros individuos llamados 'ayudantes' proporcionan cuidados a las crías (Brown 1987). Este sistema reproductivo es poco común en el mundo animal (por ejemplo, en las aves solo el 8% de las especies de paseriformes presentan cría cooperativa, Cockburn 2003), pero se ha observado en diversos grupos taxonómicos: desde las colonias de insectos eusociales (Wilson y Holldobler 2005), hasta en peces (Taborsky 2001), aves (Brown 1987) y mamíferos (Solomon y French 1997), incluidos los humanos (Kramer 2010).

En las aves, se ha demostrado que existe un claro componente filogenético en la expresión del sistema reproductor cooperativo al ser particularmente frecuente en unas pocas familias, entre las cuales se encuentran los córvidos (Arnold y Owens 1998; Cockburn 2003). Sin embargo, este sistema también responde a factores ecológicos. Estudios comparativos demuestran que la frecuencia de la reproducción cooperativa puede variar entre distintas especies de la misma familia e incluso entre distintas poblaciones de una misma especie (Baglione et al. 2002a) como respuesta a diferentes condiciones ecológicas (Arnold y Owens 1998, 1999).

Formas de reproducción cooperativa

En las últimas décadas, las modernas técnicas moleculares utilizadas para determinar con precisión las relaciones genéticas entre los individuos han revelado la verdadera diversidad y complejidad de los sistemas sociales con reproducción cooperativa. Los sistemas cooperativos en las aves varían enormemente en el tamaño del grupo, la composición, el parentesco entre sus miembros y la distribución de la reproducción entre ellos (para una revisión véase Cockburn 1998; Koenig y Dickinson 2004). El grupo social más sencillo y más frecuente viene representado por la familia, que se forma por el retraso en la dispersión de los hijos, que se quedan en el territorio natal más allá del periodo de dependencia parental y ayudan a sus padres en la cría de los nuevos hermanos (e.g. Arrendajo de Florida, *Aphelocoma coerulescens* Woolfenden y Fitzpatrick 1990; Carricero de Seychelles, *Acrocephalus sechellensis* Komdeur 1992; Cocaburra común, *Dacelo novaeguineae* Legge y Cockburn 2000). En otras especies, la formación de los grupos cooperativos es más compleja. Por ejemplo, en el Mito (*Aegithalos caudatus*), al comienzo de la temporada de cría las parejas de reproductores intentan reproducirse, pero si el nido falla precozmente, los machos que se han quedado sin pollada ayudan a otra pareja en la cría de los pollos y dirigen su ayuda preferentemente hacia los parientes más cercanos (Russell y Hatchwell 2001). Hay que destacar también que la reproducción cooperativa en las aves puede darse incluso entre individuos no emparentados, donde la pareja de reproductores es asistida por ayudantes de uno o ambos sexos con quien pueden llegar a compartir la reproducción. De hecho se conocen especies cooperativas poliándricas (donde una hembra se aparea con varios machos), poligínicas (donde un macho se aparea con varias hembras) y promiscuas. En el Martín pescador de río (*Ceryle rudis*) la pareja de reproductores generalmente acepta ayudantes emparentados pero, cuando las condiciones ambientales son malas, acoge también individuos no parientes provenientes de otros territorios (Reyer 1980). En el Carpintero bellotero (*Melanerpes formicivorus*), los grupos cooperativos se componen de hasta cuatro machos reproductores, una o dos hembras reproductoras y de uno hasta ocho ayudantes no reproductores que generalmente son hijos de años anteriores (Stacey y Koenig 1984). En el caso del Acentor común (*Prunella modularis*) no existen vínculos de parentesco entre los miembros de los grupos sociales y se observan con frecuencia grupos cooperativos formados por dos machos no emparentados y una única hembra (Davies 1990).

Evolución de la reproducción cooperativa

Aunque exista una gran variabilidad de sistemas sociales cooperativos, en la mayoría de los vertebrados, los grupos se forman por un retraso en la dispersión de los hijos, que permanecen en el territorio natal incluso después de alcanzar la madurez sexual y ayudan a sus padres en la cría de los nuevos nacidos (Emlen 1997). Sin embargo, los niveles de ayuda varían notablemente entre individuos del mismo grupo social (Cockburn 1998; Heinsohn 2004) y también existen especies en que la permanencia de los hijos en el territorio natal no implica cooperación (véase referencias citadas en Ekman 2006). Por lo tanto, la dispersión retrasada de los juveniles y la posterior decisión de ayudar a los padres en la cría pueden ser consideradas como dos decisiones independientes, y por consiguiente podrían requerir de una explicación evolutiva diferente (Hatchwell y Komdeur 2000). La clave para entender la evolución de la cría cooperativa reside por lo tanto en el estudio de dos procesos complementarios: 1) la decisión de retrasar la dispersión y 2) la decisión de ayudar en la cría.

¿Porqué retrasar la dispersión?

Las hipótesis que han sido propuestas para explicar la dispersión retrasada han sido principalmente discutidas en función de las condiciones ambientales que limitan la reproducción independiente de los juveniles. La hipótesis de las "limitaciones ecológicas" (Emlen 1982, 1994), sugiere que los juveniles retrasarían su dispersión por la falta de territorios libres y de buena calidad donde reproducirse o por los altos costes, en términos de riesgo de depredación, asociados con el abandono del lugar de nacimiento en una fase temprana de la vida. Esta hipótesis se vio avalada por numerosas evidencias empíricas que demuestran que las familias se forman en condiciones ambientales que limitan la reproducción independiente de los juveniles (e.g. Pruett-Jones y Lewis 1990; Komdeur 1992; Walters et al. 1992). Sin embargo, también ha sido criticada por su escaso valor predictivo al existir evidencias de que las limitaciones ecológicas son una condición general de la mayoría de las poblaciones de vertebrados, incluyendo las que no presentan dispersión retrasada de los juveniles (Cockburn 1996, 1998; Ekman et al. 2001).

Actualmente, la hipótesis del "nepotismo parental", también conocida como "facilitación parental" (Ekman et al. 2001; Ekman et al. 2004; Ekman 2006), representa una interesante alternativa. El termino 'nepotismo' indica tendencia a favorecer a los familiares y según esta hipótesis, los juveniles retrasarían su dispersión por los beneficios que pueden obtener prolongando la asociación con sus padres en el territorio natal, más que por las limitaciones impuestas por el medio o los altos costes de la dispersión. En particular, los padres facilitarían a los hijos el acceso a los recursos del territorio y les protegerían contra los depredadores, favoreciendo así su supervivencia hasta que encuentren un territorio donde reproducirse de forma independiente (Ekman et al. 2000). No obstante, pocos estudios han analizado en detalle los beneficios que los hijos obtienen de la asociación prolongada con sus padres, y en particular, los factores ecológicos que influyen en el nepotismo parental. En este sentido, la teoría predice que la calidad del territorio natal puede influir sobre la estabilidad del grupo, de forma que los padres invertirían en sus hijos después del periodo de dependencia solo si tienen suficientes recursos para compartir y en ausencia de competición dentro del núcleo familiar (Ekman y Rosander 1992). Aunque muchos estudios han demostrado que un elevado nivel de competición en los grupos puede influir en las relaciones sociales entre parientes (see West et al. 2001; West et al. 2002; Korb 2006; Stewart-Williams 2007), no existen estudios que hayan comprobado experimentalmente el efecto de la disponibilidad de alimento en la tolerancia parental en especies cooperativas.

¿Porqué ayudar?

Según la teoría de la evolución de Darwin (1859), la selección natural debería favorecer aquellos comportamientos que aumentan la eficacia biológica (*fitness*) de los individuos (i.e. la capacidad de un individuo de producir copias viables de los propios genes) y eliminar los comportamientos que la disminuyen. Sin embargo, la naturaleza proporciona varios ejemplos de aparente 'altruismo' entre animales, donde algunos individuos realizan acciones que podrían aumentar la eficacia biológica de otros individuos a costa de la propia. El comportamiento de los ayudantes de cría, que sacrifican la posibilidad de intentar reproducirse para ayudar en la reproducción de otros, es un claro ejemplo.

Después del ocaso de la "selección de grupo" (Wynne-Edwards 1962), la solución a la paradoja del altruismo llegó con la propuesta teórica de la "selección por parentesco" de William Hamilton (1964), que introdujo el concepto de 'eficacia biológica inclusiva' como suma de la eficacia biológica directa e indirecta de un individuo. Considerando que los parientes comparten copias de los mismos genes, Hamilton entendió que un individuo puede transmitir sus genes a la siguiente generación tanto directamente, a través de su propia reproducción, como indirectamente, favoreciendo la reproducción de sus parientes. Considerando los beneficios de la eficacia biológica indirecta, el comportamiento de ayuda en la cría no ha de considerarse 'altruista' en sentido estricto (el donante produce un beneficio a otro individuo a pesar de una obvia desventaja para sí mismo), sino que resulta beneficioso para los propios ayudantes.

La selección por parentesco se ha propuesto como base para explicar la evolución del comportamiento cooperativo, convirtiéndose en un paradigma central en la biología evolutiva. De hecho, además de su lógica convincente, numerosos estudios han revelado que la mayoría de los ayudantes están emparentados con los individuos que asisten en la reproducción (Emlen 1997; Griffin y West 2003), existiendo evidencias empíricas que demuestran la influencia del parentesco en numerosos aspectos de la vida en grupo y la cooperación entre individuos (Sherman 1977; Pravosudova et al. 2001; Russell y Hatchwell 2001; Baglione et al. 2003; Ensminger y Meikle 2005; Eberle y Kappeler 2006; Nystrand

2007; Stewart-Williams 2007). Sin embargo, como hemos visto anteriormente, la cooperación puede darse también entre individuos no emparentados (Cockburn 1998; Koenig y Dickinson 2004), lo que demuestra que la reproducción cooperativa puede promoverse en ausencia de beneficios en eficacia biológica indirecta. Por lo tanto, se ha argumentado que los beneficios indirectos deben de actuar en conjunto con otros beneficios en eficacia biológica directa (inmediatos y/o futuros) que los individuos obtienen de la vida en grupo y del comportamiento de ayuda (para una revisión véase Cockburn 1998; Clutton-Brock 2002; Bergmuller et al. 2007). En particular, la hipótesis del "pago de tributo" o *pay to stay* (Gaston 1978; véase también Kokko et al. 2002) sugiere que la contribución en la cría de los jóvenes representaría una 'renta' que los ayudantes pagan a los reproductores dominantes para ser tolerados en el grupo y acceder a los recursos del territorio. Este principio representaría un mecanismo general de regulación de la cooperación independiente del grado de parentesco entre los miembros del grupo, que podría hallarse en una amplia gama de especies con reproducción cooperativa. De hecho, en la mayoría de las sociedades con reproducción cooperativa, los ayudantes son beneficiosos para los reproductores dominantes porqué aumentan su éxito reproductor (Woxvold y Magrath 2005; Valencia et al. 2006; Canestrari et al. 2008) y su supervivencia, al aliviar su carga de trabajo durante la cría (Crick 1992; Cockburn 1998). Si existe 'pago de tributo' en estas sociedades, los dominantes deberían ajustar su nivel de agresividad hacia los ayudantes de acuerdo con el nivel de contribución de estos últimos, 'castigando' a los subordinados 'perezosos', llegando incluso a expulsarles del territorio. También se ha propuesto que los subordinados podrían prevenir el castigo del dominante incrementando los comportamientos de sumisión ('apaciguamiento preventivo' o *pre-emptive appeasement*, Bergmuller y Taborsky 2005). Sin embargo, las evidencias empíricas de la existencia de mecanismos de control agresivo de los dominantes y de apaciguamiento preventivo de los subordinados en especies cooperativas son escasas (véase por ejemplo evidencias de castigo en: Emlen y Wrege 1992; Reeve 1992; Mulder y Langmore 1993; Balshine-Earn et al. 1998; y de apaciguamiento preventivo en: Bergmuller y Taborsky 2005) y de momento, no permiten contrastar la aplicabilidad general de la hipótesis del pago de tributo.

Las relaciones sociales en la evolución de la reproducción cooperativa

Los estudios que se han llevado a cabo para explicar la evolución de la reproducción cooperativa se han centrado principalmente en los beneficios y costes del comportamiento de ayuda en la reproducción (Koenig y Dickinson 2004), mientras que las relaciones sociales entre los individuos, especialmente durante el acceso a los recursos alimenticios del territorio, han sido escasamente consideradas. Sin embargo, en todo tipo de sociedades donde los individuos comparten de forma continuada un mismo espacio (el territorio), a menudo aparecen conflictos de intereses sobre quien tiene la preferencia en el acceso a los recursos (Huntingford y Turner 1987). Los costes de vivir en grupo pueden ser distribuidos de manera desigual entre los individuos. Los dominantes podrían monopolizar el alimento y limitar el acceso a los otros miembros del grupo, donde los más subordinados podrían sufrir importantes consecuencias (Schneider 1984). En este sentido, las relaciones sociales establecidas entre los miembros del grupo pueden tener importantes consecuencias sobre la estabilidad del grupo social influyendo directamente en la dispersión de los individuos, su supervivencia y finalmente en la cooperación en la reproducción.

OBJETIVOS

El objetivo de esta tesis consiste en profundizar en el conocimiento de la evolución y ecología de las sociedades con reproducción cooperativa. La población cooperativa de Corneja negra (*Corvus corone corone*) en estudio representa un modelo ideal para investigar las dinámicas sociales dentro de los grupos y su influencia sobre la dispersión de los juveniles y la cooperación en el nido. En esta ave territorial, los grupos cooperativos se forman principalmente por el retraso en la dispersión de los juveniles, aunque también pueden acoger individuos inmigrantes que están emparentados con el reproductor del mismo sexo (Baglione et al. 2003). Tanto los hijos no dispersados como los inmigrantes pueden ayudar en la alimentación de los pollos, pero no todos contribuyen de igual manera y algunos individuos se abstienen de visitar el nido (Canestrari et al. 2005).

En esta tesis, se investigó el efecto de factores como sexo, edad y categoría social en las relaciones sociales entre los miembros de los grupos cooperativos en el acceso a una fuente experimental de alimento, con el objetivo de determinar la existencia de jerarquías de dominancia en los grupos (Artículo **I**), la existencia de beneficios de la asociación padres-hijos en los grupos (Artículos **II**, **III**), así como investigar aspectos ligados a la función del comportamiento de ayuda en el nido, testando el efecto de la contribución de los ayudantes en la alimentación de los pollos sobre las relaciones sociales en los grupos (Artículo **IV**).

MÉTODOS

Población de estudio

El estudio se ha llevado a cabo en una población de corneja negra del norte de España durante la época reproductora (Marzo-Julio), en el período entre 2003 y 2008, localizada en un área rural de 45 km^2 de la provincia de León ('La Sobarriba'). La Sobarriba se encuentra entre las cuencas fluviales de los ríos Torio y Porma, y presenta un sistema agrícola extensivo de cereales y barbecho, con pequeñas plantaciones de chopos (*Populus ssp.*) y bosquetes dispersos de roble (principalmente *Quercus pyrenaica*). La corneja negra en Europa está descrita como una especie monógama no cooperativa (Cramp y Perrins 1994), pero en la población española el 75% de los territorios está ocupado por grupos sociales cooperativos donde, además de la pareja de reproductores, hasta cinco ayudantes pueden participar en el cuidado de los pollos (Baglione et al. 2002a; Canestrari et al. 2005). Los grupos cooperativos se forman principalmente por el retraso en la dispersión de los hijos, que permanecen en el territorio natal junto a los padres incluso después de alcanzar la madurez sexual (excepcionalmente hasta 4 años). Los grupos también pueden incluir individuos inmigrantes (principalmente machos, Baglione et al. 2002a; 2002b) que están emparentados con el reproductor residente del mismo sexo (el coeficiente medio de parentesco *r* es de 0,24, Baglione et al. 2003).

La expresión del comportamiento cooperativo en la corneja negra se ha demostrado experimentalmente, y parece que se debe principalmente a factores ecológicos. En respuesta a la transferencia de huevos desde una población de cornejas no cooperativas de Suiza a unos nidos de la población cooperativa española, se observó que los pollos nacidos en ambiente cooperativo retrasaron su dispersión después del primer invierno y ayudaron a los padres adoptivos en la reproducción (Baglione et al. 2002c). Respecto a los factores ecológicos involucrados en la dispersión retrasada de los juveniles, los datos disponibles en la corneja negra descartan la hipótesis de las limitaciones ecológicas propuesta por Emlen (1982, 1994), según la cual la saturación del hábitat de cría sería un factor limitante en la reproducción independiente de los juveniles. Los resultados de un estudio comparativo entre la población española y una población no cooperativa del norte de Italia demuestran que la dispersión retrasada de los juveniles ocurre únicamente en la población cooperativa española, a pesar de vivir en un ambiente menos competitivo en términos de disponibilidad de territorios vacantes y con una densidad de población inferior (Baglione et al. 2005). Una característica de la población española es que los miembros de los grupos cooperativos son altamente territoriales y defienden el territorio y sus recursos durante todo el año (Baglione et al. 2005). Se comprobó experimentalmente que la calidad del territorio influye en la dispersión de los juveniles, al demostrar que éstos responden a una mayor disponibilidad de recursos tróficos aumentando su filopatria (Baglione et al. 2006). Estos resultados sugieren que en la población española de corneja negra podrían existir importantes beneficios relacionados con el territorio natal, capaces de influir en la dispersión de los juveniles y en la formación de los grupos cooperativos.

El comportamiento cooperativo

En los grupos cooperativos de corneja negra, que pueden ser familias monoparentales (una pareja de reproductores con hijos no dispersados), grupos mixtos (pareja de reproductores con hijos no dispersados e inmigrantes) o parejas de reproductores con uno o más inmigrantes, los hijos no dispersados y los inmigrantes inmaduros no tienen acceso a la reproducción, pero pueden obtener beneficios en eficacia biológica indirecta ayudando en la cría de los pollos. Sin embargo, los inmigrantes adultos (la madurez sexual en las cornejas se da partir del 2 año de vida, Cramp y Perrins 1994; Madge y Burn 1999) pueden compartir la reproducción con la pareja residente, generando sus propios descendientes en la pollada. La poliandria prevalece sobre la poliginia, ya que las hembras inmigrantes, además de ser muy raras en la población, solo ocasionalmente se reproducen en los grupos (Baglione et al. 2002a; 2002b). La contribución en la alimentación de los pollos es muy variable entre los miembros del grupo y algunos individuos se abstienen de cooperar (Canestrari et al. 2005). Los individuos que han obtenido acceso a la reproducción proporcionan la mayoría de los cuidados a los pollos; entre los no reproductores no hay diferencia entre los hijos no dispersados y los inmigrantes, siendo las hembras de ambas categorías sociales las que menos contribuyen (Canestrari et al. 2005). En general los costes de alimentar a los pollos son elevados para las cornejas, que durante la época de cría pierden masa corporal en proporción a su contribución en el nido (Canestrari et al. 2007). Los reproductores se benefician de la presencia de los ayudantes, que reducen su esfuerzo de aprovisionamiento a los pollos (Canestrari et al. 2007) e incrementan el éxito reproductor del grupo (Canestrari et al. 2008). Recientemente, se ha demostrado que incluso los ayudantes más 'perezosos' tienen una importante función en los grupos de corneja negra, ya que representan una fuerza de trabajo de reserva que puede compensar una reducción repentina en el aprovisionamiento total del grupo, y prevenir la reducción del éxito reproductor del grupo (Baglione et al. 2010).

Captura y marcaje

La población de estudio se lleva marcando desde 1995 con anillas de colores y placas alares que no afectan a la dinámica del vuelo y a la supervivencia de los individuos (Caffrey 2000; Canestrari et al. 2007). Los volantones se capturaron y marcaron cada año antes de abandonar el nido (28-30 días desde su nacimiento) y los adultos fueron capturados con trampas-jaula con cimbel o cepos con red específicamente diseñados para la especie (Baglione et al. 2002a), por lo que todos los miembros de los grupos en estudio eran reconocibles individualmente (véase Anexo fotográfico abajo). Durante el marcaje, se clasificó la edad de los individuos capturados en 1, 2 o > 2 años, atendiendo a la coloración interna del paladar (Svensson 1992). Se recogieron además muestras de sangre de la vena braquial de cada individuo (50 a 200 µl) para el análisis molecular del sexo y de la paternidad en los grupos (véase Métodos moleculares en Artículo **II**). Los individuos se clasificaron en las categorías sociales de reproductor, inmigrante o hijo no dispersado, en base a datos genealógicos (*pedigree data*) del grupo social y a los análisis genéticos de paternidad (véase criterios de clasificación en Artículos **I**, **II**). Todos los procedimientos de marcaje y toma de muestras fueron autorizados por la Junta de Castilla y León y ningún animal fue herido o abandonó el territorio como consecuencia de la captura.

Registro del comportamiento de alimentación en los grupos (I, II, IV)

Para el estudio de las interacciones entre los miembros del grupo social en relación al acceso al alimento, durante las épocas reproductoras entre 2003 y 2007, en 29 territorios se colocó un cebo constituido por una carcasa de pollo desplumada de 300 g aproximadamente. La carcasa se clavó al suelo en el centro del territorio para forzar a los individuos a permanecer varios minutos sobre la comida y así provocar las interacciones entre ellos. El comportamiento de los miembros del grupo cooperativo durante la alimentación se grabó con una cámara de video colocada a una distancia de 5 metros del cebo y camuflada con la vegetación circundante (véase Anexo fotográfico abajo). Para cada grupo se realizaron de 1 a 2 grabaciones de 4 horas de duración entre las 6 y las 12 h de la mañana. A partir de las grabaciones, se anotaron las interacciones en el acceso a la comida entre díadas de individuos, que permitieron analizar el comportamiento de cada individuo hacia los demás componentes del grupo social.

*Jerarquía de dominancia (**I**)*

La jerarquía de dominancia se determinó a partir del cálculo de los índices de dominancia de los miembros de 29 grupos cooperativos muestreados durante la alimentación sobre el cebo. Nueve de los grupos fueron muestreados hasta 4 veces en los años de estudio cuando su composición cambió de un año al otro debido a la muerte de un individuo, el reclutamiento de nuevos miembros o la dispersión de los hijos. En total se muestrearon 57 reproductores (33 machos y 24 hembras), 55 hijos no dispersados (36 machos y 19 hembras) y 16 inmigrantes (14 machos y 2 hembras). El índice de dominancia ('DIdom') se calculó para cada individuo a partir del resultado de las interacciones competitivas en cada relación diádica del individuo en el grupo (véase descripción detallada de los comportamientos en Tabla 2, Artículo **I**). Para testar la estructura de la jerarquía de dominancia, se calcularon los siguientes parámetros sociométricos: porcentaje de díadas asimétricas, índice de consistencia de dirección en la díada ('DCI') y transitividad de las relaciones entre múltiples díadas del mismo grupo social (véase descripción en Artículo **I**). La estabilidad de la jerarquía de dominancia en el tiempo se evaluó: 1) a corto plazo, a partir de grabaciones en video realizadas en 21 grupos cooperativos al principio (durante la puesta y incubación de los huevos) y al final (durante la primera semana después de que los pollos salieron del nido) de una misma época reproductora; y 2) a largo plazo, muestreando en dos años sucesivos cuatro grupos cuya composición se mantuvo estable. Se comprobó si el índice de dominancia de los individuos cambió en el tiempo.

*Relaciones sociales en los grupos (**II, IV**)*

A partir de las grabaciones en video de 22 grupos cooperativos (41 reproductores, 32 hijos no dispersados y 12 inmigrantes machos, Artículo **II**) y 21 grupos cooperativos (21 machos reproductores, 31 hijos no dispersados y 8 inmigrantes machos, Artículo **IV**), se recopilaron datos sobre la frecuencia y la intensidad de las interacciones en las díadas de individuos, incluyendo comportamientos no agresivos, medianamente agresivos y altamente agresivos (véase descripción detallada de los comportamientos en Tabla 1, Artículos **II**, **IV**). El comportamiento agresivo del macho reproductor hacia los demás miembros del grupo se midió calculando 1) un índice de intensidad de agresiones en cada díada y 2) la frecuencia de agresiones en cada díada. Para el artículo **II** además se examinó la existencia de asociaciones preferenciales entre los diferentes miembros del grupo sobre el cebo y se investigaron los patrones de distribución del alimento dentro de los grupos. Para ellos se calcularon el tiempo de asociación sobre el alimento en las díadas y la proporción de tiempo que cada miembro del grupo pasó alimentándose del cebo. En el artículo **IV,** para cada ayudante de cría (hijos no dispersados e inmigrantes) se evaluó: 1) la proporción de tiempo invertido en comportamientos de sumisión hacia el macho reproductor; y 2) la proporción de tiempo en alimentación con el macho reproductor.

Al final de las épocas reproductoras de 2003 y 2004, 10 grupos cooperativos (Artículo **II**) fueron asignados a un tratamiento de alimentación suplementaria como parte de un experimento dirigido a testar el efecto de la calidad del territorio en la dispersión de los hijos (véase los detalles del experimento en Baglione et al. 2006). Un año después del comienzo del tratamiento, se grabaron en video las interacciones sobre el cebo entre los miembros de los 10 grupos experimentales y 9 grupos controles siguiendo la metodología descrita anteriormente. Se testó el efecto del suplemento de alimento sobre las relaciones sociales en los grupos, es decir, en el índice de intensidad de agresiones y en la frecuencia de agresiones de los machos reproductores, así como las agresiones globales, tanto en intensidad como en frecuencia, dentro de los grupos.

Registro del comportamiento de ayuda en el nido (IV)

Los datos de la contribución individual en la alimentación de los pollos se recogieron en 21 grupos cooperativos (21 machos reproductores, 21 hembras reproductoras, 20 hijos machos no dispersados, 11 hijas hembras no dispersadas y 8 inmigrantes machos) entre 10 y 15 días después de la eclosión del primer huevo, mediante la colocación de micro cámaras de video camufladas a 2,5 metros del nido. Para cada nido se llevaron a cabo 3-5 sesiones de grabación de 4 horas cada una y en días sucesivos. Para cada miembro del grupo se midió el número de cebas (cada acto de entrega de alimento a un pollo) por hora agrupando los datos de las diferentes sesiones de grabación (Canestrari et al. 2005). La ‘contribución en el nido’ de cada ayudante (hijos no dispersados e inmigrantes) se obtuvo dividiendo el número de cebas del ayudante entre el total de cebas del grupo. Se comprobó si la agresividad de los machos reproductores y el comportamiento de sumisión de los ayudantes cambiaron durante la época reproductora (entre el principio y el final de una misma época reproductora) en función de la contribución de los ayudantes.

Registro de la respuesta a alimentos novedosos en los grupos (III)

Las carcasas de pollo utilizadas como cebo en el registro del comportamiento de alimentación en los grupos (véase arriba) constituyeron, en su primer contacto, un alimento novedoso para las cornejas, que antes de alimentarse manifestaron comportamientos típicamente neofóbicos (véase descripción de la reacción neofóbica de los individuos en Artículo **III**). Para determinar la existencia de un orden específico con que los miembros de un mismo grupo social accedieron al cebo novedoso, a partir de las grabaciones en video realizadas en 29 grupos cooperativos, se tomó nota del orden en que los individuos (reproductores, inmigrantes e hijos no dispersados) se alimentaron la primera vez del cebo. La muestra además incluyó los miembros de los grupos cooperativos que nunca se alimentaron del cebo y que se clasificaron como los más neofóbicos del grupo (Artículo **III**). En total se muestrearon 68 reproductores (37 machos y 31 hembras), 64 hijos no dispersados (40 machos y 24 hembras) y 18 inmigrantes (16 machos y 2 hembras). Para poder contrastar si el orden de acceso al cebo era debido a verdaderas diferencias individuales en los niveles de neofobia o si simplemente reflejaba la jerarquía de dominancia en el grupo, durante 2008 se llevó a cabo un experimento en 14 grupos cooperativos donde se presentaron simultáneamente dos cebos idénticos, cada uno constituido por una carcasa de pollo de ca. 300g. Los cebos se colocaron en el centro del territorio a una distancia de 10 metros entre ellos para impedir la monopolización del alimento por parte del individuo más dominante. En estos territorios se colocaron dos videocámaras, una para cada cebo, que grabaron en sincronía durante 4 horas. Para cada miembro del grupo se tomó nota del cebo elegido para alimentarse la primera vez y del orden de acceso al cebo.

Métodos estadísticos

Los análisis estadísticos se realizaron en su mayoría utilizando el programa GenStat 12.0 (VSN International, U.K.). Los datos se analizaron principalmente con modelos lineales mixtos (LMM) utilizando el método de estimación por máxima verosimilitud restringida (REML). Los modelos mixtos se caracterizan por permitir la incorporación de factores fijos y factores aleatorios (*random*) en el análisis, que permiten modelar conjuntos de datos que incluyen medidas repetidas de las mismas unidades estadísticas, en este caso del mismo individuo y/o territorio (véase descripción detallada de los modelos estadísticos en cada artículo adjunto). Los factores fijos o 'variables explicativas' que se ajustaron con menor significación al modelo (*P* > 0,1), se eliminaron de forma secuencial hasta que el modelo incluyó únicamente las variables más relevantes (procedimiento de eliminación por pasos hacia atrás, Xin y Xiao Gang 2009). Los valores de probabilidad significativos (*P* < 0,05) se obtuvieron al incluir todas las variables explicativas relevantes (*P* < 0,1) en el modelo, mientras que los valores de probabilidad de las variables no significativas se obtuvieron incluyendo cada una de las variables de forma individual en el modelo mínimo (Crawley 2002).

Anexo fotográfico

Fotos 1 y 2. Vista de dos territorios de corneja negra caracterizados por cultivos de cereal en extensivo, bosquetes dispersos de roble, prados y vegetación de lindero.

Foto 3. Trampa-jaula con cimbel y adulto de corneja negra capturado.

Foto 4. Corneja negra marcada con anillas de colores y placas alares con un código alfanumérico.

Foto 5. Montaje fotográfico basado en la metodología utilizada en las grabaciones en video de los grupos cooperativos sobre el cebo.

RESULTADOS Y DISCUSIÓN

I) Jerarquías de dominancia lineales y estables en las cornejas negras cooperativas

En los grupos cooperativos de corneja negra, el acceso al alimento estuvo regulado por jerarquías de dominancia que permanecieron estables durante toda la época reproductora y a través de los años. El cálculo de los parámetros sociométricos mostró unas jerarquías de dominancia con estructura lineal en los grupos, al ser las díadas altamente asimétricas y las relaciones entre múltiples díadas transitivas. Los machos reproductores ocuparon las posiciones más dominantes en la jerarquía, seguidos por los inmigrantes machos y los hijos machos no dispersados, que a su vez dominaron sobre las hembras reproductoras, las hijas hembras y las hembras inmigrantes (Fig. 1). De acuerdo con las observaciones realizadas sobre bandos de alimentación invernales de cornejas negras en Suiza (Richner 1989), los resultados indicaron una mayor dominancia de los machos con respecto a las hembras en los grupos cooperativos. Sin embargo, mientras que en los bandos las jerarquías son estrictas y bien definidas entre ambos sexos (Richner 1989), en los grupos cooperativos las jerarquías fueron estrictas entre los machos (reproductores > inmigrantes > hijos no dispersados) y relajadas entre las hembras, donde no se encontraron diferencias estadísticamente significativas entre las tres categorías sociales (Fig. 1).

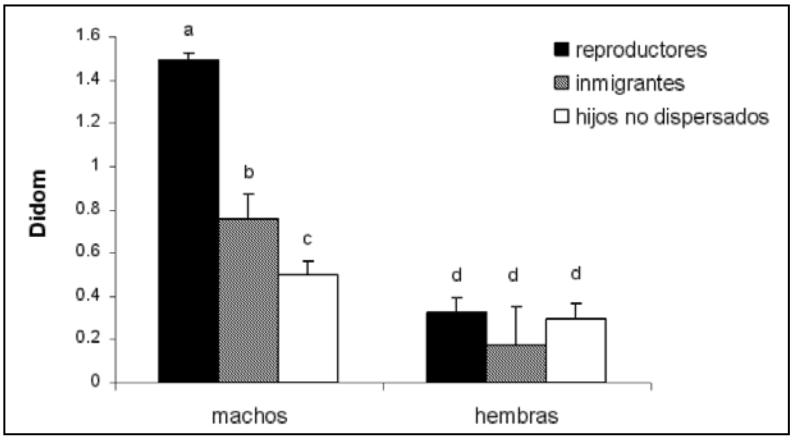

Fig. 1. Media ± SE del índice de dominancia (DIdom) de los miembros de los grupos cooperativos de corneja negra. Las letras (a, b, c, d) indican diferencias estadísticamente significativas (*P*<0,05) entre las categorías sociales.

Los patrones de dominancia observados entre los machos podrían reflejar la competición por otros recursos además del alimento, como la reproducción o la herencia del territorio. De hecho, en los grupos cooperativos de corneja negra, los inmigrantes machos no comparten parentesco con las hembras reproductoras y a menudo generan descendencia en la pollada (Baglione et al. 2002b), por lo que podrían competir con los machos reproductores dominantes para la reproducción. En cambio, los hijos machos constituyen una amenaza menor en los grupos, ya que en general comparten el territorio natal con sus padres y no se reproducen con sus madres (Baglione et al. 2002b). Todavía, estos individuos podrían ser percibidos como competidores potenciales porque, al poder retrasar su dispersión hasta los 4 años, podrían tratar de reproducirse en caso de que la madre fuera remplazada por una nueva hembra reproductora en el grupo. Por lo tanto, la competición para la reproducción actual o futura podría explicar los patrones de dominancia observados entre los machos en los grupos cooperativos. La situación es muy distinta entre las hembras que, debido al elevado recambio de hembras reproductoras en los territorios (Baglione et al. 2005), tienen una mayor probabilidad de obtener una vacante reproductora en los grupos. Por consiguiente, las hijas hembras se dispersan antes que los hijos machos y la presencia de hembras inmigrantes en los grupos es muy rara (Baglione et al. 2002a), lo que implica que el estatus de las hembras reproductoras en los grupos casi nunca se ve seriamente amenazado, explicando las relaciones de dominancia más igualitarias encontradas entre las categorías sociales femeninas.

II) Nepotismo en el acceso al alimento en los grupos cooperativos de corneja negra

En los grupos cooperativos, los machos reproductores dominantes proporcionaron a sus hijos un acceso preferencial a los recursos alimenticios del territorio. Los machos reproductores (i) atacaron a los inmigrantes machos con más frecuencia e intensidad (Fig. 2 a, b) y (ii) se asociaron preferentemente con sus hijos para compartir el alimento. Esto permitió a los hijos no dispersados pasar más tiempo alimentándose que los inmigrantes machos (Fig. 3) a pesar de su inferior rango de dominancia.

A pesar de los avances en la comprensión de la reproducción cooperativa, una gran controversia persiste sobre los factores que promueven la dispersión retrasada de los juveniles. La hipótesis del "nepotismo" sugiere que la explicación de la dispersión retrasada se encuentra en los beneficios que los hijos pueden obtener prolongando la asociación con sus padres en el territorio natal (Ekman et al. 2001; Ekman et al. 2004). Los resultados de este estudio mostraron que en la corneja negra, los hijos no dispersados obtuvieron importantes beneficios gracias a la presencia de padres nepotistas en el acceso a importantes recursos alimenticios a pesar de su bajo rango de dominancia. Estos beneficios se encuentran disponibles únicamente en el territorio natal, lo que sugiere que la tolerancia parental podría ser un factor determinante en la dispersión retrasada de los juveniles en la población cooperativa española.

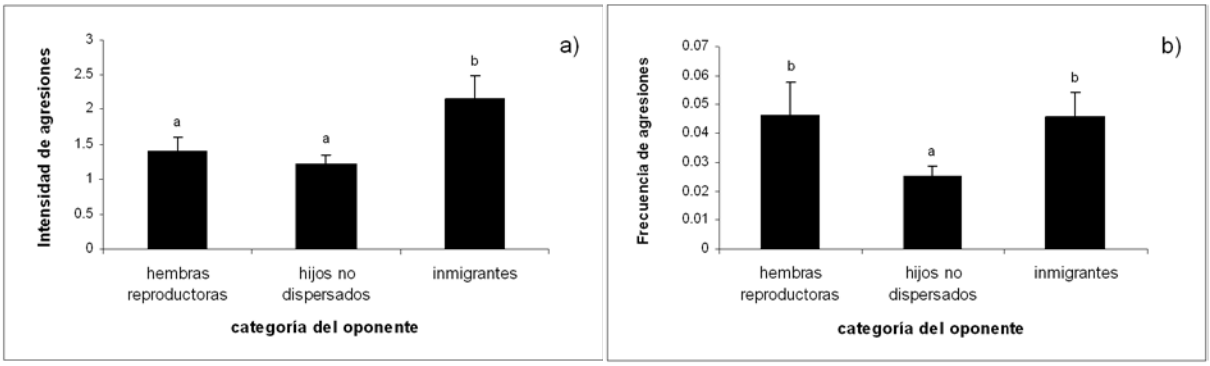

Fig. 2. a) Media ± SE del índice de intensidad de agresiones de los machos reproductores hacia las diferentes categorías sociales de los oponentes y b) Media ± SE de la frecuencia de agresiones de los machos reproductores hacia las diferentes categorías sociales de los oponentes. Las letras (a, b) indican diferencias estadísticamente significativas entre categorías (*P*<0,05).

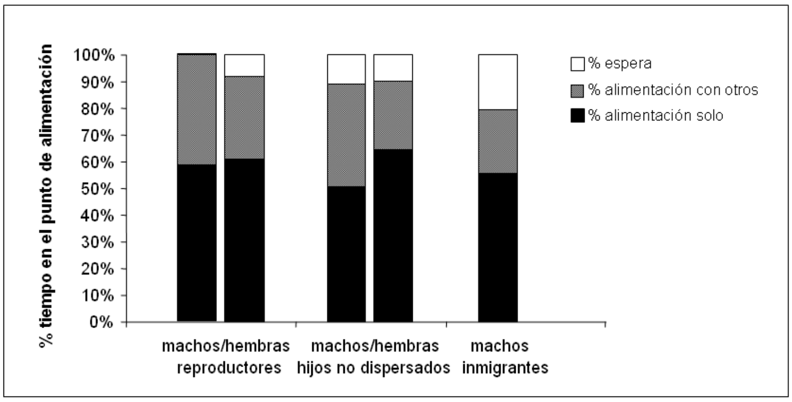

Fig. 3. Proporción de tiempo de alimentación solo, de alimentación con otros miembros del grupo y de espera mientras otro miembro del grupo se alimenta, para las diferentes categorías sociales. Las proporciones se calcularon sobre el tiempo total que el individuo pasó en el punto de alimentación.

La teoría también predice que la tolerancia parental debería de variar de acuerdo a la riqueza del territorio natal (Ekman y Rosander 1992). Baglione et al. (2006) demostraron que en las cornejas, un incremento en la disponibilidad de alimento en los territorios aumenta la filopatria de los juveniles. La variación en la tolerancia parental en función de la disponibilidad de alimento en los territorios podría ser el mecanismo próximo que explica este patrón. Sin embargo, los resultados de esta tesis mostraron que un incremento experimental en la disponibilidad de alimento en los territorios no influyó en el comportamiento agresivo de los machos reproductores y tampoco en la intensidad y en la frecuencia de agresiones globales en los grupos. Estos resultados sugieren que, en los grupos cooperativos de corneja negra, los hijos serían capaces de evaluar la calidad de su territorio natal y que podrían ejercer algún tipo de control sobre sus decisiones de dispersión en función de la abundancia de recursos.

III) Los subordinados se benefician del comportamiento exploratorio de los dominantes: respuesta a alimentos novedosos en las cornejas negras cooperativas

Los machos reproductores dominantes accedieron en primer lugar al alimento novedoso, seguidos por los inmigrantes machos, mientras que los hijos no dispersados y las hembras reproductoras fueron los últimos en alimentarse (Fig. 4). Las hembras inmigrantes muestreadas fueron excluidas de los análisis debido al escaso tamaño de muestra (*N*=2). Sin embargo, cualitativamente es interesante destacar que estas dos hembras fueron las últimas en acceder al alimento novedoso en sus grupos.

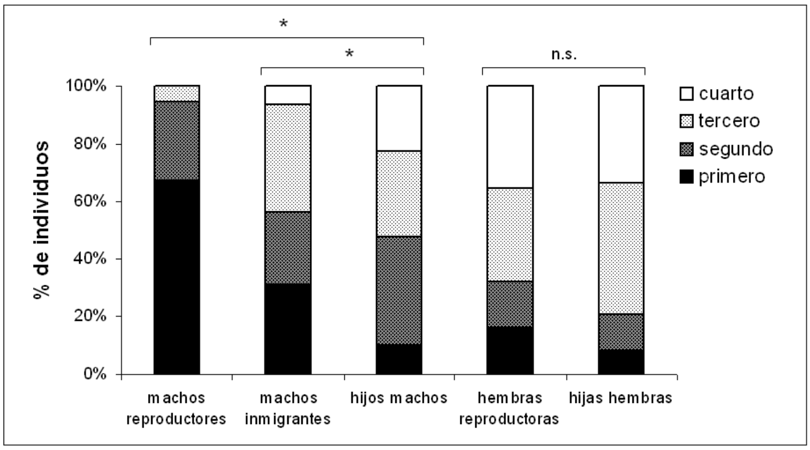

Fig. 4. Proporción de individuos que son primeros, segundos, etc. en el acceso al cebo, de acuerdo a su categoría social. Los asteriscos indican diferencias estadísticamente significativas ($P<0,05$) entre categorías sociales.

El orden de acceso al alimento, por lo tanto, reflejó el orden de dominancia en los grupos (Artículo **I**). Sin embargo, las opciones de alimentación de los subordinados no fueron limitadas por un efecto de exclusión competitiva de los machos reproductores dominantes. En los 14 grupos evaluados con dos fuentes de alimento al mismo tiempo, los subordinados (hembras reproductoras, inmigrantes machos e hijos no dispersados) optaron por alimentarse del cebo previamente utilizado por el macho dominante en lugar de alimentarse al mismo tiempo que el dominante sobre el cebo todavía inexplorado. Estos resultados sugieren que el comportamiento exploratorio de los machos reproductores dominantes permite a los subordinados reducir su neofobia en el acceso a determinadas fuentes de alimento. En particular, los hijos no dispersados, que se benefician de un acceso preferencial al alimento debido a la presencia de los padres nepotistas (Artículo **II**), no necesitarían asumir los riesgos de exploración de los alimentos presentes en el territorio natal, beneficiándose de la experiencia de los padres dominantes que comparten el alimento después de la inspección. Los beneficios que los hijos obtienen de vivir en familia en asociación con padres nepotistas y propensos a asumir riesgos, podrían ser importantes factores involucrados en la expresión de la dispersión retrasada de los juveniles en la corneja negra y en otras muchas especies cooperativas.

IV) ¿Los subordinados pagan para quedarse en los grupos cooperativos de corneja negra?

La hipótesis del "pago de tributo" predice que las relaciones sociales en los grupos cooperativos podrían estar influenciadas por los niveles de ayuda de los subordinados. Por un lado, los reproductores dominantes deberían incrementar su nivel de agresividad hacia los ayudantes 'perezosos' (Gaston 1978) y por otro lado, los ayudantes podrían apaciguar la agresividad del dominante realizando comportamientos de sumisión (Bergmuller y Taborsky 2005). Sin embargo, contrariamente a estas predicciones, en los grupos cooperativos de corneja negra en estudio, el comportamiento agresivo de los machos reproductores hacia los subordinados y el comportamiento de sumisión de estos últimos (hijos no dispersados e inmigrantes machos) no variaron durante la época reproductora en función de su contribución en el nido (Fig 5 a, b, c).

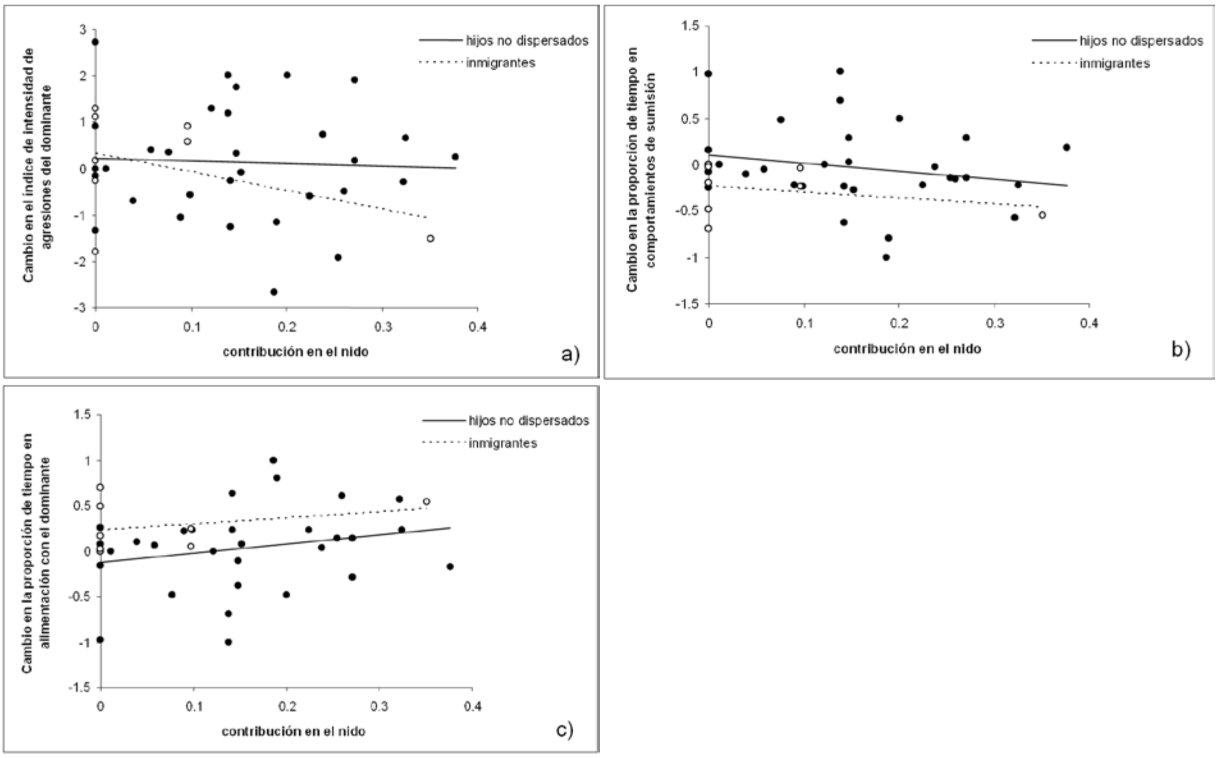

Fig. 5. Correlación entre la contribución de los ayudantes y el cambio entre el principio y el final de la época reproductora en a) el índice de intensidad de agresiones del macho reproductor dominante, b) la proporción de tiempo de los ayudantes mostrando comportamientos de sumisión y c) la proporción de tiempo alimentándose junto con el macho reproductor dominante. Puntos cerrados y abiertos representan a los hijos no dispersados y a los inmigrantes, respectivamente.

La falta de evidencias del pago de tributo en los grupos cooperativos de corneja negra se podría deber a la importante función como fuerza de trabajo de reserva que los ayudantes 'perezosos' proporcionan a los reproductores en situaciones desfavorables (Baglione et al. 2010). Datos empíricos demuestran que en esta población, cuando un miembro del grupo está temporalmente discapacitado y disminuye su contribución en el nido, los ayudantes perezosos incrementan su tasa de cebas a los pollos y los individuos que inicialmente se abstenían de cooperar empiezan a visitar el nido. El esfuerzo de estos ayudantes de 'reserva' compensa plenamente la reducción en el esfuerzo de aprovisionamiento de otro miembro del grupo, evitando una reducción en el éxito reproductor del grupo (Baglione et al. 2010). Por lo tanto, en la corneja negra y quizás en otras sociedades cooperativas, la estabilidad del grupo puede depender de la contribución potencial de los miembros del grupo además de su esfuerzo actual.

La agresividad de los dominantes hacia los inmigrantes y el sistema reproductivo

Los resultados mostraron que, en los grupos cooperativos, la categoría social del ayudante influyó significativamente en el comportamiento agresivo del macho reproductor dominante, y también en el comportamiento de sumisión de los ayudantes. Al final de la época reproductora, es decir, durante la primera semana después de que los pollos salieron del nido, los machos reproductores redujeron significativamente la intensidad de las agresiones dirigidas hacia los inmigrantes machos. Como consecuencia, los inmigrantes disminuyeron el tiempo dedicado a mostrar comportamientos de sumisión e incrementaron el tiempo dedicado a alimentarse junto con el macho reproductor dominante. En cambio, la agresividad de los machos reproductores no varió hacia sus hijos no dispersados que, por lo tanto, mantuvieron los niveles de sumisión estables durante toda la época reproductora (Fig. 6 a, b, c).

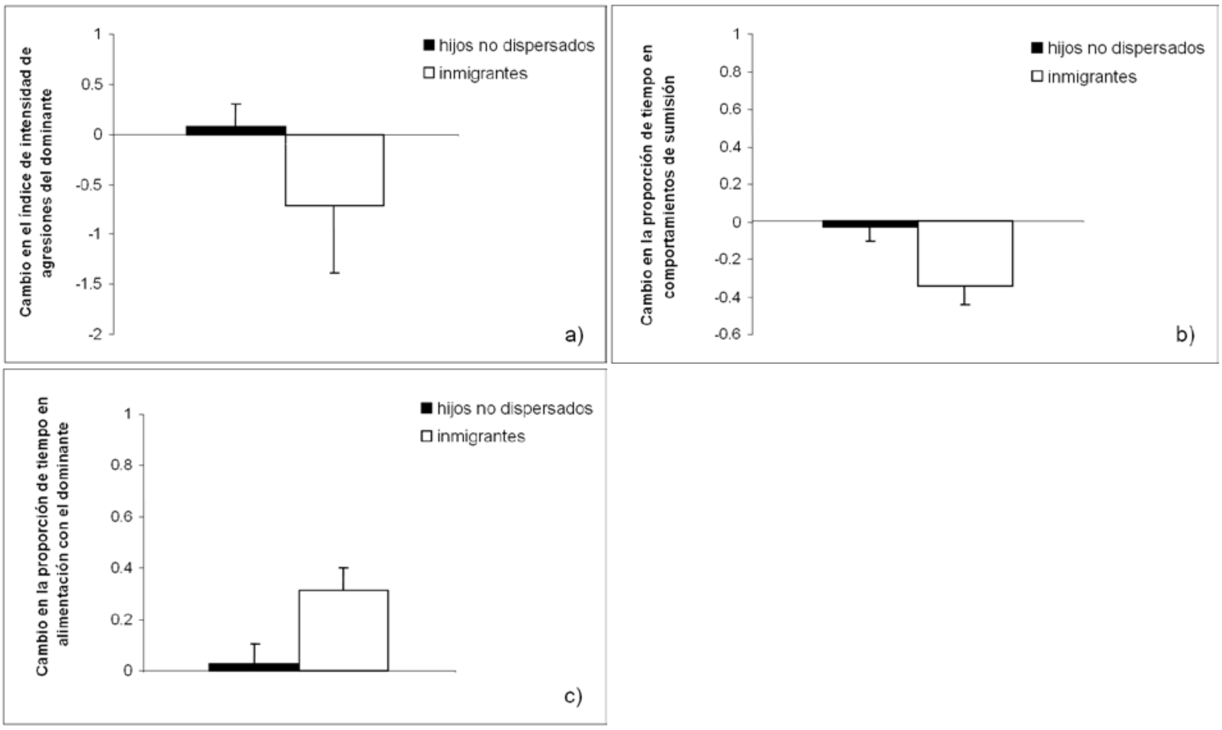

Fig. 6. Cambio en a) el índice de intensidad de agresiones del macho reproductor dominante, b) la proporción de tiempo de los ayudantes mostrando comportamientos de sumisión y c) la proporción de tiempo alimentándose junto con el macho reproductor entre el principio y al final de la época reproductora, de acuerdo con la categoría social del ayudante.

La variación en los niveles de agresión de los machos reproductores hacia los inmigrantes machos sugiere una función de la conducta agresiva en el contexto de la competición por la reproducción en los grupos. En las sociedades con reproducción cooperativa, los dominantes y los subordinados pueden compartir la reproducción (como en el caso de la corneja negra, Baglione et al. 2002b), pero el grado en que la reproducción se distribuye entre los miembros del grupo varía mucho entre especies ('reproducción sesgada' o *reproductive skew*, para una revisión véase Magrath et al. 2004; Hager y Jones 2009). Los modelos teóricos de la reproducción sesgada, sugieren que los dominantes controlan la incidencia de reproducción de los subordinados y que éstos se reproducen únicamente cuando el dominante lo permite (modelo de concesión, Vehrencamp 1979, 1983a, b), o bien, que los subordinados se reproducen porque los dominantes no son capaces de impedirlo (modelo de control incompleto, Cant 1998; Reeve et al. 1998; Johnstone y Cant 1999). El hecho de que los machos reproductores dominantes en la corneja negra mostrasen los niveles de agresividad más elevados hacia los inmigrantes machos (todos ellos adultos en esta muestra) al principio de la época reproductora (durante la puesta y incubación de los huevos), sugiere que la competencia reproductiva puede ser un factor importante que regula las relaciones sociales entre ellos. Cabe señalar que, en este período en concreto, las hembras reproductoras eran fértiles o todavía podían ser capaces de realizar una segunda puesta en el caso de depredación del nido, que se produce con frecuencia en la población de estudio (Canestrari et al. 2008). Las cornejas negras, por lo tanto, parecen encajar en el modelo del control incompleto de la reproducción sesgada, donde los machos dominantes intentan impedir la reproducción de los inmigrantes subordinados pero sin poder evitar totalmente el apareamiento (Baglione et al. 2002b).

CONCLUSIONES Y FUTURAS INVESTIGACIONES

En las especies con reproducción cooperativa, los individuos pueden obtener importantes beneficios derivados de la vida en grupo, como por ejemplo, un incremento en el número de crías por la presencia de ayudantes o una mayor supervivencia (Woxvold y Magrath 2005; Canestrari et al. 2008). Sin embargo, dentro de los grupos, los individuos también pueden competir para tratar de maximizar sus propios beneficios (West et al. 2002; Cant et al. 2006) causando conflictos que pueden influir en la estabilidad del grupo. Por esta razón, el estudio de las relaciones sociales entre los individuos puede proporcionar información relevante para la comprensión de los mecanismos de formación de los grupos y las dinámicas de la cooperación entre sus miembros.

Los resultados de esta tesis indican que, en los grupos de corneja negra con reproducción cooperativa, los individuos compiten para el acceso a los recursos alimenticios del territorio. Esta competición conduce a la formación de jerarquías de dominancia, determinadas por factores comunes a todos los grupos, donde los machos reproductores ocupan las posiciones más dominantes. Las jerarquías de dominancia y los patrones de agresividad/tolerancia entre los individuos influyen directamente en el reparto de los recursos alimenticios del territorio. Los machos reproductores dominantes pueden monopolizar la comida y se alimentan durante más tiempo con respecto a los demás miembros del grupo. Estos individuos además, proporcionan a sus hijos un acceso preferencial a los recursos alimenticios del territorio y limitan el acceso a los inmigrantes, que, a pesar de su mayor rango de dominancia, acaban alimentándose significativamente menos que los hijos no dispersados. Investigando la respuesta de los miembros de los grupos cooperativos a alimentos novedosos, se observó que los machos reproductores dominantes son los más propensos a asumir los riesgos de explorar el alimento y que su comportamiento ayuda a los subordinados a superar su neofobia y acceder al alimento. Estos resultados demuestran, por lo tanto, que en la corneja negra existen importantes beneficios que los juveniles pueden obtener prolongando la asociación con sus padres nepotistas en el territorio natal. El acceso preferencial y 'seguro' al alimento del territorio natal podría aumentar la supervivencia de los hijos que retrasan la dispersión (Ekman et al. 2000). Si así fuera, la tasa de mortalidad de los juveniles de corneja negra debería ser mayor para los hijos que se dispersan del territorio familiar que para los hijos filopátricos. Medir las tasas de mortalidad de los juveniles en función de sus decisiones de dispersión es un objetivo de trabajo futuro en la presente población de corneja negra. Otro objetivo consiste en evaluar experimentalmente la respuesta de los hijos no dispersados a un cambio del reproductor dominante en el territorio. Si los juveniles retrasan la dispersión por los beneficios que obtienen de la asociación con sus padres dominantes, al sustituir estos últimos con los inmigrantes dominantes presentes en el territorio, los hijos deberían dispersarse. Estos resultados proporcionarían evidencias contundentes de la función adaptativa de la dispersión retrasada en la corneja negra.

La vida en grupo en la corneja conduce a la cooperación entre individuos emparentados en la cría de los pollos. Los datos sobre las relaciones sociales en el acceso al alimento y la contribución de los ayudantes en la alimentación de los pollos parecen descartar la hipótesis de que la ayuda en el nido sea el tributo que los ayudantes pagan a los reproductores dominantes para ser tolerados en el territorio. En los grupos cooperativos de corneja negra, el nivel de contribución de los ayudantes en el nido no influye sobre el comportamiento agresivo del macho reproductor dominante y tampoco sobre el comportamiento de sumisión de los mismos ayudantes durante el acceso al alimento. En este trabajo se sugiere que la tolerancia del dominante hacia los ayudantes 'perezosos' podría derivar de la importante función que estos individuos ejercen en circunstancias desfavorables y que permite a los reproductores dominantes mantener constante su esfuerzo de cría (Baglione et al. 2010). Sin embargo, aunque esta función 'de reserva' pueda explicar la falta de 'castigo' por parte de los dominantes en condiciones 'normales', no se puede excluir que en situaciones desfavorables para el grupo, los dominantes puedan forzar el aprovisionamiento de los ayudantes en el nido, ya sea directamente por coacción o indirectamente al limitarles el acceso a los recursos del territorio. Los datos presentes en esta tesis no abordan esta cuestión, por lo que me propongo contrastar esta hipótesis en futuras investigaciones sobre esta población.

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Artículo I

JERARQUIAS DE DOMINANCIA LINEALES Y ESTABLES EN LAS CORNEJAS NEGRAS COOPERATIVAS

Las aves con reproducción cooperativa, en general, forman grupos cohesivos y estables que comparten un territorio durante todo el año, por lo que es probable que en algún momento lleguen a competir por los recursos. Entender como los miembros del grupo negocian el acceso a los recursos es crucial para comprender la evolución de estas sociedades, porque los conflictos pueden alterar la estabilidad del grupo y en última instancia obstaculizar la cooperación. Sin embargo, las relaciones sociales dentro de los grupos cooperativos han sido largamente olvidadas. En este trabajo, investigamos como los grupos de corneja negra con reproducción cooperativa (*Corvus corone corone*) comparten una fuente de alimento, observando las interacciones diádicas en 29 territorios que contienen hijos no dispersados de la pareja de reproductores e/o inmigrantes. Nuestros resultados mostraron jerarquías de dominancia lineales y estables en los grupos de cornejas negras, que estuvieron más definidas entre machos que entre hembras. Sugerimos que estas diferencias reflejan el nivel de competición para otros recursos además del alimento, como por ejemplo la reproducción y la herencia del territorio, que es más intensa entre machos que entre hembras. Es interesante apreciar que los inmigrantes machos dominaron a los hijos machos no dispersados, lo que sugiere que para el macho reproductor residente, que es el miembro alfa del grupo, los beneficios de la asociación con un inmigrante sobrepasan los costes de tener a sus hijos desplazados más abajo en la jerarquía. Este estudio puso al descubierto los factores clave que determinan las relaciones jerárquicas entre las cornejas cooperativas y destacó la necesidad de centrarse en las interacciones sociales en cada contexto de la vida en grupo para explicar íntegramente la dinámica de la cooperación en el nido.

Palabras clave: dominancia, jerarquía, competición, reproducción cooperativa, Corneja negra, *Corvus corone*

Linear and stable dominance hierarchies in cooperative Carrion crows

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Abstract

Cooperatively breeding birds typically form cohesive and stable groups that live year-round in all purpose territories where competition for resources is likely to arise. Understanding how group members negotiate over resources is crucial because conflicts may disrupt the stability of the group and may ultimately hinder cooperation. However, social relationships within the group have been largely neglected so far. Here we investigated how cooperatively breeding carrion crows (*Corvus corone corone*) share a food source, by observing dyadic interactions in 29 territories that contained retained offspring of the breeding pair and/or immigrants. We found that crows formed linear and stable dominance hierarchies, which were stronger for males than females. We suggest that this difference mirrors the level of competition for resources other than food, such as reproduction and territory inheritance, which is higher in males than females. Interestingly, immigrant males dominated male offspring, suggesting that, for the resident breeder, which is the alpha member of the group, the benefits of an association with an immigrant overcome the costs of having his sons pushed down in the hierarchy. Our study uncovered the key factors that determine hierarchical relationships among cooperatively breeding crows and highlighted the need of focussing on social interactions in every context of group living to fully explain the dynamic of cooperation at the nest.

Keywords: dominance, hierarchy, competition, cooperative breeding, Carrion crow, *Corvus corone*

INTRODUCTION

In animal societies, individuals that share the same territory may compete for resources such as food (Huntingford & Turner 1987), especially when it is scarce (Milinski & Parker 1991) or unevenly distributed within the territory (Isbell & Young 2002), reproduction (Huntingford & Turner 1987) and territory inheritance (Poston 1997). Direct conflicts among group members may decrease upon formation of dominance hierarchies that establish an order of access to the resources, determining a better individual investment of energy and time and reducing the risk of injures and death (Huntingford & Turner 1987; Aureli & de Waal 2000). Within a hierarchy, dominance may be influenced by sex, age (Piper 1997), body size (Persson 1985) or territory previous ownership (Bridge et al. 2000). Hierarchies can be linear when dominance is clearly established and follow a transitive order (e.g. A>B>C and A>C) or nonlinear, when the rank order is irregular and circular (e.g. A>B>C and C>A) (Martin & Bateson 2007). In general, linear dominance hierarchies remain stable over time as long as the composition of the group does not change (Senar et al. 1990; Chase et al. 2003; Graham & Herberholz 2009).

Dominance hierarchies have been described in several social organisms from insects to mammals (Izawa & Watanabe 2008 and references therein), but they have been scarcely investigated in cooperatively breeding bird species, where more than two individuals provide care to the young (Cockburn 1998). In cooperative species, groups generally form through delayed dispersal of juveniles, which help their parents in raising new young, but associations of unrelated individuals can also occur (Stacey & Koenig 1990; Hatchwell & Komdeur 2000). Studies on the evolution of cooperative breeding have primarily focused on cooperation in raising the young and competition for reproduction (reproductive skew theory, see Magrath et al. 2004 for a review), while competition for the access to the resources of the territory has been largely neglected. This lack of information hinders a full understanding of cooperative societies, because competition for resources may influence juvenile delayed dispersal as well as association of non-relatives, with important consequences for group composition and cooperation in reproduction. For example, subordinate individuals may be excluded from the best foraging areas and forced to feed in low-quality patches or where predation risk is higher (Schneider 1984), which may induce them to disperse earlier. Furthermore, the individual effort in provisioning the young among non-breeding group members in kin societies may depend on the probability of inheriting the reproductive territory in the future (Cant & Field 2001). It has been suggested that low-ranking individuals, which have smaller probabilities of inheriting the breeding position, may help more than high-ranking individuals in order to maximize their indirect fitness benefits, while high-ranking individuals may save energy for future reproduction, which may explain why in many cooperative species the helping effort is not correlated with the degree of relatedness to the young (Cant & Field 2001).

The formation of hierarchies may be especially important in cooperative species because individuals typically share all-purpose territories year round and need to reduce conflicts in order to cooperate. Cooperative species are typically long-lived (Arnold & Owens 1998) and social groups are often cohesive and stable over time (Kokko & Johnstone 1999). This may have consequences for the structure of dominance hierarchies in cooperative species. Theory predicts that: (1) continuous interactions among group members in a limited area and over a long time period will favour the formation of well defined linear hierarchies (Kaufmann 1993); (2) the stability of group composition will stabilize hierarchies over time; (3) the individual dominance rank will be influenced by intrinsic factors (e.g. sex, body size, age) consistently across groups. Alternatively, cooperative societies, particularly those that are kin-based, may be egalitarian, showing little competition for resources among group members.

In this study, we investigate the dominance hierarchies in a kin-based cooperative population of carrion crows *Corvus corone corone* in Northern Spain. Crows are long-lived birds (Cramp & Perrins 1994) and in Northern Spain they form cooperatively breeding groups of up to nine individuals that live in year-round all-purpose territories (Baglione et al. 2002a), where potential competition for food, reproduction and territory inheritance occurs. Social groups form through delayed dispersal of offspring which remain on the natal territory for up to 4 yr with one or both parents, or through immigration of relatives from other territories (Baglione et al. 2003). Both immigrants and retained offspring can help at the nest (Canestrari et al. 2005) but only adult immigrants can share in reproduction with the resident breeding pair (Baglione et al. 2002a). Here we analyse the social relationships among group members to determine whether dominance hierarchies regulate the access to food. In particular we investigate: (1) whether the access to food is egalitarian or follows a dominance hierarchy; (2) the individual factors that are correlated with dominance (sex, age, social category); (3) the structure of the hierarchy (linear vs. nonlinear) and (4) the stability of the hierarchy over time. Finally, we compare our data with previous findings on non-cooperative carrion crows and we discuss the implications of dominance hierarchies on social living and cooperation in our study population.

METHODS

Study area and population

We studied a cooperative population of carrion crow in a 45 km^2 rural area in Northern Spain (42°N, 5°W). The study area represents a traditional Spanish low intensity agricultural landscape, with a mosaic of crops, meadows, poplar and pine plantations, scrubs, oak forest patches and uncultivated land. Here, 75% of groups (three to nine crows, mode = 3) live year-round in all-purpose territories and breed cooperatively, with up to five individuals feeding the nestlings (Baglione et al. 2002a). In addition to the resident breeding pair, groups contain retained offspring that remain on the natal territory for up to 4 yr, and / or immigrants (mostly males) that are related to the resident breeder of the same sex (Baglione et al. 2003). Groups can therefore be unassisted pairs, nuclear families (a pair with retained offspring), mixed groups (a pair with both retained offspring and immigrants) or pairs with one or more immigrants. Reproduction can be shared among group members of both sexes, but retained offspring usually do not reproduce within their natal group. Polygamous mating occurs in 67% of groups containing sexually mature immigrants, with polyandry prevalent over polygyny (Baglione et al. 2002b). At the nest, individual provisioning effort is higher in individuals which produced offspring in the current brood. Among non-breeders, retained offspring and non-breeding immigrants feed the chicks at comparable rates (Canestrari et al. 2005). Territory quality influences family cohesion and cooperative behaviour. Offspring are more philopatric and more likely to help at their family's nest in territories where food resources are abundant year- round (Baglione et al. 2006; Canestrari et al. 2008a).

Individual classification and group composition

From 1995, all nestlings in the study area have been banded just before fledging (30 d old) with a unique combination of colour rings and patagial wing tags (Caffrey 2000) and 105 adults were caught with walk-in baited cages or 'snap traps' (Baglione et al. 2002a). A study on American crows (*Corvus brachyrhynchos*) showed that patagial wing tags did not affect survival and social interactions (Caffrey 2000). In our population no crows were injured or abandoned the nest or territory as a consequence of capture, nor did the wing tags affect survivorship (Canestrari et al. 2007). We collected between 50 and 200 µl of blood from the brachial vein of each banded individual for sex determination using P2 / P8 molecular method (Griffiths et al. 1998). The birds were aged as one, two and older than 2 yr according to the internal colour of the upper mandible (Svensson 1992). For this study, observations were collected between 2003 and 2007 on 29 territories where the history of the groups (three to eight individuals, mode = 4) was known due to constant effort in catching and banding adults and fledglings since 1999 (Table 1). Thirteen of those territories were sampled two to four times in different years. In nine territories the composition of the groups had changed, due to death of one individual, recruitment of new member (young born on the same territory or immigrants) or dispersal of offspring. In the remaining four territories the groups remained unchanged. In our analyses, we controlled for repeated measures of the same individual and territory where appropriate (see "Statistical methods").

In nuclear families we classified as retained offspring all individuals that were still living in their natal territory, while the remaining two adult birds were classified as breeders. We classified as immigrant any individual that was born in a different territory and joined an established group. Sexually mature male immigrants often sire offspring alongside the 'resident breeder' (Baglione et al. 2002b), which is defined here as the male that had been

Table 1. Sample sizes used in the analyses.

Question addressed	**Years**	**Number of different territories***	**Number of known dyads**	**Number of individuals**
Factors influencing dominance hierarchy	2003–2007	29 (13)	285	57 breeders (33♂, 24♀) 55 offspring (36♂, 19♀) 16 immigrants (14♂, 2♀)
Dominance hierarchy stability:				
Over short term (same group sampled at the beginning and at the end of the breeding season)	2003–2007	21 (11)	186	40 breeders (22♂, 18♀) 37 offspring (24♂, 13♀) 11 immigrants (9♂, 2♀)
Over long term (same group sampled in different years)	2004–2005	4	30	7 breeders (4♂, 3♀) 4 offspring(2♂, 2♀) 4 male immigrants

*In brackets the number of territories that were sampled more than once in different years (see text for details) living in the territory before the arrival of immigrants. Note that this classification of resident male breeders (also 'male breeders' hereafter) and adult male immigrants reflects the previous ownership of the territory rather than the breeding status.

The individuals considered in our sample were individually recognizable. In groups containing one unbanded breeder, sex could be inferred by the sex of the other breeder (14 females and 5 males). In four groups, the two unbanded breeders could be distinguished by their different sizes. The observations of these groups involved the use of a camouflaged digital scale attached to a chicken carcass that attracted the birds to the video-recording spot (Canestrari et al. 2007). Because in this population males are significantly heavier than females (Canestrari et al. 2007) we could identify each breeder based on their relative weight. In other two groups the breeding female and an immigrant bird were unbanded. These individuals were initially excluded from the sample, but based on the results of this study they could be classified *a posteriori* due to their dominant / submissive behaviour. The two breeding females were therefore included in the analyses, while the unbanded immigrants were not because their sex was unknown. Removing the two females from the sample never involved qualitative changes in the results. Because reproduction in crows is rare before the third year (Madge & Burn 1999) and as only one of 44 breeders studied so far in this population has been younger than 3 yr, all unbanded breeders were aged as adults (Canestrari et al. 2007). The final sample included 57 breeders, 16 immigrants and 55 retained offspring. According to the question addressed, the data set was reduced to the sub-sample that was relevant for statistical testing (see Table 1 for details). All bird manipulations were authorized by Junta de Castilla y León.

Dominance hierarchy

We determined the dominance hierarchy by using two different dominance indices from which we calculated the ordinal rank of each group member. The 'DIdom' index (Lamprecht 1986) provides a measure of how dominant an individual is with regard to other group members and is calculated as the number of animals dominated by an individual / the number of animals with which that individual interacted. DIdom ranges between 0 (absolutely submissive) and 1 (absolutely dominant), and considers the performance of an individual in all contested dyads, providing detailed information about the distances between adjacent ordinal ranks (Langbein & Puppe 2004). The 'normalized David's score' (DS, De Vries et al. 2006) calculates dominance ranks by using the proportion of wins and loses by each individual within each dyad, while taking the relative strength of the opponents into account (David 1988).

Between 2003 and 2007 we calculated the dominance indices of 128 group members of 29 different territories, based on interactions among individuals feeding on an experimental food source. A chicken carcass of approximately 300 g was tied to the ground and allowed group members to feed and interact for approximately 2 h. We video-recorded the interactions with a video-camera placed 5 m away from the bait and disguised with vegetation. For each group, in March and April, we carried out one or two observation bouts of 4 h between 06:00 and 12:00 h, for a total of 360 h of observation. Overall, we sampled 387 dyads comprising 33 breeding males, 24 breeding females, 55 retained offspring (36 males and 19 females) and 16 immigrants (14 males, two females) (Table 1). We based our analyses on the outcome of competitive interactions within dyads of individuals that included unaggressive behaviours, mild forms of aggression and overt forms of aggression (see Table 2 for a detailed description of interactions).

Table 2. Description of the behaviours observed in the dyads. Individual A: first member of the dyad. Individual B: second member of the dyad.

Interaction type	Times observed	Definition
(1) Unagressive food monopolization 1	102	Individual A feeds while B takes food furtively, adopting an inconspicuous posture, keeping the body low and parallel to the ground and stretching the neck to reach the food beyond the reach of A’s beak
(2) Unaggressive food monopolization 2	257	Individual A feeds on the bait while individual B waits closely. Individual B starts feeding when individual A leaves
(3) Displacement	85	Individual A moves directly towards individual B and continues moving through the point of intersection while B moves away
(4) Intimidation	106	Individual A intimidate B using the beak, but without a physical contact. Individual B leaves food item and waits for food or leaves the feeding site
(5) Chase	35	Individual A flaps the wings and adopt a conspicuous posture, inflating head and chest and chases B
(6) Fight	4	Individual A physically attacks B using pecks, bill snaps and kicks

We evaluated the dominance status of individuals within every dyadic relationship based on a clear winner/loser criterion. For each dyadic interaction, we defined the 'loser' as the individual that first stopped fighting, turned away from an attack, tried to flee or was displaced from a location, fed furtively or waited for food while the opponent was feeding. We defined the 'winner' as the individual that did not turn away from a fight, displaced the second individual from the feeding spot and ate while the second individual fed furtively or waited for food. Within a dyad, the 'dominant' was defined as the individual that won more than 50% of the agonistic interactions recorded during the observational period (Jackson & Winnegrad 1988). Typically, crows consumed very little food on the feeding spot as they cached most of the meat in their territory. During the observations bouts therefore, crows were continuously flying to and from the feeding spot, so that individuals of each dyad met repeatedly on the bait. We defined as 'event' every encounter on the bait of the two individuals of a dyad. Each event finished when one or both individuals left the feeding site and the next one started when the individuals met again. Agonistic behaviours within an event might be non-independent and this could affect our assessment of dyadic dominance based on counting victories (see above). To avoid this, for events with multiple interactions, we assigned one victory to the individual of the dyad that won more interactions within that event.

Dominance linearity within groups

Linear dominance hierarchies are those in which dyadic relationships are asymmetric and triadic relationships are transitive (Martin & Bateson 2007). Asymmetry occurs when one individual in a dyad consistently wins a disproportionate number of interactions. Transitivity occurs when individual A is dominant over B, B is dominant over C and A is dominant over C, whereas if A>B>C but C>A dominance is circular. In our study, in 102 dyads individuals never interacted ('unknown dyads' hereafter, Langbein & Puppe 2004). In the remaining 285 known dyads, we determined the number of wins of each member and we calculated dyadic asymmetry as the percentage of dyads with a significant asymmetric outcome tested with two-tailed binomial sign test (Lehner 1996). For this analysis we considered only dyads with six or more interactions (113 known dyads) because with less interactions and a binomial probability of $P = 0.5$ it was not possible to reject the null hypothesis, which is that the dyad was symmetric. Finally, we calculated the 'directional consistency index' (DCI, van Hooff & Wensing 1987) that quantified the degree of asymmetry of wins within dyadic relationships. It ranges from 0 to 1, where high values indicate that, among pairs of individuals who interact multiple times, wins are highly asymmetrical. We measured transitivity of relationships across multiple dyads within the same social group as the number of circular dominance relationships in the group. Dominance in the group tends to be transitive if the proportion of triads in which relationships are circular is less than that expected by chance (Appleby 1983).

Linearity is often measured with the Landau index (h) or de Vries's corrected index (h^1) (De Vries 1995). However, we could not use these indexes because most groups did not fulfil the requirements, namely having more than six members interacting at high frequencies (Appleby 1983; Isbell & Young 2002).

Dominance hierarchy stability

In order to determine the stability of the dominance hierarchy over time, in 21 groups we repeated video recorded observations (bouts of 4 h between 06:00 and 12:00 h) twice, at the beginning of the breeding season (egg laying and incubation) and at the end (the first week after fledging), and we checked whether the DIdom index of group members changed. Overall, we sampled 22 breeding males, 18 breeding females, 37 retained offspring (24 males and 13 females) and 11 immigrants (9 males and two females). In addition, in four territories where group composition did not change across years, we collected data in two successive years. Here we recorded behaviour of four breeding males, three breeding females, four retained offspring (two males and two females) and four male immigrants.

Statistical methods

Statistical analyses were performed using GENSTAT 12.0. Because the individual ordinal ranks obtained from the DIdom and David's score indices were equivalent (Spearman's rank correlation: $r_s = 0.909$, $N = 128$ individuals, $P < 0.001$) we used for the statistical analyses only DIdom index, which was normalized using arcsine square root transformation. All data were analysed with linear mixed models (LMM) using the restricted maximum likelihood method (REML). Individual identity and territory identity were fitted as random factors. Potential explanatory variables that gave non-significant results ($P > 0.1$) were sequentially removed until the model only included significant terms. Significant probability values were derived from having all significant terms fitted in the model together, whereas those of non-significant terms were obtained from having all significant terms in the model and each non-significant term fitted individually (Russell et al. 2003). If relevant, when an interaction term was significant in an LMM, we performed further analyses to determine the main effect of each individual term, testing separately the effect of one term for each category of the other (Engqvist 2005).

Ten groups in our sample had been food supplemented year-round as part of a field experiment designed to investigate the effect of territory resources on dispersal and helping behaviour (for details on methodological procedures see Canestrari et al. 2007; Canestrari et al. 2008a). A preliminary statistical analysis showed that food supplementation treatment did not significantly affect the DIdom of group members (*N* = 30 fed individuals, *N* = 46 unfed individuals; experimental treatment: Wald = 0.85, d.f. = 1, 58.9, *P* = 0.360; results of LMM that included the following variables on individual DIdom: Experimental treatment -fed / unfed-, sex, age, individual category -breeder, retained offspring and immigrant-, individual category*sex; random factors: Individual identity and territory identity). Therefore, fed groups were included in the sample.

To investigate the factors determining dominance rank, we tested the effect of the following variables on individual DIdom: Year, individual category (breeder, retained offspring and immigrant), sex, age, individual category*sex. To test the stability of the dominance hierarchy over time in 21 groups sampled at the beginning and at the end of the same breeding season, we tested the effect of the following variables on individual DIdom: Year, period (beginning / end of the breeding season), individual category, sex, age, individual category*sex. LMM could not be used to test the stability of the hierarchy across years because of the small sample size (four groups, Table 1); therefore Spearman's rank correlation was used instead.

RESULTS

Dominance hierarchy

The ordinal rank of group members derived from 'DIdom' and 'normalized David's score' indices of dominance indicate that breeding males were the most dominant group members, followed by male immigrants, male retained offspring, breeding females, female retained offspring and female immigrants (Fig. 1). The interaction between category and sex significantly influenced individual DIdom, as breeding status conveyed a dominant position to males only (Fig. 1, Table 3), while year and age had no significant effect (Table 3). When we re-ran the analysis for each social category separately, we found that males were dominant over females both in breeders (Wald = 268.61, d.f. = 1, 25.6, $P < 0.001$) and in retained offspring, although for the latter the effect of sex was non-significant (Wald = 2.87, d.f. = 1, 51.8, $P = 0.09$; Fig. 1). Immigrants could not be tested because of the small sample size (only two females). However, qualitatively, it is interesting to note that those two immigrant females were the most subordinate in their group. Interestingly, we also found that the male lowest rank category, i.e. retained offspring, were still dominant over all the females in their group, regardless of the social status of the latter (Wald = 4.14, d.f. = 1, 44.8, $P = 0.042$; Fig. 1). The analysis carried out for separate sexes revealed a clear hierarchy among males, with breeders on the top, immigrants in the middle and retained offspring at the bottom (Wald = 194.18, d.f. = 2, 168, $P < 0.001$), with significant differences between the three categories (Fig. 1), as shown by the *post hoc* comparison performed with VMPROCEDURE available in GENSTAT 12.00 (Payne 2009). On the contrary, the social category had no significant effect on individual DIdom among females (Wald = 3.09, d.f. = 2, 23, $P = 0.24$; Fig. 1). This result did not change qualitatively when we excluded the two immigrant females from the analysis. In addition we also found that the level of aggressiveness was higher in males, where 58% of dyads showed aggressive interactions (type 3–6; Table 2) compared with 34% of females dyads (Fisher's exact test: two-tailed $P = 0.02$; $N = 145$).

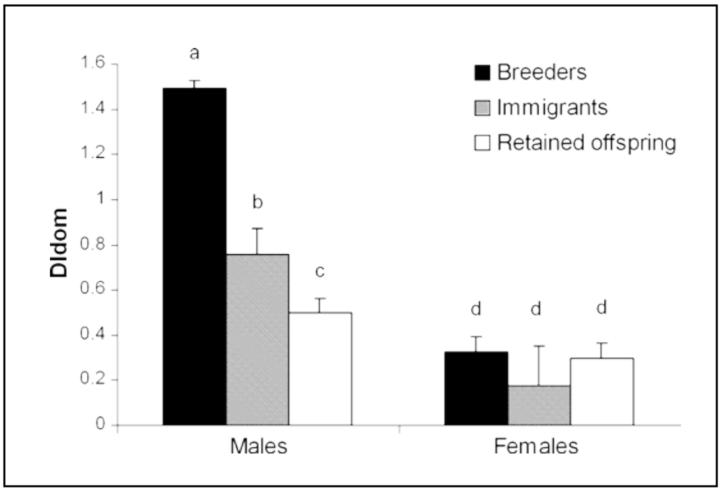

Fig. 1. 'Mean' ± SE normalized DIdom (normalized using arcsine square root transformation) of members of crows groups. Different letters (a, b, c, d) indicate statistical differences ($P < 0.05$) between social categories.

Table 3. Model summary of the factors affecting dominance hierarchy.

Model terms	**Wald statistic**	***df***	***P***	**Random term estimated variance component ± SE**
Dominance hierarchy model				
Individual identity*				-0.016 ± 0.015
Territory identity*				0.007 ± 0.007
Year	5.26	4, 68.8	0.274	
Individual category	174.43	2, 62.1	<0.001	
Sex	182.50	1, 69.1	<0.001	
Age	1.87	1, 63.3	0.177	
Individual category*Sex	69.06	2, 93.4	<0.001	

*Random factors

Dominance linearity within groups

The results of antagonistic interactions and the calculation of sociometric parameters showed clear linear dominance hierarchies within groups, where known dyads were highly asymmetric and triadic relationships were transitive. Out of the 285 known dyads, 258 were 'one-way dyads' (with wins only for one individual), 23 were 'two-way dyads' (with more wins for one individual) and four were 'tied dyads' (with the same number of wins for both individuals). According to the two-tailed binomial tests 92.9% of known dyads with six or more interactions (N = 113) were significantly asymmetric. DCI was 0.95 and we did not observe circular dominance relationships in any group.

Dominance hierarchy stability over time

In 21 groups sampled at the beginning and at the end of the same breeding season, dominance hierarchies proved stable over time. When controlling for the significant effect of the interaction between sex and category neither year, period (beginning or end of the breeding season) nor age had a significant effect on individual DIdom (Table 4). In four groups sampled over successive years, individual DIdom values were highly correlated (Spearman's rho correlation: $r_s = 0.993$, $N = 15$, $P < 0.001$).

Table 4. Model summary of the factors affecting dominance hierarchy stability.

Model terms	**Wald statistic**	***df***	***P***	**Random term estimated variance component ± SE**
Dominance hierarchy stability model				
Individual identity*				-0.008 ± 0.022
Territory identity*				0.006 ± 0.009
Year	4.50	4, 23.3	0.372	
Period (beginning or end of the breeding season)	1.26	1, 126.2	0.264	
Individual category	91.21	2, 55.1	<0.001	
Sex	104.80	1, 60.5	<0.001	
Age	1.46	1, 91.8	0.231	
Individual category*Sex	37.68	2, 68.1	<0.001	

*Random factors

DISCUSSION

Cooperative groups of carrion crows were not egalitarian in sharing food resources. The access to food was regulated by dominance hierarchies, showing that there is competition for resources in this kin-based society. The individual dominance rank was correlated with sex and social category consistently across groups. In general, males dominated over females and resident male breeders were the most dominant, followed by male immigrants, male offspring, female breeders, female offspring and female immigrants. It should be noted that immigrant females are rare in cooperative groups and only two could be sampled for this study. Hereafter, when discussing results involving female dominance, we will refer to female breeders and female retained offspring only.

Theory predicts that linear and stable hierarchies arise in animals living in groups smaller than 10 individuals and with stable composition over time (Kaufmann 1993; Jameson et al. 1999). Larger group sizes may lead to irregularities in the hierarchical order (Jameson et al. 1999) and a faster turnover of individuals may hinder individual recognition and learning from past antagonistic experiences, leading to unstable dominance relationships (Drews 1993). In this study we showed that cooperatively breeding groups of carrion crows, which are cohesive and stable over time (Baglione et al. 2002a), showed linear hierarchies that remained stable throughout the breeding season and across years.

The dominance hierarchy in carrion crows presented three interesting features: (1) dominance relationships were more defined and strict among males than among females; (2) immigrants were dominants over retained offspring; (3) the breeding females were subordinate to their sons. Here, we discuss the possible explanations and consequences of these patterns.

Consistent with observations of winter flocks in Switzerland (Richner 1989), our results also indicated a significant effect of sex on the individual dominance rank in cooperatively breeding groups of carrion crows. However, interestingly, while in winter foraging flocks the hierarchies are strict and well defined within both sexes (Richner 1989), in cooperatively breeding groups hierarchies were clear among males (resident breeders>immigrants> retained offspring) but relaxed among females. Compared to the big winter flocks of unrelated birds, Spanish crow social groups are enlarged families (Baglione et al. 2003) where kinship may decrease competition for food (Ekman et al. 2001). According to this, females in the studied families were egalitarian in sharing food. However, the fact that the male hierarchies persisted in a kin-based social environment suggests that, for this sex, dominance ranks not only regulate the access to food but also to other limited resources, such as reproduction and territory inheritance, for which males compete more strongly than females. This idea is supported by the fact that, in experimental conditions of food abundance, the dominance hierarchies among kin group members did not relax. In the social groups of crows in Spain, immigrant males are generally unrelated to the breeding female and often sire some offspring in the brood (Baglione et al. 2002b). Male retained offspring probably threaten less the paternity of other male group members, because they usually live with their parents and have no potential mates within their natal group. Indeed, male offspring reproduction has never been observed so far (Baglione et al. 2002b). However, they may still be perceived as current or future potential competitors for reproduction because they can stay at home for up to 4 yr and may try to mate if their mother is replaced by new unrelated breeding females. Competition for current or future reproduction may therefore explain the patterns of dominance between males in the groups. The situation is different for females, which have a higher probability of obtaining a breeding vacancy due to the higher turnover of breeding females in the territories (Baglione et al. 2005). As a consequence, daughters disperse earlier than sons and female immigration into established groups is very rare. Therefore, in cooperatively breeding groups, the breeding status of the female is virtually never seriously challenged, explaining the egalitarian relationships among female group members.

Besides reproduction, immigrant males and male offspring can also compete for inheriting the territory after the death of the breeding male. This may also contribute to the formation of a hierarchy, where we expect that dominant individuals have primary access to the resource. According to this prediction, out of seven cases of territory inheritance documented in our population upon disappearance of the dominant breeding male, six involved an immigrant male and only one a retained offspring (V. Baglione own data). Again, competition for territory inheritance is less likely among females, which do not queue as long as males for a breeding position outside the natal territory (Baglione et al. 2005).

Several other studies on cooperative species documented intra-group competition for reproduction (Cockburn 1998) and some showed that dominance hierarchies and / or direct conflicts among group members were correlated to this kind of competition. In Florida scrub jays (*Aphelocoma coerulescens*) where groups form only through offspring delayed dispersal, the dominance order is very similar to the one found in carrion crows: Male breeders are the most dominant, followed by male offspring, female breeders and juveniles (Woolfenden & Fitzpatrick 1977). Like in crows, there is competition for reproduction among males, but not among females due to incest avoidance of retained daughters. In cooperative Mexican jays (*Aphelocoma ultramarina*), where groups form through delayed dispersal of offspring and immigration of unrelated individuals, more than one female can breed and they compete for reproduction. In this species males generally dominate over females, but in several groups the order is inverted (Barkan et al. 1986). In Arabian babblers (*Turdoides squamiceps*) the dominance hierarchies are generally linear, older individuals dominate over younger ones and males dominate over females. However, the stability of the hierarchy weakens in groups where there are several competitors for the breeding position (Zahavi 1990).

An unexpected finding of our study was the dominant position of male immigrants over male offspring. According to the theory of nepotism (Ekman et al. 2001), breeding males should not tolerate male immigrants in their territories if they hinder the access to the resources to their sons. Furthermore, adult immigrants can mate with the breeding female, reducing the paternity of the dominant male. This raises the question of why the resident breeding male does not evict the immigrant. One possible explanation is that these costs are compensated by the benefits accrued by the immigrant to the dominant male. Indeed, immigrants can be highly efficient helpers at the nest, especially when they participate in reproduction, increasing fledgling production significantly (Canestrari et al. 2008b) and lighten the workload of the resident breeder (Canestrari et al. 2007). Alternatively, the dominant breeder may be unable to chase the immigrant away from his territory, so that the association between the two represents a 'best of a bad job' for the dominant male. However, this possibility is unlikely because crows seem to be very efficient in expelling conspecific intruders from their territories (Baglione et al. 2005) and form long-lasting associations only with their relatives (Baglione et al. 2003).

In our study groups, male offspring occupied dominant positions over breeding females, despite being younger (in our sample, only seven of 36 male offspring were older than 2 yr). This supremacy reflects the general effect of sex on crow dominance hierarchies (Richner 1989) and may allow the sons to contribute to guarding the breeding female during her fertile period. Theory predicts that, in cooperatively breeding societies, dominant offspring may increase their indirect fitness by hindering extra-pair mating of their mother, hence avoiding the dilution of their relatedness with the chicks they contribute to raise (Welbergen & Quader 2006). This may happen in crows, where indeed polyandrous females mate only with males of their group (i.e. the dominant males and his related immigrant), but seem unable to do so with males of other groups (Baglione et al. 2002b). The "mother guarding" hypothesis is intriguing, but has received little support so far. The carrion crow may be a suitable model for a compelling empirical test.

CONCLUSIONS

In this paper we uncovered the hierarchical structure of cooperatively breeding groups of carrion crows, where dominance ranks are determined by factors that are constant across groups and indicate that individuals, especially males, compete for resources within their territory. This is likely to affect the stability of the group and ultimately the dynamics of cooperation at the nest. We believe that understanding the consequences of hierarchies on individual social strategies will contribute to explain how cooperative breeding is maintained in our study population of crows and that focussing on social interactions in every context of group living is likely to provide insights on the dynamics of helping at the nest in most cooperatively bird species.

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Artículo II

NEPOTISMO EN EL ACCESO AL ALIMENTO EN LOS GRUPOS COOPERATIVOS DE CORNEJA NEGRA

La dispersión retrasada de los juveniles es el principal mecanismo que lleva a la formación de las sociedades con reproducción cooperativa. Se ha sugerido que los padres promueven la filopatría de los hijos proporcionándoles un acceso preferencial a los recursos alimenticios del territorio y que la tolerancia de los padres puede venir afectada por la calidad del territorio. Sin embargo, pocos estudios han evaluado esta hipótesis en especies de vertebrados que viven en familias. En este estudio, demostramos que en los grupos de corneja negra (*Corvus corone corone*) con reproducción cooperativa, que contienen juveniles no dispersados e/o individuos inmigrantes, los machos reproductores dominantes se comportaron de forma nepotista en el acceso a una fuente de alimento experimental, (1) atacando a los inmigrantes con más frecuencia e intensidad y (2) asociándose preferentemente con sus hijos para compartir el alimento. Esta 'facilitación parental' permitió a los hijos no dispersados pasar más tiempo alimentándose que los inmigrantes, a pesar de su inferior rango de dominancia. También demostramos que un aumento experimental de la disponibilidad de alimento durante todo el año en los territorios, no incrementó la tolerancia de los machos reproductores y tampoco influyó en el conjunto de las agresiones en los grupos. Esto indica que la mayor filopatría de los hijos observada en los territorios suplementados con alimento comparado con los territorios no suplementados, no es una consecuencia de un entrono social más benigno. Más bien sugiere que los hijos evalúan la calidad de su territorio natal y ajustan su comportamiento de dispersión en consecuencia.

Palabras clave: dispersión retrasada, nepotismo, facilitación parental, calidad del territorio, Corneja negra, *Corvus corone*

Nepotistic access to food resources in cooperatively breeding carrion crows

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Abstract

Offspring delayed dispersal is the principal mechanism leading to formation of kin-based societies. It has been suggested that parents promote offspring philopatry by providing them with preferential access to the food resources of the territory and that parental tolerance may be affected by territory quality. However, few studies have addressed this hypothesis in kin-living vertebrate species. Here, we show that in cooperative breeding groups of carrion crows (*Corvus corone corone*) containing retained offspring and immigrants, dominant breeding males behaved nepotistically on an experimental source of food by (1) attacking immigrants with more frequency and intensity than offspring and (2) associating preferentially with their offspring on the feeding spot and sharing food with them. This parental facilitation allowed the offspring to spend more time feeding than higher-rank immigrants. We also found that a year-round experimental food supplementation neither increased breeding males' tolerance nor relented the overall aggressiveness in the groups. This indicates that higher natal philopatry observed on fed territories compared to unfed ones is not a consequence of a more benign social environment. Rather, it suggests that offspring value territory resource wealth and adjust the timing of dispersal accordingly.

Keywords: delayed dispersal, nepotism, parental facilitation, territory quality, Carrion crow, *Corvus corone*

INTRODUCTION

Family living occurs in a wide range of taxa and sets the scene for cooperatively breeding kin societies where more than two individuals provision the young (Emlen 1997). The family is defined as a social unit where offspring forego dispersal and interact with the parents on the natal territory past the age of independence (Emlen 1994). In most bird species with delayed dispersal, offspring forego personal reproduction and aid their parents in rearing new siblings (Emlen 1997; Brown 1987). However, delayed dispersal must convey benefits to the offspring, independent from the indirect fitness gained through helping, as proven by the many species where offspring "stay at home" but refrain from provisioning the young (see Ekman 2006 and references therein).

The idea that offspring stay at home as a "best of a bad job" strategy when ecological constraints (e.g., habitat saturation or predation risk) hinder dispersal (Emlen 1994) has been criticised for its low power in predicting family living across species and populations (Cockburn 1998). A more comprehensive hypothesis suggests that families form when the natal territory offers benefits that offspring cannot find elsewhere (Ekman et al. 2001, 2004; Ekman 2006). In particular, philopatric offspring may gain direct fitness benefits from a prolonged association with their parents through, for example, preferential access to the resources of the territory and/or defence against predators. Such "parental facilitation" or "nepotism" has been shown for example in the Siberian jay (*Perisoreus infaustus*), where first year survival is higher for offspring that stay in the natal territory with their nepotistic parents than for those that emigrate and join a group of unrelated individuals (Ekman et al. 2000).

Although nepotism has a great potential for explaining the evolution of family living, its generality is still unclear as few studies have analysed in detail the benefits that offspring derive from remaining with their parents and the ecological factors that promote parental facilitation. In this study on cooperatively breeding carrion crows (*Corvus corone corone*), we investigated whether offspring enjoy preferential access to the food in their natal territory and whether aggressive interactions among group members changed according to the amount of food resources available in the territory. Carrion crows in NW Spain form social units that comprise a breeding pair, its retained offspring and/or immigrants that are related to the resident breeder of the same sex (Baglione et al. 2003). Groups live year-round in all purpose territories where the access to food resources is regulated by linear dominance hierarchies, with resident breeding males always at the top of the hierarchy, followed by male immigrants and male offspring, which are dominant over all the females in their group, including their mothers (Chiarati et al. 2010). Here, we first investigated the frequency and intensity of the aggressive behaviour of the dominant breeding males toward subordinate group members on an experimental source of food. Subsequently, we examined whether there were preferred associations of individuals on the bait, exploring the patterns of food sharing within the group.

METHODS

Study area and population

We studied a cooperative population of carrion crow in a 45 km^2 agricultural area in northern Spain (42° N, 5° W). In 75% of the territories, groups between three and nine individuals (mode = 3) breed cooperatively with up to five individuals feeding the nestlings (Baglione et al. 2002a). In addition to the resident breeding pair, groups contain offspring that remain on the natal territory for up to 4 years, and/or immigrants (mostly males) that are related with the resident breeder of the same sex (mean $r = 0.24$; Baglione et al. 2003). Groups can therefore be unassisted pairs, nuclear families (a pair with retained offspring), mixed groups (a pair with both retained offspring and immigrants), or pairs with one or more immigrants. Reproduction can be shared among group members of both sexes, but retained offspring do not reproduce within their natal group. Polygamous mating occurs in 67% of groups containing sexually mature immigrants, with polyandry prevalent over polygyny (Baglione et al. 2002b). More details on the mating system and cooperative behaviour are given in previous papers (Canestrari et al. 2005, 2008; Baglione et al. 2006).

Bird capturing and banding

From 1995, all nestlings in the study area were captured in the nest just before fledging (30 days after hatching) and free-flying individuals were caught with walk-in baited cages or “snap traps” (Baglione et al. 2002a). All captured individuals were banded with a unique combination of colour rings and patagial wing tags (Caffrey 2000). It has been shown that patagial wing tags did not affect survival and social interactions in a wild population of American crows *Corvus brachyrhynchos* (Caffrey 2000). In our population, no crows were injured or abandoned the nest or territory as a consequence of capture and wing tags did not affect survivorship (Canestrari et al. 2007). At the time of capture, the birds were aged as 1, 2 and older than 2 years according to the internal colour of the upper mandible (Svensson 1992). For sex and paternity determination (see Molecular methods), we collected between 50 and 200 µl of blood from the brachial vein of each banded individual (Baglione et al. 2002b).

Field data collection

Between 2003 and 2007, we collected data on 26 groups holding different territories to investigate the aggressive behaviour of dominant males on food and the existence of preferred feeding associations between group members. For each observation bout, a chicken carcass of approximately 300 g was tied to the ground in the middle of the territory. We video recorded the interactions with a video camera placed 5 m away from the bait and disguised with vegetation. Recording bouts lasted 4 h and took place between 06:00 and 12:00 in March and April (the beginning of the breeding season). As the bait was usually consumed in 2 h, the duration of the recording bout allowed sampling all interactions among group members at the feeding spot.

Individuals were classified as resident breeders, immigrants, or retained offspring. We classified as 'immigrant' any individual that was born in a different territory and joined an established group. In territories with immigrants, we classified as 'resident breeder' the breeding adults that had been living in the territory before the immigrant arrived. We classified as 'retained offspring' every nondispersing juvenile that was sired by the current resident breeding male. Offspring parentage could be inferred from pedigree data in seven nuclear families (extra-group copulations have never been observed in this population and retained offspring do not breed in the natal territory, so that parentage in nuclear families can be reliably attributed to the current breeding pair, see Baglione et al. 2002b). In other 19 groups, parentage needed to be confirmed by molecular testing (see below) because some non-dispersing juveniles were born before the current breeding male was caught and banded. Four of these groups were excluded from the sample because paternities could not be resolved (see "Molecular methods" section), so that the final sample comprised 22 groups. Eight territories, where group composition changed due to death of one individual, recruitment of new member (young born on the same territory or immigrant) or dispersal of offspring, were sampled two to four times over different years. In our analyses, we controlled for repeated measures of the same individual and territory where appropriate (see "Statistical methods" section). All individuals in our sample were individually recognisable because all, or all but one, were banded. In 14 groups, the only unbanded individual was a breeding female recognised by her incubating behaviour. Another two groups contained one unbanded immigrant which was excluded from the analyses because its sex could not be determined. Because reproduction in crows is rare before the third year (Madge and Burn 1999) and since only one of the 44 breeders studied so far in this population was younger than 3 years, the unbanded breeding females were aged as adults (Canestrari et al. 2007). Overall, we sampled 41 breeders, 32 retained offspring, and 12 male immigrants.

At the end of the breeding seasons 2003 and 2004, some groups were assigned to a year-round food-supplementation treatment, as part of a controlled experiment that tested the effect of territory quality on offspring dispersal (see detail on the procedure in Baglione et al. 2006). After 1 year, we video recorded interactions on bait among members of ten food-supplemented and nine unfed control groups following the same procedure described above. Because no significant effect of the treatment was found on breeding males' aggressions towards other group members nor on the overall frequency and intensity of aggressions among group members (see "Results" section) these groups were included in the sample for all subsequent analyses.

Molecular methods

Genomic DNA was extracted from blood samples using the DNeasy Blood & Tissue Kit (Qiagen™) following manufacturer's instructions. We genotyped each individual using six polymorphic microsatellite markers previously used to estimate parentage in *C. corone* (Baglione et al. 2002b). Products of polymerase chain reaction (PCR) were run on an automated sequencer 3130xl (Applied Biosystems, ABI) using GeneScan™ 500 ROX™ Size Standard (ABI). Alleles were called using GENEMAPPER 3.7 (ABI).

We used IDENTITY4 (Wagner and Sfec 1999) to estimate genetic descriptors (see additional data in Supplementary Material). Deviations from Hardy–Weinberg expectations were tested using a probability (exact) test as implemented in the software GENEPOP (http://genepop. curtin.edu.au) developed after Raymond and Rousset (1995). Details on the Markov chain method used to estimate the *P* value were as follows: dememorization (1,000), batches (100), and iterations per batch (1,000).

The average number of alleles per locus was 5.17 (SD = 2.48). Average expected heterozygosity was 0.62 (SD = 0.05), whereas average observed heterozygosity was 0.63 (SD = 0.02). All loci showed an estimated frequency of null alleles lower than 5% (Supplementary Material). There was no indication of deviation from Hardy–Weinberg when tested over all samples and loci ($\chi^2 = 15.56$, df = 12, $P = 0.21$). None of the loci deviated from Hardy–Weinberg expectations (Probability test, Supplementary Material).

Total paternity exclusion probability (PEP) was 0.951. PEP varied among loci, ranging from 0.182 (locus Ase18) to 0.594 (locus Ck.5A4B). After confirming the power of the set of six microsatellite loci, we proceeded with paternity assignment excluding a male as putative father when a mismatch in at least one of the studied loci was found.

Of the 19 groups tested, results confirmed the paternity of dominant males for all retained offspring in 15 groups that were therefore included in the sample ($N = 20$ retained offspring). Four groups were excluded because offspring paternities could not be assigned unambiguously due to the high relatedness between the dominant male and the male immigrant.

We used two PCR-based protocols to determine the sex of banded carrion crows. First, we used the P2/P8 method (Griffiths et al. 1998) and then males were confirmed using primers 3007 and 3112 as described by Ellegren and Fridolfsson (1997). Amplification products were separated and visualised using a Bioanalyzer 2100 with DNA 1000 Assay chip (Agilent Technologies).

Video recorded data analysis

From the video recordings, we collected data on the frequency and intensity of interactions within dyads of individuals that included unaggressive behaviours, mild forms of aggression, and overt forms of aggression (see Table 1 for a detailed description of interactions). We also measured the time that individuals spent feeding on the bait and the time “at the feeding spot”, defined as the time spent within a radius of 1.5 m from the bait, regardless of whether the individual was eating or not.

We measured the intensity of the aggressive behaviour of the dominant male (breeding males’ ‘aggression score’) towards other group members with an index that was calculated as follows. First, we ranked agonistic interactions according to an increasing level of aggressiveness (0 = no aggression to 6 = intense aggression) as indicated in Table 1. Then, for each dyad involving the dominant males, we applied the following formula:

$$\left[\sum_{i=1}^{6} \left(X_i \cdot n_i \right) \Big/ n_{total} \right]$$

where, X_i represents the score of a given interaction i, n_i is the number of times that interaction was recorded and n_{total} is the total number of interactions recorded in the dyad. The obtained aggression scores were normally distributed (Kolmogorov–Smirnov test, d = 0.095, $P > 0.20$). Besides the information relative to the average level of aggressiveness (aggression score), we also analysed the frequency of agonistic interactions to better describe the social relationships within dyads. We measured breeding males' 'frequency of agonistic interactions' as the number of agonistic behaviours recorded in which the breeding male monopolised food or threatened/attacked the opponent (i.e. sum of unaggressive food monopolisation 1, unaggressive food monopolisation 2, displacement, intimidation, chase and fight, see Table 1) divided by the total time the two individuals of the dyad were observed together at the feeding spot. To calculate the overall level of aggressiveness within the group ('group aggression score'), we summed up the scores (see Table 1) of all interaction occurred in the group and divided it by the total number of interactions recorded in that group. To calculate the overall frequency of aggressions within the group ('group aggression frequency'), we divided the total number of agonistic interactions occurred in the group by the total time where at least two individuals were simultaneously present at the feeding spot.

Table 1. Description of the behaviours observed in the dyads at the feeding spot.

Behavioural interactions (*i*)		**Score (*X*)**
Feeding alone	Individual A feeds while there are no other birds within a radius of 1.5 m from the bait	–
Feeding together	Individual A shares the bait with individual B	0
Unaggressive food monopolisation 1	Individual A feeds while B takes food furtively, adopting an inconspicuous posture, keeping the body low and parallel to the ground and stretching the neck to reach the food beyond the reach of A's beak	1

→

Unaggressive food monopolisation 2	Individual A feeds while individual B waits close by. Individual B starts feeding when individual A leaves	2
Displacement	Individual A moves directly towards individual B and continues moving through the point of intersection while B moves away	3
Intimidation	Individual A threatens B using the beak, but without a physical contact. Individual B leaves food item and waits for food or leaves the feeding site	4
Chase	Individual A flaps the wings and adopt a conspicuous posture, inflating head and chest, and pursues B	5
Fight	Individual A physically attacks B using pecks, bill snaps and kicks	6

Individual A: first member of the dyad. Individual B: second member of the dyad.

We measured the 'individual proportion of time at the feeding spot', dividing the time that an individual spent at the feeding spot by the total time that all group members spent at the feeding spot. Because no significant effect of the individual category and sex was found (see "Results" section), showing that group members did not differ in the time spent around the bait, in the next step, we analysed how individuals budget their time at the feeding spot. In particular, we focussed on possible differences in the proportion of time during which they were actually eating. The 'individual proportion of time feeding' was therefore calculated dividing the time that an individual spent feeding on the bait by the total time that the same individual spent at the feeding spot.

To determine if there were preferred associations of group members on the food source, we classified the dyads into eight categories: breeding male–retained offspring, breeding male–immigrant, breeding male–breeding female, breeding female–retained offspring, breeding female–immigrant, retained offspring–retained offspring, retained offspring–immigrant and immigrant–immigrant. For each dyad, we calculated the 'association time' as the total time in which two individuals were recorded feeding together divided by the time in which each of them was recorded eating with any group member, i.e. (A + B)/[(A + any group member) + (B + any group member)].

Statistical methods

Statistical analyses were performed using GENSTAT 12.0 and Microsoft Excel-Pop tools (http://www.cse.csiro.au/poptools). Unless stated otherwise, all data were analysed with linear mixed models (LMM) using the restricted maximum likelihood method (REML), where individual identity and territory identity were fitted as random factors (see description of each analysis below), to account for repeated measures of the same individual and territory. Potential explanatory variables with *P* values > 0.1 were sequentially removed until the model only included relevant terms (backwards stepwise elimination procedure; Xin and Xiao Gang 2009). Significant probability values ($P < 0.05$) were derived from having all relevant terms ($P < 0.1$) fitted in the model together, whereas those of nonsignificant terms were obtained by fitting them individually to the minimal model (Crawley 2002). *Post hoc* analyses were performed with VMPROCEDURE available in GENSTAT 12.00 that explores differences between means with t statistics using the approximate number of residual degrees of freedom printed by REML (Payne 2009).

To analyse whether food supplementation significantly influenced breeding males' aggression score and frequency of agonistic interactions, we run LMMs where experimental treatment (fed/unfed), group size, opponent's category, opponent's sex, and opponent's age were entered as explanatory variables and breeding male identity as random factor. The sample comprised only the data collected in 2004 and 2005, i.e. the period when the supplementation experiment was carried out. Because all breeding males were sampled only on one territory, "territory identity" coincided with "breeding male identity" in this analysis, and therefore it was not included as random term. We also analysed the effect of food supplementation on the overall aggression rate within groups (group aggression score and group aggression frequency). Due to small sample size (10 fed groups and nine unfed groups), LMM could not be used, and a t test for independent samples was performed instead. One limitation of this univariate approach was that group size could not be controlled for. However, this is unlikely to have affected our results, because the average group size did not significantly differ between fed and unfed groups (average size of fed groups ± SD = 3.8 ± 0.63; unfed groups: 3.77 ± 0.66; t test for independent sample, $t = 0.07$, $P = 0.87$).

To investigate whether breeding males were more tolerant in sharing food with their own offspring than with other group members, we analysed breeding males' aggression score and frequency of agonistic interactions using LMMs, where group size, year, opponent's category (breeding female, retained offspring and immigrant), opponent's sex, and opponent's age were fitted as explanatory variables and breeding male identity as random factor. To determine whether there were preferential associations between group members, we carried out two tails Monte Carlo permutation tests following the method of Bejder et al. (1998). Briefly, the original association time data set was randomised 10,000 times to obtain an expected distribution. For each dyad category ($N = 8$), a Monte Carlo analysis was run to test whether the observed means of association time differed significantly from those expected if individuals associated randomly.

To analyse whether there were differences between group members in the proportion of time at the feeding spot and the proportion of time feeding (normalised using arcsine square root transformation) we carried out LMMs that included group size, year, sex, age and individual category (breeder, retained offspring or immigrant) as explanatory variables. Territory identity was entered as random factor, as well as individual identity, because some groups were sampled more than once, in different years (see above). Subsequent LMMs also analysed the differences among categories of individuals in the proportion of time they foraged alone on the bait and together with any other group member.

RESULTS

Effect of food supplementation

Experimental food supplementation neither affected significantly dominant breeding males' aggression score ($F_{1,8.8} = 0.21$, $P = 0.65$) nor his frequency of agonistic interactions ($F_{1,3.4} = 0.68$, $P = 0.46$). Moreover, fed and unfed groups did not differ in terms of overall intensity of aggressiveness among group members (group aggression score: t test for independent samples, $t = -1.265$, $P = 0.48$) nor of overall frequency of agonistic interactions (group aggression frequency: t test for independent samples, $t = -0.952$, $P = 0.35$).

Aggressiveness

The category of the opponent significantly influenced breeding males' aggression score (Table 2). Immigrants were attacked with more intensity than retained offspring and breeding females, with no significant *post hoc* differences between the latter two categories (Fig. 1a).

Opponent's age and sex, year and group size had no significant effect (Table 2). When we analysed breeding males' frequency of agonistic interactions we found again an effect of the category of the opponent (Table 2), with immigrants and breeding females attacked with similar frequency and significantly more than retained offspring (Fig. 1b).

Table 2. Model summaries of the factors affecting breeding males' aggression score and breeding males' frequency of agonistic interactions

Model terms	***F***	***df***	***P***	**Random term estimated variance component ± SE**	**Average effect ± SE**
Breeding males' aggression score					
Individual identity[a]				−0.05 ± 0.11	
Year	1.07	4, 41.5	0.38		
Group size	0.35	1, 49.8	0.56		
Category opponent	4.93	2, 78.1	0.01		
Sex opponent	2.92	1, 40.1	0.09		
Age opponent	0.70	1, 49.6	0.41		
Minimal model					
Constant					1.59 ± 0.12
Category opponent					
Breeding females					0
Retained offspring					−0.15 ± 0.27
Immigrants					0.74 ± 0.33
Breeding males' frequency of agonistic interactions					
Individual identity[a]				0.00004 ± 0.0002	
Year	1.53	4, 21.3	0.23		
Group size	1.09	1, 20.0	0.31		
Category opponent	3.91	2, 75.0	0.02		
Sex opponent	0.03	1, 39.3	0.86		
Age opponent	0.28	1, 63.0	0.60		
Minimal model					
Constant					0.05 ± 0.007
Category opponent					
Breeding females					0
Retained offspring					−0.02 ± 0.009
Immigrants					−0.002 ± 0.01

[a] Random factor

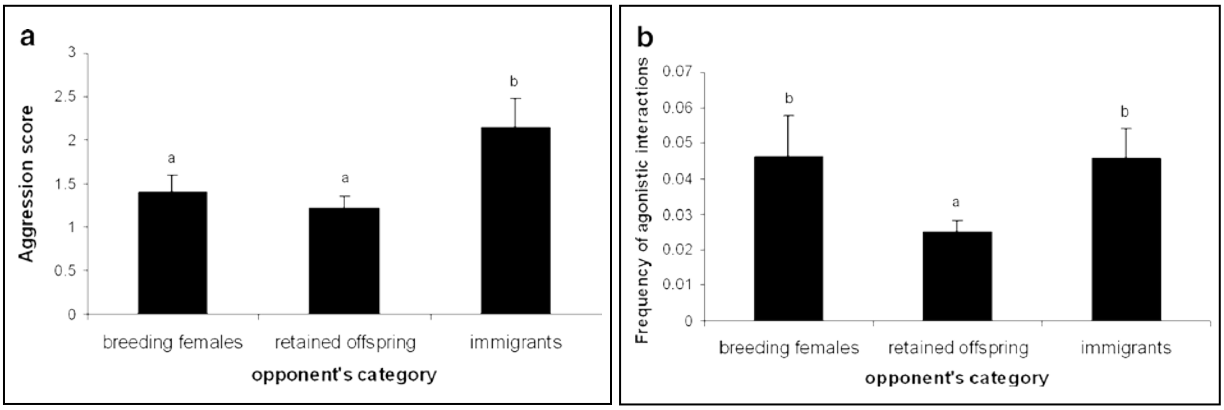

Fig. 1. a) 'Mean' ± SE breeding males' aggression score towards different categories of opponents. b) 'Mean' ± SE breeding males' frequency of agonistic interactions towards different categories of opponents. Different letters (a, b) indicate statistical differences ($P < 0.05$).

Associations on the food

The Monte Carlo analysis revealed that breeding males and their offspring spent significantly more time feeding together on the bait than expected by chance (mean association time for dyads comprising breeding males and their retained offspring =0.362, $N = 34$; mean association time for all dyads sampled = 0.272, $N = 126$, $P = 0.01$). All other categories of dyads showed random association times.

Time at the feeding spot and time feeding

We found that the proportion of time individuals spent at the feeding spot was inversely correlated with group size. Moreover, we found that age correlated, though not significantly, with the individual proportion of time at the feeding spot, with juveniles spending more time at the feeding spot than adults, irrespective of individual category and sex (Table 3). Conversely, individual category and sex influenced the proportion of time feeding (Table 3). Breeding males spent significantly more time eating the bait than any other group members and retained offspring fed significantly longer than immigrants (Fig. 2). The latter result was unlikely to be explained by an effect of age, with offspring allocating more time feeding on the bait merely because they were less efficient in foraging. Age was controlled for in the analysis and returned a non-significant result (Table 3). In addition, to further investigate the effect of age on the proportion of time feeding, we ran a new LMM restricted to the sample of retained offspring, where all age categories (1, 2 and older than 2 years) were represented. Again, age showed no effect ($F_{1,35.5}$ = 0.34, P = 0.57), dismissing an explanation based on feeding efficiency. The significant difference between social categories, was not caused by the proportion of time that each individual fed alone on the bait, which was similar for all categories (effect of individual category on the proportion of time feeding alone: $F_{2,69.0}$ = 0.31, P = 0.73) but by the time they spent feeding together with other group members (effect of individual category on the proportion of time feeding together with another group member: $F_{2,22.4}$ = 7.96, P = 0.003; and sex: $F_{1,7.5}$ = 25.95, P = 0.001). The *post hoc* comparison showed that immigrants were significantly less likely to share the bait with another group member than retained offspring and breeding males.

Table 3. Model summaries of the factors affecting the individual proportion of time at the feeding spot and the individual proportion of time feeding of all group members.

Model terms	***F***	***df***	***P***	**Random term estimated variance component ± SE**	**Average effect ± SE**
Proportion of time at the feeding spot					
Individual identity[a]				0.007 ± 0.006	
Territory identity[a]				−0.001 ± 0.002	
Year	0.46	4, 36.8	0.76		
Group size	11.0	1, 25.1	0.003		
Individual category	1.30	2, 78.2	0.28		
Sex	1.79	1, 49.3	0.19		
Age	3.43	1, 88.0	0.07		
Minimal model					
Constant					0.39 ± 0.01
Group size					−0.06 ± 0.02
Proportion of time feeding					
Individual identity[a]				34.0 ± 22.7	
Territory identity[a]				2.0 ± 10.6	
Year	0.45	4, 67.2	0.78		
Group size	1.97	1, 55.5	0.17		
Individual category	14.62	2, 75.8	<0.001		

→

Sex	5.48	1, 61.4	0.02	
Age	0.91	1, 103.1	0.34	
Minimal model				
Constant				86.90 ± 1.95
Individual category				
Breeders				0
Retained offspring				−9.17 ± 2.54
Immigrants				−19.09 ± 3.96
Sex				
Males				0
Females				−6.03 ± 2.58

[a] Random factors

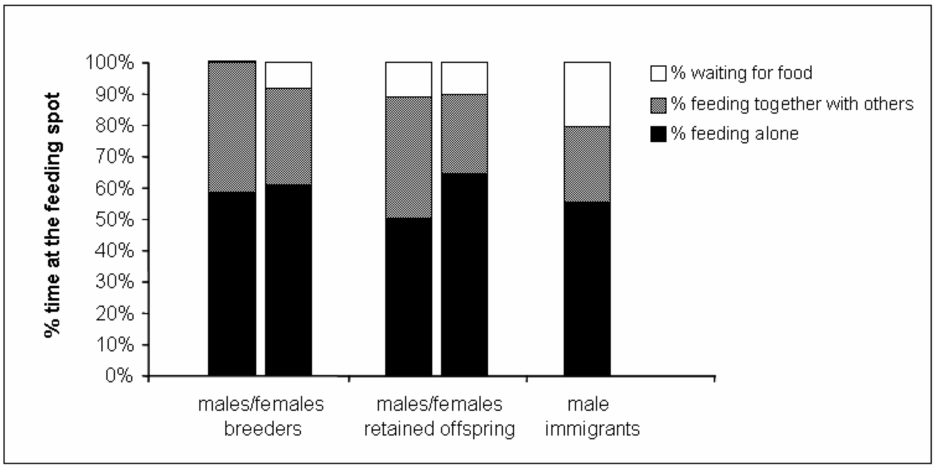

Fig. 2. Proportion of time feeding alone, feeding together with any other group member and waiting for food for group members of different categories. Proportions are calculated on the individual total time spent at the feeding spot.

DISCUSSION

Despite the advances in our understanding of cooperative breeding, a large controversy persists on the factors that promote family living in vertebrates. In territorial bird species, the benefits obtained from the association with the parents and the natal site may be the key to explain offspring delayed dispersal (Ekman et al. 2004). In this study on cooperatively breeding carrion crows, we showed that retained offspring, unlike immigrants, enjoyed preferential access to food resources due to the nepotistic behaviour of their father.

Crow social groups are highly hierarchical on food sources, with breeding males at the top and male immigrants dominating retained offspring and breeding females (Chiarati et al. 2010). However, here we found that offspring fed more on an experimental food source than more dominant immigrants and that they could do so because they joined their father at the feeding spot and shared food with him. Such preferential association was possible because the breeding male was more tolerant towards his offspring than to other group members. Carrion crows therefore show how retained offspring obtain direct benefits from the presence of their nepotistic father. Such benefits are available only on the natal territory suggesting that parental tolerance could be an important factor leading offspring to delay dispersal in this species.

Male's nepotism in carrion crows may be a kin-selected trait, as tolerant fathers are likely to increase the survival of their offspring by preferentially sharing the food with them. A non-exclusive explanation, however, could be that such favouritism is a consequence of the fact that offspring, unlike immigrants, challenge neither the dominant breeding position within their natal group, because of lack of unrelated potential mates to copulate with, nor the dominance hierarchy, being usually younger than immigrants and of lower rank. This explanation seems unlikely, because dominant males showed higher frequency of aggression towards the breeding female compared to the offspring, in spite of the fact that the breeding female occupies the lowest rank in the group and is obviously not a sexual competitor. Admittedly, however, disentangling these hypotheses is difficult in crows. The Siberian Jay, another kin-living corvid where social relationships have been studied deeply, provides an interesting comparison. In this species, retained offspring suffer less aggression from both male and female breeders compared to unrelated immigrant birds (Ekman et al. 1994), so that they can spend more time at protected feeding sites and high-quality food sources than immigrants (Nystrand 2007, 2006). Griesser et al. (2006) showed that offspring survive significantly better than immigrants (Griesser et al. 2006), suggesting that the benefits in term of offspring fitness are likely to play a role in maintaining parental nepotism in this species.

Although parental nepotism has a great potential for explaining delayed dispersal in many kin-living species, only a few other studies have investigated in detail the benefits that offspring derive from remaining with their parents and results are contrasting. Similar to results on Carrion crow and the Siberian jay, in the Seychelles warblers (*Acrocephalus sechellensis*) there is the evidence of parental facilitation in natal dispersal and in the consequent acquisition of a territory (Eikenaar et al. 2007). Furthermore, in Mexican jays (*Aphelocoma ultramarina*), the unusual pattern of high social status of yearlings over adult group members has been interpreted in terms of payoff asymmetries and parental facilitation (Barkan et al. 1986). Conversely, in a communal breeding mammal, the African banded mongoose (*Mungos mungo*) nepotism was not observed (Gilchrist 2004). In this species, adults escort pups during their period of dependence, providing protection against predators, but show no preference for their own offspring (Gilchrist 2004). Differences among species in patterns of nepotism may exist because of variation in the relative costs and benefits of nepotistic behaviours, kin recognition abilities, or variation in the availability of opportunities for nepotism (see Wenseleers 2007; Zinck et al. 2009; Van Horn et al. 2004; Mateo 2002). To test the generality of the hypothesis, more studies on different social systems are needed.

Effect of territory quality on parental nepotism

Theory predicts that family stability is influenced by territory quality (Emlen 1995). In most kin-based societies, families live in year-round territories (Arnold and Owens 1999) where resources can be depleted if the group is too large, with immediate negative consequences on survival or reproductive success of the breeders (Clutton-Brock 1991). This suggests that parents should only invest in offspring beyond independence if they have enough resources and in the absence of intra-family competition (Covas and Griesser 2007). Therefore, parental nepotism should vary according to family wealth (Ekman and Rosander 1992). This idea is supported by recent studies that showed that an experimental reduction of food resources induced offspring to disperse (Dickinson and McGowan 2005), whereas an experimental food supplementation increases offspring philopatry (Baglione et al. 2006). However, it is unclear to what extent parents influence the dispersal strategy of their offspring.

Several studies have shown that high levels of competition can influence social relationships among relatives (see Korb 2006; Stewart-Williams 2007; West et al. 2001, 2002). Although available data on bird species indicate that parental nepotism is maintained also in winter, when resources are scarce (Scott 1980; Ekman et al. 1994; Pravosudova et al. 2001; Dickinson and McGowan 2005), no studies have analysed experimentally the effect of food shortage on parental aggressive behaviour in birds. Such studies are needed to fully explore the relative role of parent and offspring decisions in shaping natal dispersal strategies in kin-living birds.

Baglione et al. (2006) showed that an experimental increase in year-round food availability in territories increased offspring philopatry. Differences in parental nepotism between fed and unfed groups may be the proximate mechanism that links territory quality and delayed dispersal. However, the results of this study showed that experimentally increased food availability did not determine an overall decrease in aggressiveness among group members, and that fathers in fed territories did not increase their tolerance towards their offspring or any other subordinate. These results suggest that offspring are capable of evaluating the quality of their home and that they can exert some control on the timing of their dispersal, adjusting it to territory wealth.

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Supplementary Material

Characteristics of six polymorphic microsatellite loci used for parentage analysis in 56 individuals of *Corvus corone*. Listed are number of alleles per locus (NA), observed (H_0) and expected (H_E) heterozygosity rates, null allele frequency (NAF), paternity exclusion probability (PEP), and *P*-values obtained from the tests on Hardy-Weinberg segregation (HW). The last column refers to the fluorescent dye used to mark the forward primer. All markers were originally described by Tarr & Fleischer (1998), but locus Ase18 (Richardson et al. 2000).

Locus	**NA**	**Size (bp)**	H_E	H_0	**NAF**	**PEP**	**HW**	**Dye**
Ck.5^{a}5F	9	139-168	0.735	0.839	-0.06	0.525	0.556	HEX
Ck.5^{a}4B	7	111-123	0.790	0.839	-0.027	0.594	0.057	NED
Ck.5^{a}4D	5	105-113	0.638	0.642	-0.003	0.382	0.205	NED
Ck.B6D	4	146-155	0.601	0.607	-0.004	0.324	0.449	HEX
Ck.5^{a}5G	4	189-199	0.492	0.446	0.034	0.249	0.351	6-FAM
Ase18	2	196-206	0.477	0.429	0.033	0.182	0.404	6-FAM

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Artículo III

LOS SUBORDINADOS SE BENEFICIAN DEL COMPORTAMIENTO EXPLORATORIO DE LOS DOMINANTES: RESPUESTA A ALIMENTOS NOVEDOSOS EN LA CORNEJA NEGRA COOPERATIVA

Las sociedades cooperativas se forman principalmente cuando los hijos prolongan la asociación con sus padres. Se ha sugerido que los hijos retrasan su dispersión debido a los beneficios que obtienen de esta asociación. En este trabajo demostramos que en los grupos con reproducción cooperativa de corneja negra (*Corvus corone corone*), los padres al ser más propensos a asumir riesgos facilitan a sus hijos el acceso a fuentes de alimento novedosas y potencialmente peligrosas. En los grupos de cornejas, los machos reproductores dominantes, que comparten el alimento de forma nepotista con sus hijos, realizaron el primer contacto con el alimento novedoso seguidos por los inmigrantes machos, mientras que los hijos no dispersados y las hembras reproductoras fueron los últimos. Este orden reflejó el rango de dominancia de los individuos en el grupo, sin embargo no estuvo determinado por la interferencia social. En grupos testados con dos fuentes idénticas de alimento novedoso que no pudieron ser monopolizadas por un solo individuo, los subordinados se alimentaron únicamente de la fuente de alimento que fue anteriormente explorada por el macho dominante. Esto sugiere que las decisiones de forrajeo de las cornejas estuvieron afectadas por el miedo al alimento y que el comportamiento exploratorio de los machos reproductores dominantes ayudó a los subordinados a superar su neofobia. Las jóvenes cornejas sin experiencia por lo tanto, se beneficiaron de vivir en familias obteniendo el acceso a los recursos alimenticios sin incurrir con los riesgos de la exploración.

Palabras clave: dispersión retrasada, neofobia, facilitación parental, reproducción cooperativa, Corneja negra, *Corvus corone*

Subordinates benefit from exploratory dominants: response to novel food in cooperatively breeding carrion crows

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Abstract

Kin-based societies typically form when offspring prolong their association with the parents. It has been suggested that offspring delay natal dispersal because of the benefits that such association conveys. Here we show that in cooperatively breeding carrion crows (*Corvus corone corone*), risk-prone fathers facilitate the access to novel and potentially dangerous food to their offspring. In crow groups, dominant breeding males, which share food nepotistically with their offspring, made the first contact with a novel food, followed by male immigrants, whereas retained offspring and breeding females were last. This order mirrored the dominance ranks in the group, but it was unlikely to be enforced through social interference. In groups that were simultaneously presented with two identical novel food sources that could not be monopolised by one individual, subordinates only used the one that was first explored by the dominant male. This suggests that foraging decisions in crows were affected by the fear of the novel food and that the explorative behaviour of the dominant breeding male provided cues that helped subordinates to overcome their neophobia. Young and inexperienced crows therefore benefited from living in families by gaining access to food without incurring the risk of exploring.

Keywords: delayed dispersal, neophobia, parental facilitation, cooperative breeding, Carrion crow, *Corvus corone*.

INTRODUCTION

Cooperative breeding societies are characterised by individuals providing care to young that are not their offspring (Brown 1987). Natal delayed dispersal is typically a prerequisite for cooperative behaviour in vertebrates, because helpers are often offspring that remain in the natal territory past the age of independence and aid their parents in rearing new siblings (Emlen 1997). Therefore, investigating the mechanisms that lead offspring to 'stay at home' is crucial to understand the evolution of cooperative breeding (Hatchwell and Komdeur 2000). The hypothesis of "parental facilitation" (or nepotism) suggests that offspring delay dispersal because of the benefits obtained from the prolonged association with their parents in the natal territory (Ekman et al. 2001; Ekman et al. 2004; Ekman 2006). In the Siberian Jay (*Perisoreus infaustus*), for example, it has been shown that tolerant parents provide preferential access to food resources for their offspring, as well as protection against predators (Ekman et al. 1994; Griesser 2003; Griesser and Ekman 2004, 2005; Nystrand 2007). However, the generality of this hypothesis is still unclear, because few studies have analysed in detail the benefits that offspring derive from remaining with their parents.

Neophobia, defined as the hesitancy to approach a novel food item, object or place, is an important factor influencing the foraging behaviour of animals (Greenberg 2003). Neophobia is an indicator of an animal's internal state of risk perception as well as its propensity to take risks (Wilson et al. 1994). Studies across species showed differences in individual response to novel stimuli. Such variability has been explained with relative costs and benefits of exploration, which depend on ecology and social organisation (Mettke-Hofmann et al. 2002; Bergman and Kitchen 2009). In some species, dominant individuals explore novelties (Drea 1998; Dingemanse and de Goede 2004; Soma and Hasegawa 2004), while in other species subordinates are more risk prone (Katzir 1983; Di Bitetti and Janson 2001; Stahl et al. 2001). It has been proposed that high competition for resources may decrease neophobia in subordinates, which need to be faster in feeding to avoid the monopolisation of food by the dominants (Greenberg 2003). Social facilitation, too, can help to overcome neophobia, especially when a kin or an affiliated individual acts as 'demonstrator' (Swaney et al. 2001; Benskin et al. 2002; Soma and Hasegawa 2004; Stowe et al. 2006) and particularly in the case of adult-infant combinations (Aisner and Terkel 1992; Avery 1996; Cadieu and Cadieu 2004; Voelkl et al. 2006).

In most cooperatively breeding societies, individuals live for long periods within the same social unit sharing territory resources year-round (Arnold and Owens 1999). Contrary to large groups of unrelated individuals, in cooperative groups characterised by high levels of relatedness, competition between group members is expected to be low. Therefore, subordinates may not need to take the risk of exploring an unfamiliar food or place if tolerant and more experienced dominants will do it and will share the resource after inspection. The advantage of living with risk prone parents may therefore be an incentive for offspring to delay dispersal.

Here we analysed the behaviour of wild carrion crows (*Corvus corone corone*) towards an unfamiliar food source. Carrion crows in northern Spain live in cooperatively breeding kin groups, which comprise a breeding pair, its offspring and/or immigrants that are related to the same sex breeder (Baglione et al. 2003). Linear and stable hierarchies regulate the access to food in the group, with resident breeding males occupying the alpha position, followed by male immigrants and male retained offspring, which are dominant over all the females in their group (Chiarati et al. 2010). We investigated i) whether there were differences among individuals in the latency in feeding for the first time on a single novel source of food, ii) whether individual latency decreased with familiarisation and iii) whether there was a consistent pattern across groups in the order of access to the bait among individuals of different categories (breeders, offspring and immigrants). An order that mirrored the dominance rank could either be explained by social interference among group members, where dominants prevent subordinates from feeding, or by true differences in neophobia. To disentangle these two effects some groups were provided simultaneously with two identical novel sources of food. If the order of access was caused by social interference, we expected subordinates to approach the food item that was not used by the dominant group member and therefore to decrease their latency in starting feeding. Conversely, if neophobia determined the feeding behaviour, subordinates should approach the food previously inspected by the dominant, with no difference in latency between the two feeding conditions (one food source / two food sources).

METHODS

Study area and population

We studied a cooperative population of carrion crow in a 45 km² agricultural area in northern Spain. Crow groups form through offspring delayed dispersal and/or immigration of individuals (mostly males) that are related to the resident breeder of the same sex (mean *r* = 0.24, Baglione et al. 2003). Both retained offspring and immigrants can help at the nest and, within a group, up to five individuals participate in nestling care (Canestrari et al. 2005). Details on the mating system and cooperative behaviour are given in previous papers (e.g. Baglione et al. 2002; Canestrari et al. 2008a; Canestrari et al. 2008b). Cooperative groups are organised in linear and stable hierarchies where resident breeding males are the most dominant (Chiarati et al. 2010).

Bird capturing and banding

Free-living crows were caught with walk-in baited cages or “snap traps” while nestlings were captured in the nest just before fledging (see Baglione et al. 2002 for details). All captured individuals were banded with colour rings and patagial wing tags (Caffrey 2000). No crows were injured or abandoned the nest or territory as a consequence of capture and wing tags did not affect survivorship (Canestrari et al. 2007). At the time of the capture, the birds were aged as one, two, and older than two years according to the internal colour of the upper mandible (Svensson 1992). We collected between 50 and 200 µl of blood from the brachial vein of each banded individual for sex determination using P2 / P8 molecular method (Griffiths et al. 1998).

Field data collection

Response to novel food. During the breeding seasons (March-July) 2003 - 2007 we video-recorded 29 cooperative groups (three-eight individuals per group, mode = 4) foraging on a novel food source. One plucked chicken carcass of approximately 300 g was nailed to the ground in the middle of the territory and pieces of plastic bags (that were also nailed to the ground and removed immediately after the observations) were placed all around to make the bait more conspicuous. The bait triggered neophobic reactions in crows. The birds often made alarm calls during several minutes watching the food source from nearby trees. Then they typically landed a few meters away, but only one individual initiated the approach to the food. Nervousness increased at 0.5 m from the bait, when the bird started keeping the body low and parallel to the ground and stretching the neck to reach the food. When a crow touched the carcass it jumped back several times (as described in ravens by Heinrich 1988) and showed pileal erection (Coppinger 1969) until it finally started feeding. Only after the first bird begun feeding without fear other group members initiated the approach to the bait showing the same fearful behaviours.

We video-recorded the behaviour of group members with a video-camera placed five meters away from the bait and disguised with vegetation. Nine territories, where group composition changed over the years due to death of individuals, recruitment of new members (young born on the same territory or immigrants) or dispersal of offspring, were sampled two to four times in different years. In our analyses, we controlled for repeated measures of the same individual and territory (see Statistical methods). For each of the 29 groups, we carried out one observation bout of four hours between 06:00 and 12:00 h sampling a total of 68 breeders (37 males and 31 females), 64 retained offspring (40 males and 24 females) and 18 immigrants (16 males and 2 females). From the video-recorded observations, we measured the latency of each group member in feeding for the first time on the bait ('individual latency' hereafter) and the order in which individuals started feeding ('order of access' hereafter). Individual latency was measured from the start of the recording (i.e. as soon as the bait had been nailed to the ground). If the entire social group did not show up during the first recording bout, the carcass was removed and presented again the following day. The empty bout was not considered in the calculation of individual latency. During the breeding season, crows spend the whole daylight time in their territories. Because of the high cohesion of groups (Baglione et al. 2002), it is very unlikely that once the bait was discovered part of the group overlooked it. Therefore, individuals that never touched the bait were given latency equal to the total observation time.

Effect of familiarisation. In order to determine whether the latency in starting feeding decreased with familiarisation, in 21 groups we repeated video recorded observations once during the breeding season with an interval of 1 to 72 days (mean number of days ± SE = 25 ± 3.8). Overall, the sample included 42 breeders (21 males and 21 females), 39 retained offspring (25 males and 14 females) and 11 immigrants (9 males and 2 females).

Social interference *versus* neophobia. In a group, dominants may prevent subordinates from feeding. To test whether individual latency and the order of access to the bait were determined by intra-group social interference rather than individual neophobia, in 2008 we carried out an experiment in 14 groups, where we presented simultaneously two identical plucked chicken carcasses. The feeding spots were located in the middle of the territory, 10 m apart to avoid individual food monopolisation. In eight territories the baits were visually separated by natural shrubs whereas in the remaining six territories the birds feeding on any of the baits could see the other. We placed two synchronised video cameras to record each bait for 4 hours. For each individual we collected data on 1) the first choice of bait, 2) the latency in feeding and 3) the order of access to the food in each bait. In this experiment we sampled 28 breeders (14 males and 14 females), 31 retained offspring (14 males 17 females) and 9 male immigrants.

Statistical methods

Statistical analyses were performed using GENSTAT 12.0. Individual latencies used in statistical analyses were log-transformed (Zar 1998) and transformed data were normally distributed (Kolmogorov-Smirnov test, $d = 0.06$, $P > 0.20$). Unless stated otherwise, we analysed data with linear mixed models (LMMs), using the restricted maximum likelihood method (REML), including both fixed and random terms. Potential explanatory variables with $P > 0.1$ were sequentially removed until the model only included relevant terms (backwards stepwise elimination procedure, Xin and Xiao Gang 2009). Significant probability values ($P < 0.05$) were derived from having all relevant terms ($P < 0.1$) fitted in the model together, whereas P values of non-significant terms were obtained by fitting them individually to the minimal model (Crawley 2002). *Post hoc* analyses were performed with VMPROCEDURE available in GENSTAT 12.0 that explores differences between means with t-statistics using the approximate number of residual degrees of freedom printed by REML (Payne 2009). All LMMs included year, territory identity and individual identity as random factors.

Response to novel food. In 29 groups tested with one unfamiliar food item we investigated the factors influencing i) log-transformed individual latency and ii) the order of access to the food. In the first LMM we fitted group size, sex, age, individual category (breeders, retained offspring or immigrants) and the interaction between individual category and sex as explanatory variables. The second LMM contained sex, age, individual category and the interaction between individual category and sex.

Familiarisation with novel food. In 21 groups sampled twice during the breeding season, we analysed the effect of chronological bout order on log-transformed individual latency to test whether it decreased with familiarisation with the food. In the LMM we added chronological bout order (first / second video recording session), the interactions between individual category and chronological bout order and the interaction between sex and chronological bout order to the explanatory variables listed in the previous LMM on response to novel food (see the individual latency LMM above). After this, we tested whether familiarisation was affected by the time interval between the two feeding sessions. To do so, we ran a new LMM where we correlated the difference of individual latency between the first and second video recording session with number of days elapsed, group size, sex, age, individual category and the interaction between individual category and sex.

Social interference *versus* neophobia. First we asked whether adding the second bait reduced the latency of subordinate individuals (immigrants, retained offspring and breeding females). The sample included territories tested with one and two food sources (N = 29 and 14 respectively). Log transformed individual latency was analysed with a LMM that included treatment (one/two food sources), group size, sex, age, individual category and the interaction individual category*sex, individual category*treatment and sex*treatment as explanatory variables. Subsequently, using Fisher exact tests and binomial tests we investigated whether i) the proportion of subordinates (i.e. group members other than the dominant male) that approached the novel food before breeding males differed between territories tested with one or two separated food sources; ii) in groups tested with two separated food sources subordinates chose to feed first on the item previously inspected by the dominants; iii) a visual occlusion between the baits influenced the explorative behaviour of the subordinates.

RESULTS

Response to novel food. Individual latency was significantly affected by the interaction between category and sex, because breeding status correlated with shorter latency in males only, with dominant males being faster in approaching the bait (Table 1; Fig. 1). Group size and age had no significant effect (Table 1). When we re-ran the analysis for separate sexes we found that male breeders approached the food faster than immigrants and retained offspring ($F_{2,\ 61.8} = 14.81$, $P < 0.001$) with no significant *post hoc* differences between the latter two categories. On the contrary, the social category had no significant effect on individual latency among females ($F_{2,\ 58.5} = 0.39$, $P = 0.67$; Fig. 1). The analyses carried out for each social category separately revealed that breeding males approached the food item faster than breeding females ($F_{1,\ 24.7} = 39.04$, $P < 0.001$) whereas in retained offspring the effect of sex was non-significant ($F_{1,\ 55.6} = 2.24$, $P = 0.14$; Fig.1). Immigrants could not be tested because only two females were sampled.

Table 1. Response to novel food: i) LMM summary of the factors affecting Individual latency and ii) LMM summary of the factors affecting Individual order in reaching the food.

Model terms	***F***	***df***	***P***	**Random term estimated variance component ± SE**
Individual latency				
Individual identity*				0.04 ± 0.02
Territory identity*				0.03 ± 0.02
Year*				0.04 ± 0.03
Group size	3.16	1, 53.9	0.08	
Individual category	7.28	2, 133.6	<0.001	
Sex	23.80	1, 98.5	<0.001	
Age	0.73	1, 244.7	0.39	
Individual category*Sex	3.51	2, 139.4	0.03	
Individual order				
Individual identity*				0.34 ± 0.08
Territory identity*				0.02 ± 0.02
Year*				-0.001 ± 0.007
Individual category	21.03	2, 180.4	<0.001	
Sex	44.93	1, 127.5	<0.001	
Age	0.90	1, 155.4	0.34	
Individual category*Sex	6.91	2, 162.3	0.001	

*Random factors

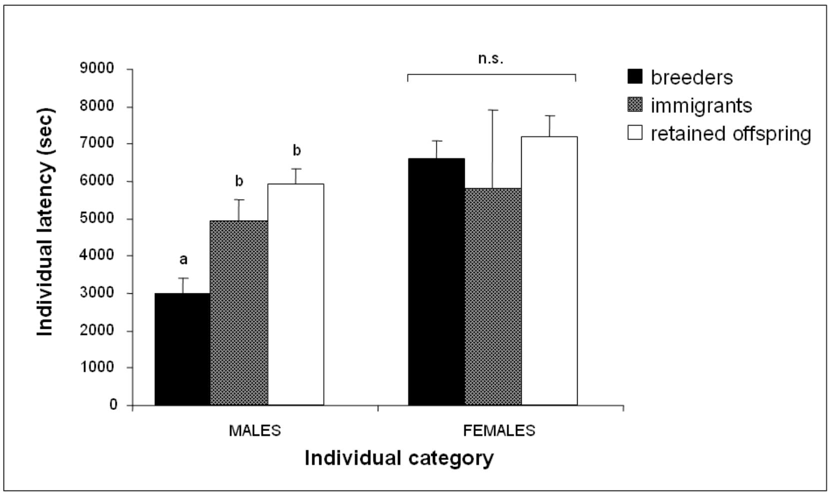

Fig. 1. 'Mean' ± SE latency to approach the novel food source of members of crow groups. Different letters (a, b) indicate significant differences (P<0.05) between social categories.

Results of the LMM also showed a significant effect of the interaction between category and sex on the individual order of access to the food (Table 1). Male breeders were first in feeding, followed by male immigrants, whereas retained offspring and breeding females were last (Fig. 2). When we re-ran the analysis for separate sexes we found a clear order among males, with breeders on the top, immigrants in the middle and retained offspring at the bottom ($F_{2,\ 112.6}$ = 31.43, P < 0.001), with significant *post hoc* differences between the three social categories (Fig. 2). On the contrary, the social category had no significant effect among females ($F_{2,\ 58.1}$ = 0.72, P = 0.49). The analyses carried out for each social category separately showed that breeding males fed before breeding females ($F_{1,\ 38.8}$ = 74.13, P < 0.001) and that male retained offspring fed before female retained offspring, although in this case the effect of sex was statistically non-significant ($F_{1,\ 58.7}$ = 3.76, P = 0.06). Immigrants could not be tested separately because of the low number of females sampled. However, qualitatively, it is interesting to note that the two immigrant females were last in accessing the food in their group. All previous statistical analyses were repeated excluding the two immigrant females from the sample and the results did not change qualitatively.

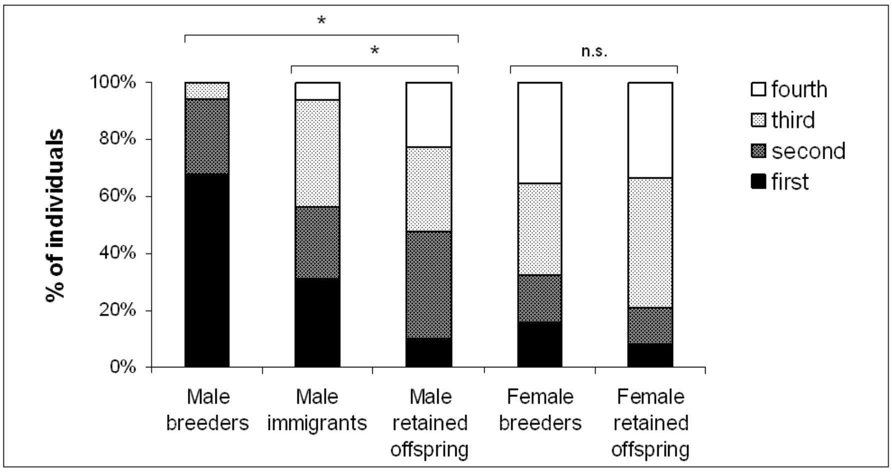

Fig. 2. Proportion of individuals being first, second, etc. in reaching the bait according to their social category. Comparisons with asterisks indicate significant differences (P<0.05).

Familiarisation with novel food. In groups sampled twice, individuals showed shorter latency in the second video recording bout (effect of chronological bout order: $F_{1,\ 123.4}$ = 22.74, P < 0.001). Relative differences in latency among social categories remained consistent over time as shown by a lack of significant interactions between individual category*chronological bout order ($F_{2,\ 127.1}$ = 0.25, P = 0.77) and sex*chronological bout order ($F_{1,\ 128.7}$ = 0.07, P = 0.79). Breeding males showed a shorter latency (category*sex: $F_{2,\ 72.5}$ = 3.59, P = 0.03), while group size and age had no significant effect ($F_{1,\ 42.8}$ = 2.81, P = 0.10 and $F_{1,\ 45.0}$ = 0.13, P = 0.72 respectively), confirming the previous results. Moreover, the difference in individual latency over successive video recording sessions was not correlated with the time interval between the two bouts ($F_{1,\ 45.6}$ = 0.59, P = 0.44), showing that crows recognised the food item regardless of the number of days elapsed from the first exposure, within the experimental time span (2-72 days).

Social interference *versus* neophobia. Results of the LMM showed that the addition of a second bait did not reduce the latency of subordinate individuals (effect of treatment: $F_{1,\ 3.7}$ = 0.21, P = 0.67; sex*treatment: $F_{1,\ 269.4}$ = 0.44, P = 0.50; individual category*treatment: $F_{2,\ 265.7}$ = 0.75, P = 0.47). Consistent with previous results, the interaction between individual category and sex significantly influenced individual latency, with breeding males being the least neophobic in their groups ($F_{2,\ 178.0}$ = 4.63, P = 0.01).

We did not find significant differences in the proportion of subordinates approaching food before the breeding male among territories tested with one or two food items. Nineteen of 113 subordinates (17.0%) did so in territories provided with one bait compared to 9 of 54 (17.0%) where two baits were present (two-tailed Fisher's exact test: $P = 1.0$). Due to the rarity of exploratory subordinates, no further statistical analyses could be done to detect differences between immigrants, retained offspring and breeding females. In the 14 groups tested with two separate food sources, we did not find significant differences in the proportion of subordinates feeding before the breeding male among territories tested with or without visual separation (five of 31 subordinates did so in territories tested with visual separation compared to four of 23 tested without visual separation; two-tailed Fisher's exact test: $P = 1.0$). Subordinates significantly preferred to eat for the first time from the feeding source already used by the dominant male rather than from the unexplored one (45 of 54 subordinates; two-tailed binomial test: $P < 0.001$).

DISCUSSION

Like other corvids (Katzir 1983; Heinrich 1988; Dally et al. 2008), carrion crows proved to be neophobic towards a novel food source as shown by their cautious approach, their nervousness while delivering the first pecks and the decrease of latency in starting feeding after familiarisation with the bait. In this study we showed that breeding males made the first contact with a novel and potentially dangerous food resource, followed by male immigrants, while retained offspring and breeding females were last. This order mirrored the dominance hierarchy in the group (Chiarati et al. 2010) and could therefore be due either to the effect of competition and social interference among group members or to individual differences in the degree of neophobia (or a combination of both). However, the fact that subordinates, in the presence of two identical baits that could not be monopolised by the alpha male, were not faster in starting to eat and consistently chose the bait already used by the dominant male suggests that their foraging decisions were affected by the fear of the unfamiliar food and that they benefited from the explorative behaviour of the breeding male to overcome their neophobia. Available data from other cooperatively breeding species also show that individuals can use social cues from more experienced conspecifics to reduce their neophobia towards novel foods (Forkman 1991; Thornton 2008) and novel foraging patches (Midford et al. 2000).

The fact that, in crows, breeding males were consistently less neophobic compared with the rest of group members in any of the experimental settings might derive from a combination of their larger experience in assessing the risk of novel situations and the generally relaxed competition for food within the group. Compared to flocks of unrelated individuals where competition for resources may force subordinates to explore novelties (e.g. *Corvus monedula*, Katzir 1983; *Branta leucopsis*, Stahl et al. 2001), crow social groups are cohesive and stable families (Baglione et al. 2003) where high levels of relatedness promote food sharing, especially between the father and his offspring. Dominant breeding males are more likely to share food with their offspring than with immigrants, towards which they behave more aggressively (Chiarati et al. 2011). In this situation, offspring do not need to hurry over a new source of food and can benefit from experienced and risk-taking fathers that will share the resources after inspection. The benefits that offspring derive from the prolonged association with parents in the natal territory may be the key to explain delayed dispersal in vertebrates (Ekman et al. 2004). In crows, living with elder kin provides young crows with access to 'risk free' food. This advantage of family living has never been highlighted before in the context of the evolution of delayed dispersal, but it is likely to be common in social species and may contribute to delayed natal dispersal in young and inexperienced offspring.

An interesting result of the experiment with two baits was that immigrant males also chose to eat the food previously explored by the dominant male, in spite of being less tolerated than offspring at the feeding spot (Chiarati et al. 2011). This contrasts with the pattern found in groups of Siberian Jays, where immigrants take higher risk and forage on less protected feeding sites (Nystrand 2007). We suggest that the difference may be explained by the social organisation of the two species. In social living Siberian Jay, immigrants are unrelated to the dominant breeding pair, which harasses them when they try to approach the best foraging sites, forcing them to feed in dangerous conditions to attain the equivalent energy intake (Nystrand 2007).

Conversely, immigrants in carrion crow are related to the same sex dominant breeder (Baglione et al. 2003) and are highly efficient helpers at the nest, increasing fledging production significantly (Canestrari et al. 2008a) and reducing the workload of the resident breeders (Canestrari et al. 2007). Immigrants are therefore valuable group members, and this may explain why competitive interactions on a food source rarely escalate into physical aggressions (see description of agonistic behaviors in Chiarati et al. 2010). Under these circumstances, immigrants may also benefit form the explorative behavior of the dominant male, because the cost of exploration on their own may be larger than the cost of suffering aggressions at the feeding spot.

The high level of neophobia showed by the breeding females is also worth noting. Like the breeding males, breeding females are adult birds, and should therefore be equally competent in assessing the risks of a novel situation, but this does not translate into similar degrees of neophobia. One possible explanation is that, due to high male competition for breeding openings, which are in short supply in this population (Baglione et al. 2005), the breeding males are a biased subsample of above average bold individuals, so that their low degree of neophobia could be interpreted as a behavioural syndrome. This would not be the case of females, for which competition for breeding positions is relaxed due to higher mortality and consequent higher turnover in the territories (Baglione et al. 2005).

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Artículo IV

¿LOS SUBORDINADOS PAGAN PARA QUEDARSE EN LOS GRUPOS COOPERATIVOS DE CORNEJA NEGRA?

La hipótesis del "pago de tributo" propone que el comportamiento de ayuda observado en los sistemas con reproducción cooperativa representa una 'renta' que los subordinados pagan a los dominantes para ser tolerados en su territorio. Esto implica que 1) los reproductores dominantes puedan 'castigar' los ayudantes que no proporcionan ayuda suficiente, o como se ha sugerido recientemente, que 2) los ayudantes perezosos puedan evitar el castigo mostrando comportamientos de sumisión. Sin embargo, en este estudio mostramos que en la corneja negra (*Corvus corone corone*), el comportamiento agresivo de los machos reproductores dominantes y el comportamiento de sumisión de los ayudantes subordinados durante la época reproductora no estuvieron relacionados con el nivel de contribución en el nido de los ayudantes subordinados. En cambio, la agresividad del dominante y el comportamiento de sumisión de los ayudantes estuvieron influenciados por la categoría social del ayudante (hijo no dispersado/inmigrante). Al final de la época reproductora, los machos reproductores dominantes redujeron significativamente sus agresiones hacia los machos inmigrantes, que en consecuencia redujeron sus comportamientos de sumisión e incrementaron el tiempo invertido alimentándose junto con el macho dominante. Sugerimos que la falta de evidencias de 'pago de tributo' en los grupos cooperativos de corneja negra, puede derivar de la importante función como fuerza de trabajo de reserva que los subordinados 'perezosos' desempeñan para los reproductores dominantes, que les permite afrontar situaciones desfavorables y prevenir una reducción del éxito reproductor del grupo.

Palabras clave: reproducción cooperativa, comportamiento de ayuda, pago de tributo, apaciguamiento preventivo, Corneja negra, *Corvus corone*

Do subordinates pay to stay in cooperatively breeding carrion crows?

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Abstract

The “pay to stay” hypothesis proposes that helping behaviour observed in cooperative breeding systems represents a ‘rent’ that subordinates pay to the dominants in order to be tolerated in their territory. This implies that 1) dominant breeders should punish helpers that do not provide sufficient help, or, as recently suggested, that 2) lazy helpers should prevent punishment by displaying submissive behaviours. However, here we show that in carrion crows (*Corvus corone corone*), the aggressive behaviour of the dominant breeding males and the submissive behaviour of subordinate helpers over the breeding season were not related to the level of contribution at the nest of subordinate helpers. Instead, dominant aggressiveness and subordinate submissive behaviours were influenced by helper’s category (retained offspring / immigrants). At the end of the breeding season, dominant breeding males reduced significantly their aggressions towards immigrant males, which in turn decreased the frequency of submissive behaviours and increased the time spent eating together with the dominant males. Conversely, no changes occurred in the social relationships between the alpha males and their offspring throughout the breeding season. We suggest that the observed lack of punishment of ‘lazy’ subordinates in crows is explained by their hidden insurance function, because these individuals can compensate for any sudden reduction in the provisioning effort of the group.

Keywords: cooperative breeding, helping behaviour, pay to stay, pre-emptive appeasement, Carrion crow, *Corvus corone*.

INTRODUCTION

Cooperatively breeding societies are characterized by individuals called 'helpers' that provide care to non-descendant young (Brown 1987). Kin selection theory (Hamilton 1964) explains the evolution of cooperative behaviour of helpers through the indirect fitness benefits that individuals gain from provisioning related young. Although several studies demonstrated the influence of relatedness on many aspects of group living and cooperation among individuals (Sherman 1977; Pravosudova et al. 2001; Russell and Hatchwell 2001; Baglione et al. 2003; Griffin and West 2003; Ensminger and Meikle 2005; Eberle and Kappeler 2006; Nystrand 2007; Stewart-Williams 2007), kin selection does not provide an explanation for helping among unrelated individuals. In several cooperative societies (e.g. *Ceryle rudis*, Reyer 1980; *Melanerpes formicivorus*, Stacey and Koenig 1984; *Turdoides squamiceps*, Zahavi 1990), relatedness among group members varies greatly and both related and unrelated individuals care for the young. Thus, it has been argued that indirect fitness benefits must act in combination with direct fitness benefits that individuals derive from group living and helping behaviour via improved future survivorship and reproduction (for a review see Cockburn 1998; Clutton-Brock 2002; Bergmuller et al. 2007). In particular, the "pay to stay" hypothesis proposes that helping represents a 'rent' that subordinates pay to the dominant breeders to be tolerated in their territory and to gain access to resources (Gaston 1978; see also Kokko et al. 2002). This may represent a general regulatory mechanism of group cohesion and cooperation, which is independent of the kinship among group members, and is likely to be applicable to a wide range of cooperative breeding species. Indeed, in most cooperative systems, helpers are beneficial to the dominants because helping increase their reproductive success (Woxvold and Magrath 2005; Valencia et al. 2006; Canestrari et al. 2008) and their survival, owing to workload-lightening in raising the young (Crick 1992; Cockburn 1998). If 'pay to stay' applies to these societies, in groups with asymmetric dominance relationships, dominants should 'punish' or evict helpers that do not provide sufficient help (Clutton-Brock and Parker 1995), adjusting their level of aggression according to helpers' contribution to young provisioning. However, empirical evidence for punishment in cooperative breeding societies is scarce (e.g. in birds: Emlen and Wrege 1992; in mammals: Reeve 1992; Mulder and Langmore 1993; in fish: Balshine-Earn et al. 1998). A possible reason for this is that punishment may be prevented by 'pre-emptive appeasement' by which helpers influence the level of tolerance of dominants through submissive behaviours (Bergmuller and Taborsky 2005). For example, in the cichlid *Neolamprologus pulcher*, helpers that had been experimentally prevented from participating in territory defence increased their submissive behaviours when allowed back into the group (Bergmuller and Taborsky 2005).

In this study on a cooperatively breeding population of carrion crows (*Corvus corone corone*), we examined how the contribution to chick provisioning by helpers influenced their social relationships with the dominant member of the group, i.e. the breeding male. Crow social groups consist of a breeding pair and subordinate helpers at the nest that are either offspring of one or both breeders or immigrants related to the same sex breeder (Baglione et al. 2002a; Baglione et al. 2003; Chiarati et al. 2010). Crows pay high costs for feeding the chicks (Canestrari et al. 2007) and breeders benefit from the cooperation of helpers in terms of increased reproductive success (Canestrari et al. 2008) and lightening of provisioning workload (Canestrari et al. 2007). However, helping effort varies largely among group members and groups often comprise subordinates that refrain from visiting the nest (Canestrari et al. 2005; Baglione et al. 2010). To find evidences of 'pay to stay' in this society we analysed the relationship between the aggressive behaviour of dominant breeding males and the level of contribution of subordinate helpers, as well as the relationship between helpers' contribution to chick feeding and their submissive displays. If subordinates pay to stay in the group, we expect the breeding male to increase the frequency and/or intensity of aggressive behaviours towards less cooperative helpers compared to helpful ones. Moreover, if pre-emptive mechanisms (Bergmuller and Taborsky 2005) are used by subordinate crows to prevent dominant aggressions, we expect lazy helpers to show submissive behaviours at higher frequency compared to hard-working group members.

METHODS

Study area and population

We studied a cooperative population of carrion crows in a 45 km² rural area in northern Spain characterised by a traditional low intensity agricultural landscape. Cooperative groups are cohesive families that live year-round in all purpose territories and breed cooperatively, with up to five individuals feeding the nestlings (Baglione et al. 2002a). In addition to the resident breeding pair, groups contain non-dispersing offspring, which can stay on the natal territory for up to four years, and/or immigrants (mostly males) that are related to the resident breeder of the same sex (mean *r* = 0.24, Baglione et al. 2003). Unlike retained offspring that do not breed in their natal territory, adult immigrants often share reproduction with the resident breeders (Baglione et al. 2002b). Both retained offspring and immigrants can help in feeding the nestlings, but group members do not contribute equally and some individuals completely refrain from visiting the nest (Canestrari et al. 2005). In general, individuals that generated offspring make larger contributions to chick provisioning. Among nonbreeders, retained offspring and immigrants do not significantly differ in their provisioning effort, being females of both categories the least helpful at the nest (Canestrari et al. 2005). Recently it has been shown that the presence of 'lazy' helpers in groups represents an insurance workforce for breeders because the former compensate for a sudden reduction of the overall provisioning effort of the group, preventing a reduction of the reproductive success of the group (Baglione et al. 2010).

Field methods and data collection

We studied levels of 'contribution to chick provisioning', 'aggressions' and 'submissive behaviours' between 2003 and 2007 in 21 cooperative groups (three-eight individuals per group, mode = 4), where crows were individually recognisable. Nestlings were captured in the nest just before fledging whereas free-living crows were caught using walk-in baited cages or 'snap traps' (for details on capture methods see Baglione et al. 2002a). At the time of the capture, individuals were aged as one, two, and older than two years according to the internal colour of the upper mandible (Svensson 1992) and 50-200 µl of blood were collected from the brachial vein of each individual for P2 / P8 molecular sexing (Griffiths et al. 1998). Individuals were banded with colour rings and patagial wing tags (Caffrey 2000). No crows were injured or abandoned the territory as a consequence of capture and wing tags did not affect survivorship (Canestrari et al. 2007).

Video recordings at the nest. Data on individual contribution to chick feeding in groups were collected between 10 and 15 days after the first egg hatched by placing camouflaged micro cameras 2.5 m away from the nest (see Canestrari et al. 2005 for further details). For each nest we collected 3-5 recording bouts of four hours in subsequent days, sampling a total of 42 breeders (21 males and 21 females), 31 retained offspring (20 males and 11 females) and 8 immigrant males. We measured the individual provisioning effort, pooling data from the different bouts, as the number of feeds per hour, where every 'feed' is the act of delivering food to a chick's open gape. This is a good measure of provisioning effort in crows because it correlates with the amount of food carried by an individual in its crop (Canestrari et al. 2005). For each helper (retained offspring / immigrants) we calculated the 'contribution to chick provisioning' as the number of feeds of the individual divided by the total number of feeds of the group.

Video recordings on food. Data on aggressions and submissive behaviours were obtained from video recording observations carried out when group members were foraging on a plucked chicken carcass of approximately 300 g nailed to the ground in the middle of the territory. To determine whether the dominant breeding male adjusted his level of aggressiveness to the contribution of helpers to chick provisioning, in each group we carried out video recorded observations on food (bouts of four hours between 06:00 and 12:00 h) twice, at the beginning of the breeding season (i.e. during egg laying and incubation) and at the end (i.e. during the first week after chick fledging). Overall, we sampled 21 breeding males and 39 subordinate helpers (20 male retained offspring, 11 female retained offspring and 8 male immigrants). From the video-recordings on food, we collected data on dyadic interactions, which included unaggressive behaviours, mild forms of aggression and overt forms of aggression (see Table 1 for a detailed description of interactions). We measured the intensity of the aggressive behaviour of the dominant male (breeding males' 'aggression score') towards subordinate helpers with an index that was calculated by ranking behavioural interactions observed in the dyad according to an increasing level of aggressiveness (from score 0 = no aggression to score 6 = intense aggression as indicated in Table 1), applying the following formula:

$$\left[\sum_{i=1}^{6} \left(X_i \cdot n_i \right) \Big/ n_{total} \right]$$

where X_i represents the score of a given interaction i, n_i is the number of times that interaction was recorded and n_{total} is the total number of interactions recorded in the dyad. To further describe the social relationships within dyads, we also calculated breeding males' 'frequency of agonistic interactions' as the number of agonistic behaviours directed towards a given helper (i.e. unaggressive food monopolisations during which subordinate takes food furtively or waits for food, displacement, intimidation, chase and fight, see Table 1) divided by the total time that the two individuals spent together within a radius of 1.5 m from the bait (i.e. the total time of the dyad). We also analysed helpers' submissive behaviours towards the dominant male. We defined as 'submissive behaviours' any attempt to avoid

Table 1. Description of the behaviours observed in the dyads at the feeding spot. Individual A: dominant breeding male. Individual B: subordinate helper.

Behavioural interactions (*i*)		**Score (*X*)**
Feeding together	Individual A shares the bait with individual B	0
Unaggressive food monopolisation 1	Individual A feeds while B takes food furtively, adopting an inconspicuous posture, keeping the body low and parallel to the ground and stretching the neck to reach the food beyond the reach of A's beak	1
Unaggressive food monopolisation 2	Individual A feeds while individual B waits close by. Individual B starts feeding when individual A leaves	2
Displacement	Individual A moves directly towards individual B and continues moving through the point of intersection while B moves away	3
Intimidation	Individual A threatens B using the beak, but without a physical contact. Individual B leaves food item and waits for food or leaves the feeding site	4
Chase	Individual A flaps the wings and adopt a conspicuous posture, inflating head and chest, and pursues B	5
Fight	Individual A physically attacks B using pecks, bill snaps and kicks	6

confrontation with the dominant male by feeding furtively or waiting aside while the dominant male was feeding on the bait (see unaggressive food monopolisations in Table 1). We calculated helpers' 'proportion of time showing submissive behaviours' dividing the time that the helper spent feeding furtively or waiting aside by the total time of the dyad. We also calculated helpers' 'proportion of time eating together with the dominant male', dividing the time that the helper and the dominant breeding male fed together on the bait divided by the total time of the dyad.

Statistical methods

Statistical analyses were performed using GENSTAT 12.0. Data were analysed with linear mixed models (LMMs) using the restricted maximum likelihood method (REML). Potential explanatory variables with $P > 0.1$ were sequentially removed until the model only included relevant terms (backwards stepwise elimination procedure, Xin and Xiao Gang 2009). Significant probability values ($P < 0.05$) were derived from having all relevant terms ($P < 0.1$)

fitted in the model together, whereas *P* values of non-significant terms were obtained by fitting them individually to the minimal model (Crawley 2002). In the results, values for nonsignificant interactions are omitted. All LMMs included dominant breeding male identity as random factor to account for repeated measures of the same individual in different dyads within the group. Because all breeding males were sampled only on one territory, 'territory identity' coincided with 'dominant breeding male identity', and therefore it was not included as random term.

We first investigated whether the dominant males adjusted their level of aggressiveness towards subordinate helpers according to their contribution to chick provisioning. In two separate LMMs we analysed the factors influencing the difference between the beginning and the end of the breeding season in 1) breeding males' aggression score and 2) breeding males' frequency of agonistic interactions. In all models, we fitted year, helper's contribution, group size, helper's category (retained offspring / immigrants), helper's sex, helper's age and interactions between helper's contribution * helper's category, helper's contribution * helper's sex and helper's contribution * helper's age as explanatory variables. The interaction between helper's category and sex was omitted because no immigrant females were sampled.

In the next step we examined the behaviour of the subordinate helpers. We analysed the factors influencing the difference between the beginning and the end of the breeding season in 1) the helpers' proportion of time showing submissive behaviours and 2) the helpers' proportion of time feeding together with the dominant male. The LMMs included the same independent variables and random factor listed above.

RESULTS

The frequency and intensity of aggressive behaviours showed by breeding males towards subordinate helpers did not change over the breeding season according to the contribution of the latter to chick provisioning (Table 2, Fig. 1 a). However, both variables were influenced by helper's category (retained offspring / immigrants, Table 2). The analyses revealed that dominant males reduced the intensity of their aggressions towards immigrants at the end of the breeding season, whereas showed no change towards their offspring (Table 2, Fig. 2 a). When we analysed breeding males' frequency of agonistic interactions we found

Table 2. Model summaries of the factors affecting the difference in i) breeding males' aggression score and ii) breeding males' frequency of agonistic interactions, at the beginning and at the end of the breeding season. Average effects ± SE are provided for significant terms.

Model terms	*F*	*df*	*P*	**Random term estimated variance component ± SE**	**Average effect ± SE**
Breeding males' aggression score					
Breeding male identity*				0.385 ± 0.516	
Year	1.28	4, 9.3	0.34		
Group size	1.25	1, 6.1	0.30		
Helpers' contribution	0.66	1, 33.9	0.42		
Helpers' category	3.93	1, 39.1	0.05		
Helpers' sex	0.01	1, 38.0	0.90		
Helpers' age	1.35	1, 30.2	0.25		
Minimal model					
Constant					0.019 ± 0.27
Helpers' category					
Retained offspring					0
Immigrants					-1.12 ± 0.56
Breeding males' frequency of agonistic interactions					
Breeding male identity*				0.0006 ± 0.0004	
Year	0.84	4, 19.2	0.52		
Group size	0.02	1, 17.5	0.88		
Helpers' contribution	1.69	1, 27.4	0.20		
Helpers' category	3.23	1, 31.6	0.08		
Helpers' sex	0.09	1, 33.0	0.77		
Helpers' age	3.04	1, 33.6	0.09		
Minimal model					
Constant					0.013 ± 0.006
Helpers' age					0.014 ± 0.008
Helpers' category					
Retained offspring					0
Immigrants					-0.037 ± 0.02

*Random factor.

again an effect of the category of the subordinate helpers, although in this case it was not statistically significant, with immigrants experiencing a reduction in the frequency of aggressions received by dominant males at the end of the breeding season (Table 2). Moreover, we found that age correlated, though not significantly, with the breeding males' frequency of agonistic interactions, with adult helpers receiving more aggressions than juveniles (Table 2).

Results also showed that the change in submissive behaviours of subordinates over the breeding season did not depend on their contribution to chick provisioning (Table 3, Fig. 1 b, c). However, immigrants decreased the time spent showing submissive behaviours and increased the time eating together with the dominant breeding male at the end of the breeding season (Table 3), whereas retained offspring showed no significant change (Fig. 2 b, c).

Table 3. Model summaries of the factors affecting the differences in i) helpers' proportion of time spent in submissive behaviours and ii) helpers' proportion of time eating together with the dominant breeding male. Average effects ± SE are provided for significant terms.

Model terms	***F***	***df***	***P***	**Random term estimated variance component ± SE**	**Average effect ± SE**
Time showing submissive behaviours					
Breeding male identity*				0.035 ± 0.081	
Year	1.11	4, 13.7	0.39		
Group size	0.02	1, 8.4	0.87		
Helpers' contribution	1.77	1, 34.5	0.19		
Helpers' category	4.36	1, 36.3	0.04		
Helpers' sex	0.61	1, 35.9	0.44		
Helpers' age	0.01	1, 34.0	0.96		
Minimal model					
Constant					-0.025 ± 0.076
Helpers' category					
Retained offspring					0
Immigrants					-0.33 ± 0.158 →

Time eating together with the dominant male					
Breeding male identity*				0.038 ± 0.090	
Year	1.09	4, 14.3	0.39		
Group size	0.01	1, 11.1	0.93		
Helpers' contribution	2.19	1, 33.4	0.14		
Helpers' category	4.17	1, 35.4	0.04		
Helpers' sex	0.34	1, 35.4	0.56		
Helpers' age	0.01	1, 33.0	0.93		
Minimal model					
Constant					0.025 ± 0.079
Helpers' category					
Retained offspring					0
Immigrants					0.348 ± 0.17

*Random factor

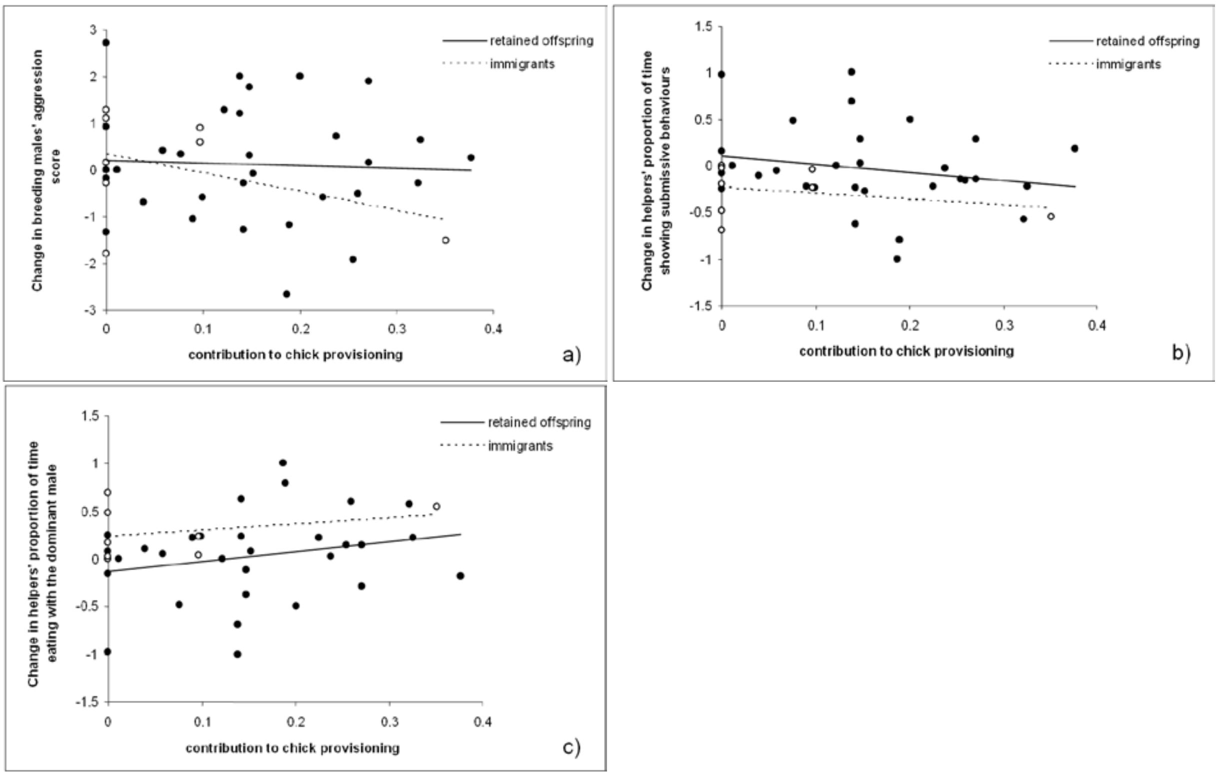

Fig. 1. Correlation between the contribution of helpers to chick provisioning and the change, between the beginning and the end of the breeding season, in a) breeding males' aggression score, b) helpers' proportion of time showing submissive behaviours and c) helpers' proportion of time eating together with the dominant breeding male. Solid and open dots represent retained offspring and male immigrants respectively.

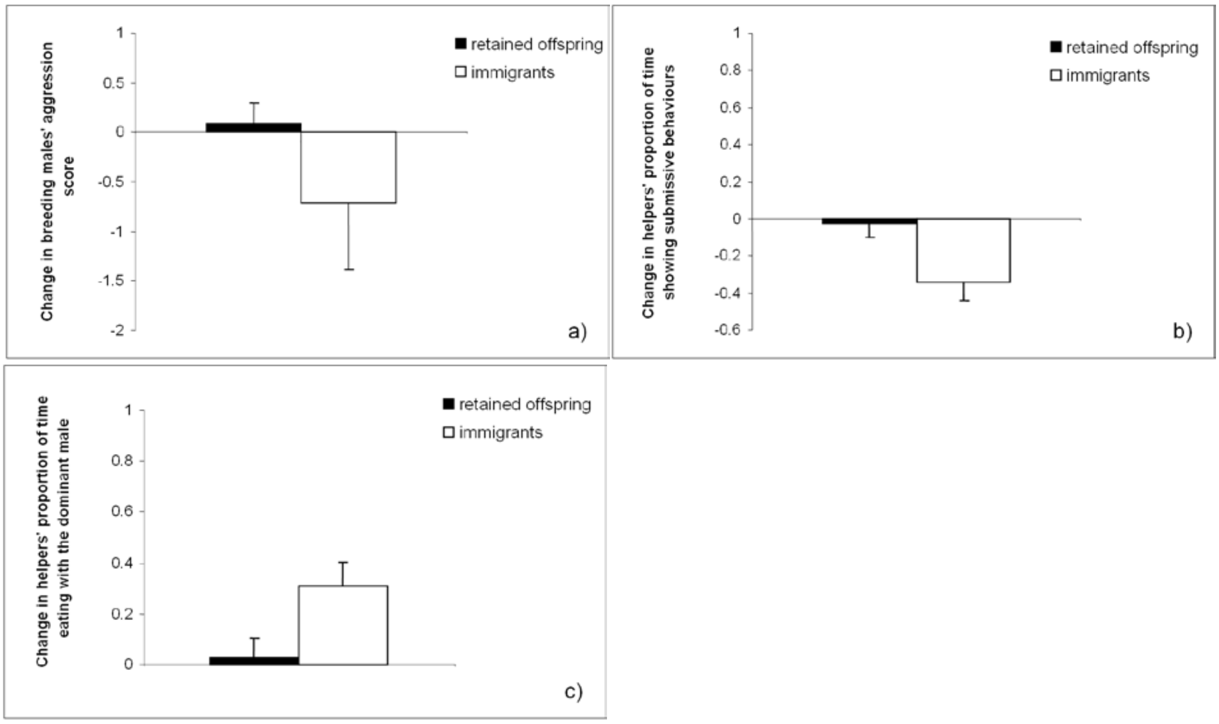

Fig. 2. Change in a) breeding males' aggression score, b) helpers proportion of time showing submissive behaviours and c) helpers proportion of time eating together with the dominant breeding male, between the beginning and the end of the breeding season, according to the social category of helpers.

DISCUSSION

The "pay to stay" hypothesis predicts that social relationships in cooperative groups should be influenced by helpers' levels of contribution to the young. On the one hand, dominant breeders may punish lazy helpers (Gaston 1978) and on the other hand, the latter may appease dominant aggressiveness showing submissive behaviours (Bergmuller and Taborsky 2005). However, in this study on cooperative crows, we found that the level of contribution of subordinate helpers neither influenced the aggressive behaviour of the dominant breeding males nor the submissive behaviour of subordinate helpers on an experimental source of food.

Kokko et al. (2002) proposed that dominants would demand effort primarily from (and direct any aggression towards) less related same-sex helpers, whose presence constitutes a reproductive threat and consequently conveys higher costs for the dominants compared to their sons. This has been shown, for example, in the cooperative breeding cichlid *Neolamprologus pulcher*, where groups consist of a breeding pair and several helpers of different size classes. Bruintjes and Taborsky (2008) showed that when helping demands raise, large helpers, which are a greater threat for breeders with regard to territory take-over, pay generally more than small ones to remain tolerated in the breeders' territory. Similarly, in the cooperative groups of crows in Spain, immigrant males often sire some offspring in the brood (Baglione et al. 2002b), threatening the paternity of the resident male breeder. Therefore, alpha males should demand helping effort primarily from immigrants. However, again, our data did not fit this prediction, as shown by the non significant effect of the interaction between the category of subordinate helpers and their helping effort on both the aggressiveness of dominant males and the submissive behaviour of subordinate helpers. However, as only eight immigrants could be sampled for this study, we can not exclude that the lack of a significant effect of immigrants' contribution on dominant males' aggressiveness might be merely due to the limited sample size.

Absence of evidence of pay to stay in the carrion crows raises the question of why lazy subordinates are tolerated in the group. We suggest that this may be due to the insurance function of apparently uncooperative group members that has been recently uncovered in this study population (Baglione et al. 2010). Experimental data showed that when a care giver is temporally impaired and decreases its nest attendance, the 'laziest' members of the group get into action and compensate for the sudden provisioning failure, preventing a loss of reproductive success. Such hidden function of lazy subordinates may explain why dominants' aggressiveness did not correlate with the current effort of subordinate helpers. However, this does not exclude that dominants may enforce helping when circumstances are unfavourable. Future research should aim at manipulating breeding conditions (e.g. food availability, workforce, etc.) to fully explore whether paying a rent is context dependent in the carrion crow.

Dominants' aggressiveness towards immigrants and reproductive system

In crow groups, the only factor that influenced the variation in dominant males' aggressiveness and subordinates' submissive behaviour throughout the breeding season was the category of helpers. Unlike offspring, immigrant males experienced a significant reduction in the level of aggressions received by the dominant breeding males. Accordingly, immigrants also reduced the time spent in submissive behaviours and increased the time spent eating together with the dominant male.

The change in aggression levels towards immigrant males suggests a function of the aggressive behaviour of dominant breeding males in the context of reproductive competition. In cooperatively breeding systems, dominants and subordinates may share reproduction (like in the case of the carrion crow, Baglione et al. 2002b), but the extent to which reproduction is distributed among group members varies widely among species ('reproductive skew', see Magrath et al. 2004; Hager and Jones 2009 for a review). 'Concession models' of reproductive skew assume that the distribution of reproduction among group members is under the full control of a single dominant individual, which may allow subordinates to reproduce as an incentive to remain in the group (Vehrencamp 1979, 1983a, b). However, the assumption that dominants have a complete control over breeding has been questioned and new 'incomplete control models' have been developed and predict that subordinates breed when dominants are unable to prevent them from doing so (Cant 1998; Reeve et al. 1998; Johnstone and Cant 1999). Therefore, the final distribution of reproduction in cooperative groups may reflect the relative ability of dominants and subordinates to enforce their particular optimal degree of skew. The fact that crow breeding males showed the highest levels of aggressiveness towards immigrant males (all of them adults in this sample) at the beginning of the breeding period (egg laying and incubation) suggests that reproductive competition may be an important factor regulating the social relationships between them. It should be noted that, at the time of the first video recording, i.e. when breeding males proved most aggressive towards immigrants, breeding females were either fertile or still able to lay a new clutch in case of nest predation, which occurs frequently in our population (Canestrari et al. 2008). Our crows therefore seem to fit well into an 'incomplete control model' of reproductive skew, where dominant males attempt to prevent the reproduction of subordinate immigrants, but cannot totally prevent them from mating (Baglione et al. 2002b).

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experiments comply with the law of the country they were performed, and all bird manipulations were authorised by Junta de Castilla y León.

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