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LA EVOLUCIÓN DE LA COMPETENCIA AGRESIVA ENTRE CRÍAS HERMANAS EN ESPECIES DE AVES ALIMENTADAS POR LOS PADRES

TESIS

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PRESENTA

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"In 'modern' Ethology nobody pays the slightest attention to anything but the 'why'. It is a very peculiar situation: we have a science dealing with the causal explanations of observations but the collection of the basic observations is no longer considered a part of the science" (Nielsen 1958, p. 564).

"Description is never, can never be, random; it is in fact highly selective, and selection is made with reference to the problems, hypotheses and methods the investigator has in mind" (Tinbergen 1963).

"Contempt for simple observation is a lethal trait in any science, and certainly in a science as young as ours" (Tinbergen 1963).

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Resumen — La competencia entre las crías por la inversión parental, generalmente en forma de alimento entregado por los padres, ha sido descrita en organismos tan diversos como son los insectos, los mamíferos y las aves. En una minoría de especies las crías compiten no solo mediante solicitud y rebatiña, sino también atacando violentamente a sus hermanos por mordidas, picotazos y arañazos que pueden causar lesiones a los hermanos y en ciertos casos hasta la muerte. La competencia agresiva entre crías hermanas ha sido más estudiada en aves, y generalmente se describe como implicando el establecimiento de una jerarquía basada en relaciones de dominancia-subordinación entre pares de crías. Las crías dominantes generalmente tienen mayor probabilidad de supervivencia y una mayor tasa de crecimiento que sus hermanos subordinados. Durante los más de 30 años transcurridos desde los primeros estudios sobre la competencia agresiva entre crías de aves se ha acumulado un extenso conocimiento de los mecanismos que influyen sobre la expresión de este comportamiento, en comparación, el conocimiento de su ontogenia y evolución ha avanzado muy poco.

La presente tesis tenía tres objetivos principales: (1) identificar algunas características que han facilitado la evolución de la competencia agresiva entre crías de aves alimentadas por los padres, (2) describir el desarrollo de la agresión en la garza garrapatera e identificar los agentes que influyen sobre los patrones de variación temporal de la tasa de agresión, y (3) identificar los mecanismos que influyen sobre la ontogenia de la competencia agresiva y el establecimiento de la jerarquía en nidadas de tres crías de la garza garrapatera. Primero, se realizó un análisis comparativo tomando en cuenta las relaciones filogeneticas entre las especies con el propósito de identificar correlaciones entre dos medidas cuantitativas de la competencia agresiva y cinco caracteres: dos relacionados con la historia de vida, dos con el comportamiento y uno con la morfología. Segundo, mediante un estudio descriptivo en campo se cuantificó la alimentación y agresión de las crías en nidadas de dos crías de la garza garrapatera para identificar los agentes que influyen sobre el desarrollo y variación temporal de la tasa de agresión. Finalmente, mediante un segundo estudio empírico en campo se cuantificó la agresión, concesión y despliegues agresivos de las crías en nidadas de tres crías de la garza garrapatera para identificar los posibles mecanismos que influyen sobre el establecimiento y mantenimiento de la jerarquía en esta especie.

Los resultados del estudio comparativo permitieron identificar tres caracteres, la alimentación indirecta, las nidadas pequeñas y los periodos de nidada largos, que parecen haber facilitado la evolución de la competencia agresiva entre crías de aves alimentadas por los padres. Los resultados del primer estudio de campo ponen en duda la hipótesis de que la alimentación directa influye sobre la distribución interespecífica de la competencia agresiva, y que presenta una influencia próxima de la competencia agresiva. Los resultados sugieren que los patrones de variación temporal de la tasa de agresión temprano en el periodo de nidada pueden ser explicados por el establecimiento temprano de la jerarquía. Finalmente, los resultados del segundo estudio empírico de campo sugieren que en las nidadas de la garza garrapatera la evaluación de la capacidad agresiva del oponente y el entrenamiento para ganar son los mecanismos clave que influyen sobre el establecimiento y mantenimiento de la jerarquía, además los resultados sugieren que las crías subordinadas no están entrenadas para perder.

Abstract — Sibling competition for parental investment has been reported in species as diverse as insects, mammals and birds. In a minority of species offspring compete not only through begging and scrambling but also by violently attacking siblings with pecks, bites or scratches which may cause lesions and in some cases even death. Aggressive sibling competition has been most studied in birds where it is generally described as involving the establishment of a dominance hierarchy based on pairwise dominance-subordination relationships. Dominant chicks generally have better survival probabilities and faster growth rates than broodmates since they bias food distribution in their favour. During the more than 30 years since the first studies of broodmate aggression we have accumulated a large amount of knowledge about the mechanisms which influence the expression of this behaviour but comparatively our knowledge of the ontogeny and the evolution of broodmate aggression has advanced very little.

This thesis had three main objectives: (1) identify some of the agents which have facilitated the evolution of aggressive broodmate competition in parentally fed altricial species, (2) quantify development of aggression in the cattle egret and identify the agents which have a proximate influence on the temporal variation in rates of aggression and (3) identify the mechanisms which influence the ontogeny of aggression and hierarchy establishment and maintenance in three chick broods of the cattle egret. First, a phylogenetic comparative analysis was undertaken to identify correlations between two quantitative measures of aggressive competition and five proposed facilitators of the evolution of broodmate aggression: two related to life history characteristics, two behavioural characteristics and two morphological characteristics. Second, in an empirical field study feeding and aggression were quantified in two chick broods of the cattle egret to identify the agents which have a proximate influence on the temporal variation in rates of aggression. Finally, in a second empirical field study aggression, concession and aggressive displays were quantified in cattle egret three chick broods in order to identify the possible mechanisms influencing ontogeny of aggression and concession as well as hierarchy establishment and maintenance in this species.

The results of the phylogenetic comparative analysis identified three characteristics, indirect feeding of chicks, long nestling periods and small broods, which appear to have facilitated the evolution of aggressive competition in parentally fed bird species. The results of the first empirical study did not support the hypothesis that direct feeding favours the use of aggressive competition and that it also has a proximate influence on temporal variation in rates of aggression. Results suggest that temporal variation in rates of aggression early in the nestling period can be explained by hierarchy establishment. Finally, the results of the second empirical field study suggest that assessment of the opponents' aggressive capabilities and trained winning are key mechanisms influencing hierarchy establishment and maintenance in cattle egret broods. The results also suggest that subordinate chicks of this species are not trained as losers.

INTRODUCCIÓN

La competencia entre individuos por el acceso a los recursos es un principio clave de la teoría de evolución por selección natural de Darwin (1859). Poco más de cien años después de la publicación de la obra de Darwin, Hamilton (1964) propuso la teoría de la selección por parentesco, según la cual la selección natural favorecerá conductas altruistas (o moderación del egoísmo) dirigidas hacia otros individuos siempre y cuando el beneficio para el otro individuo, multiplicado por el grado de parentesco entre ambos, sea mayor al costo que incurre el individuo que realiza la conducta. En un sentido adaptativo, bajo esta teoría han podido explicarse conductas aparentemente costosas en interacciones donde un individuo incurre en un costo, mientras otro obtiene el beneficio. Un caso donde puede aplicarse la teoría de la selección por parentesco es en el cuidado parental: la conducta altruista por parte de los padres hacia sus crías puede ser vista como un extremo dentro de un continuo en la variación de conductas de aparente sacrificio individual en beneficio de otro individuo. El nivel de sacrificio dependerá en parte del grado de parentesco que comparten los individuos involucrados (Hamilton 1964). Sin embargo, Trivers (1974) demostró que, aunque el grado de parentesco es generalmente alto dentro de una familia, las relaciones no siempre son armoniosas. Según Trivers (1974), si las crías tienen algún control sobre la distribución de la inversión parental, éstas deberían exigir un mayor nivel de inversión de lo que sería óptimo para los padres. Las tendencias egoístas de las crías no sólo fomentan un conflicto padre-hijo, sino también competencia entre las crías por obtener mayor inversión parental.

Dentro de taxa tan diversos como son los insectos, los mamíferos y las aves, las crías hermanas compiten por la inversión parental, que generalmente se manifiesta como la cantidad de alimento que los padres proveen a las crías (Mock y Parker 1997). Esta competencia entre crías ha sido estudiada más ampliamente en aves, en las cuales existe una sorprendente variación en las distintas formas de competencia por el alimento. En la mayoría de las aves las crías compiten por el alimento por solicitud y rebatiña (revisión en Wright y Leonard 2002). La primera consiste en realizar despliegues llamativos muchas veces acompañados de vocalizaciones rítmicas y estímulos visuales que comunican a los padres el estado nutricional de las crías (Kilner 1997; Wright y Leonard 2002). Los padres responden a la solicitud de las crías ofreciendo alimento y puesto que los recursos generalmente son limitados, emerge una situación de competencia entre crías de una nidada (Leonard et al. 2000; Neuenschwander et al. 2003). Bajo condiciones ambientales desfavorables, la competencia por alimento puede resultar en la muerte por inanición de la (o las) cría(s) menos competitiva(s), lo cual tiene como consecuencia la reducción de la nidada (Lack 1947).

En una minoría de especies de aves las crías no sólo compiten por solicitud, sino también atacando violentamente a sus compañeros de nidada mediante picotazos, mordidas y empujones (competencia agresiva: Mock y Parker 1997; Drummond 2002). En las especies altriciales con competencia agresiva la eclosión de los huevos es asincrónica; es decir que los huevos de una misma nidada eclosionan con una diferencia de varias horas o incluso días. La eclosión asincrónica confiere una ventaja en edad y tamaño a las crías que eclosionan primero, quienes desde edades tempranas atacan violentamente a sus compañeros de nidada. Las crías dominantes intimidan a los contrincantes y distorsionan el patrón relativo de solicitud, obteniendo así acceso prioritario al alimento (Drummond

2002). En especies como la gran garza blanca (*Casmerodius albus*, Mock y Parker 1997), el bobo de patas azules (*Sula nebouxii*, Drummond et al. 1986), el águila negra (*Aquila verreauxi*, Gargett 1980) y el cucaburra común (*Dacelo novaeguineae*, Legge 2000) las crías menores tienen menor probabilidad de supervivencia que sus hermanos mayores, debido directa (a través de lesiones) o indirectamente (a través de inanición o expulsión del nido) a la agresión recibida (Mock y Parker 1997; Drummond 2001b).

Existe una marcada variación interespecífica en cómo se manifiesta la competencia agresiva entre hermanos; principalmente se distingue entre siblicidio facultativo y obligado. En el primero se establece una jerarquía que generalmente sigue el orden de eclosión. Las crías mayores son más agresivas y menos sumisas que las menores, quienes son poco agresivas y en ciertos casos responden a los ataques con posturas estereotipadas de sumisión (Drummond et al. 1986; Mock y Parker 1997). La supervivencia de las crías menores parece depender de la disponibilidad de los recursos, y en años con recursos abundantes puede emplumar toda la nidada. Si los recursos escasean, las crías dominantes intensifican su agresión, privando de alimento a sus compañeros de nidada o directamente causando su muerte (Drummond et al. 1986). En especies con siblicidio obligado la cría mayor ataca violenta e implacablemente a la cría menor causando, en la gran mayoría de los casos, su muerte pocos días después de la eclosión. Un ejemplo notable es el del águila negra, donde en una nidada la cría mayor atacó continuamente a su hermano menor durante sus 72 horas de vida, picoteándolo 1569 veces en 38 enfrentamientos (Gargett 1978). La escasez de alimento no parece haber sido la causa del ataque puesto que había presas en el nido y la hembra intentó alimentar a la cría mayor mientras ésta atacaba continuamente a la cría menor (Gargett 1978). En las especies con siblicidio obligado, las crías menores no presentan conductas de sumisión, sino que aunque generalmente se encuentran asediadas, pueden responder agresivamente a los ataques e inclusive pueden iniciar enfrentamientos (Drummond et al. 2003). Esta clasificación de las especies con base en la naturaleza facultativa u obligada del siblicidio no implica una dicotomía, sino que representa dos extremos dentro de un continuo de variación (Newton 1977; Simmons 1988).

La competencia agresiva entre crías puede ser estudiada desde los cuatro enfoques distintos definidos por Tinbergen (1963): la ontogenia, los mecanismos que influyen sobre la expresión del comportamiento, su función y su evolución. Las áreas que cubren estas preguntas presentan cierto grado de traslape, pero es útil distinguir entre ellas e importante resaltar que para obtener un entendimiento completo y coherente de un comportamiento es necesario prestar atención a cada una de las preguntas así como a su integración (Tinbergen 1963). En los más de treinta años que han transcurrido desde los primeros estudios que reportaron competencia agresiva entre las crías cabe la pregunta de si hemos desarrollado un conocimiento equitativo de su ontogenia, mecanismos, función y evolución.

Ontogenia de la competencia agresiva

Tinbergen (1963) definió el fenómeno de interés en el estudio de la ontogenia como: "el cambio en la maquinaria del comportamiento durante el desarrollo" (p. 424). El estudio de la ontogenia debe incluir una descripción de los cambios de la conducta con la edad del individuo junto con un análisis de los mecanismos que influyen sobre su desarrollo. En el caso de la competencia agresiva, existe poca información sobre los cambios de la conducta agresiva en relación a la edad de las crías. Además, se sabe poco sobre las respuestas de las crías subordinadas y el desarrollo de su conducta. Se conoce que la agresión inicia a edades muy tempranas, y que la victima generalmente es agredida desde algunas horas a algunos días después de su eclosión (Drummond 2001b). Por ejemplo, en un estudio en el pelícano blanco (*Pelecanus onocrotalus*) la cría mayor inició el ataque a su compañero de nidada cuando éste aún no había salido completamente del cascarón (Cooper 1980). En la garza real (*Ardea cinerea*) la agresión entre las crías se observó por primera vez a la edad de 7 días (Milstein et al. 1970).

En especies con siblicidio obligado la agresión generalmente se concentra en edades tempranas y es intensa hasta que la cría menor muere (Gargett 1978; Meyburg 1987). En especies con siblicidio facultativo, la agresión observada dentro de una nidada parece aumentar con la edad de las crías y posiblemente esté relacionada con el desarrollo de sus capacidades motrices y sensoriales (Drummond et al. 1986). Ciertos estudios sugieren que la agresión disminuye después del establecimiento de la jerarquía. Por ejemplo, en la garza garrapatera (*Bubulcus ibis*) se ha sugerido que la jerarquía se establece a las 3 semanas de edad de la cría mayor, posterior a lo cual decrecen notablemente los niveles de agresión (Mock y Lamey 1991). En un estudio en el bobo de patas azules (*Sula nebouxii*) la intensidad de la agresión de la cría mayor fue modesta entre los 5 y los 10 días de edad, fue cuatro veces mayor entre los 10 y los 20 días de edad y disminuyó progresivamente durante los 40 días siguientes. Por su parte, la cría menor inició y presentó un pico modesto de agresión entre los 5 y los 10 días de edad, después de los cuales la agresión disminuyó y permaneció en niveles cercanos a cero (Drummond et al. 1986). En el cucaburra común la agresión fue más intensa en los primeros días después de la eclosión de la cría menor, en ciertos casos causando su muerte (Legge 2000).

La información que tenemos de los mecanismos que influyen en el desarrollo del comportamiento agresivo proviene, principalmente, de investigación realizada en el bobo de patas azules. En un estudio donde se enfrentó experimentalmente a dos crías únicas, o a una cría única con una cría dominante o subordinada de nidadas de dos crías, se demostró una influencia de la experiencia social sobre el comportamiento de las crías (Drummond y Osorno 1992). La experiencia social temprana de las crías determinó su comportamiento al enfrentarse a un polluelo desconocido, independientemente de la experiencia social del polluelo desconocido. Las crías dominantes atacaron al polluelo desconocido, mientras que las crías subordinadas no fueron agresivas y respondieron con sumisión al ser atacadas. En contraste, en crías sin experiencia social (crías únicas), la dirección de la relación de dominancia dependió de las diferencias de tamaño y edad entre las crías. En ciertos casos la experiencia social pareció predominar sobre la influencia de una ventaja en tamaño y edad, pues crías subordinadas enfrentadas a crías dominantes menores y más pequeñas fueron incapaces de dominarlas (Drummond y Osorno 1992). En un experimento subsiguiente, Drummond y Canales (1998) mostraron que la experiencia social temprana tiene un efecto fuerte, aunque reversible, de entrenamiento tanto sobre crías dominantes como subordinadas. El entrenamiento como subordinado parece tener un efecto más persistente que el entrenamiento como dominante, posiblemente porque la situación experimental, la cual se enfrentó a una cría dominante con una cría única más grande y una cría subordinada con una cría única más pequeña, reforzó el entrenamiento como subordinado y contrarrestó el entrenamiento como dominante (Drummond y Canales 1998). Un estudio descriptivo detallado del desarrollo de la conducta agresiva y tendencias de sumisión en nidadas de 2 y 3 crías del bobo de patas azules resaltó la importancia inicial de la diferencia en tamaño y edad (resultado de la eclosión asincrónica) en las interacciones tempranas entre las crías, así como la influencia del entrenamiento que surge como consecuencia de las repetidas interacciones entre las crías (Valderrábano et al. en prensa). En conjunto, estos estudios demuestran que los papeles que adoptan las crías dentro de una jerarquía resultan de la interacción entre las diferencias en capacidades agresivas causadas por la eclosión asincrónica y el entrenamiento de las crías como ganadoras o perdedoras (Bernstein 1981).

La influencia de las hormonas en las conductas de agresión y sumisión también ha sido explorada; sin embargo, nuestro conocimiento se limita a dos especies del género *Sula*. En estudios en el bobo de patas azules, la testosterona y sus metabolitos sólo fueron detectables en crías de 0 a 12 días de edad y no se encontraron diferencias entre crías dominantes y subordinadas (Ramos-Fernandez 1993; Nuñez-de la Mora et al. 1996). Las crías subordinadas de 15 a 20 días de edad presentaron niveles de corticosterona 109% más elevados que sus hermanos dominantes (Nuñez-de la Mora et al. 1996) y dichos niveles disminuyeron con la edad independientemente del estatus social de las crías (Ramos-Fernández 1993). Crías dominantes enfrentadas experimentalmente a una cría única presentaron un incremento en los niveles de corticosterona, al mismo tiempo que incrementaron su agresión. Por el contrario, crías subordinadas bajo la misma situación experimental no presentaron un cambio significativo en sus niveles de corticosterona (Nuñez-de la Mora et al. 1996). Esto sugiere que en esta especie la corticosterona interactúa con la experiencia social, favoreciendo la conducta agresiva en crías dominantes y la conducta sumisa en crías subordinadas (Nuñez-de la Mora et al. 1996), aunque la causalidad no ha sido determinada. En el bobo de Nazca, donde el siblicidio es obligado, los niveles de testosterona en crías mayores y en segundas crías aumentaron durante los enfrentamientos previos al siblicidio, decreciendo un día después del siblicidio (Ferree et al. 2004), lo que sugiere que en esta especie la testosterona posiblemente esté tendiendo una influencia sobre la conducta agresiva.

Mecanismos que influyen en la expresión de la competencia agresiva

La mayoría de los estudios sobre la competencia agresiva se han enfocado en los mecanismos que influyen en su expresión (Drummond 2001b). Este sesgo ha resultado en un mejor conocimiento de los mecanismos que de la ontogenia, función o evolución de la competencia agresiva. A continuación se da una breve reseña sobre los principales mecanismos que se han propuesto para explicar la competencia agresiva.

- *Cantidad de alimento*

Estudios descriptivos en varias especies sugieren que la agresión entre hermanos está asociada a los eventos de alimentación (David y Berrill 1987), aumenta cuando la cantidad de alimento entregada por los padres disminuye (Braun y Hunt 1983; Fujioka 1985b; Drummond et al. 1986; Forbes 1991), cuando la temperatura es inclemente o en territorios con baja disponibilidad de recursos (Braun y Hunt 1983; Young y Millar 2003). Estudios experimentales en bobos de patas azules (Drummond y Garcia-Chavelas 1989; Nuñez-de la Mora et al. 1996), gaviotas pata negra (*Rissa tridactyla*; Irons 1992), águilas pescadoras (*Pandion haliaetus*; Machmer e Ydenberg 1998) y en el arao aliblanco (*Cepphys grylle*; Cook et al. 2000) han mostrado que las crías incrementan su agresión conforme se reduce su ingesta (revisión en Drummond 2001a). Por ejemplo, un experimento en el bobo de patas azules, donde se juntaron 2 crías subordinadas previamente privadas de alimento en diferente grado, resultó en que la cría con mayor privación de alimento se volvió dominante (Rodríguez-Gironés et al. 1996).

No obstante, se ha argumentado que en las garzas las crías no ajustan su agresión a la cantidad de alimento ingerido (Mock et al. 1987a; Mock y Parker 1997). Estudios descriptivos en la gran garza azul (*Ardea herodias*) y la garza garrapatera no encontraron la relación negativa entre frecuencia de alimentación y agresión predicha por la hipótesis (Ploger y Mock 1986; Sullivan 1988). Además, en la gran garza blanca la tasa de agresión de las crías no parece estar relacionada con la frecuencia de alimentación en nidadas naturales: en nidadas experimentales donde las crías recibieron un suplemento alimenticio, éstas no redujeron su agresión, tampoco hubo diferencias en la frecuencia de agresión en nidadas experimentales alimentadas a mano con diferentes cantidades de alimento (Mock et al. 1987a). Sin embargo, este estudio ha sido criticado porque por un lado no se controlaron el efecto de la edad de las crías y el tamaño de la nidada, factores que podrían influir sobre la agresión. Por otro lado, el complemento de alimento no fue ingerido por las crías que normalmente emiten la mayoría de la agresión, la provisión de alimento en las nidadas experimentales fue insuficiente y todas las crías fueron excepcionalmente agresivas (Drummond 2001a). Por último, dos estudios descriptivos en garzas garrapateras sí encontraron una relación negativa entre la ingesta y la tasa de agresión de las crías (Fujioka 1985a; Creighton y Schnell 1996).

En especies con siblicidio obligado la cantidad de alimento no parece ser un factor limitante puesto que la cría menor generalmente muere a los pocos días de la eclosión aún cuando hay alimento disponible en el nido (e. g. Gargett 1978; Meyburg 1974). Por ello, se ha sugerido que en estas especies la intensidad de la agresión y la probabilidad de supervivencia de la cría menor no están bajo la influencia de la cantidad de alimento (Gargett 1978; Meyburg 1978; Sumba y Pomeroy 1984; Gerhardt et al. 1997; Margalida et al. 2004). Sin embargo, el único estudio experimental realizado en una especie con siblicidio obligado en el cual se manipuló la ingesta de las crías mostró que aunque la frecuencia de agresión no parecía estar afectada por la privación de alimento, la frecuencia de intentos de expulsión del nido de la cría menor por parte de la mayor aumentó en las nidadas privadas de alimento (Osorno y Drummond 2003).

- *Método de alimentación*

La manera en la cual los padres transfieren el alimento a las crías también podría influir en la competencia agresiva. La hipótesis del método de alimentación (originalmente hipótesis del tamaño de la presa; Mock 1985) sugiere que se favorece la competencia agresiva cuando el alimento pasa directamente del pico del adulto al pico de la cría (alimentación directa), puesto que la agresión supuestamente permite monopolizar el alimento. En contraste, cuando el alimento es depositado sobre el piso del nido (alimentación indirecta) y es accesible a todas las crías la agresión es ineficaz para competir por el alimento (Mock 1985; Drummond 2001a). Estudios realizados con garzas parecen apoyar esta hipótesis puesto que muestran que las crías alimentadas de manera directa son más agresivas que las crías alimentadas de manera indirecta (Mock 1985; Mock et al. 1987a, b). Pero, dichos estudios han sido criticados por no controlar por variables que también podrían influir sobre la agresión (Drummond 2001a).

En ciertas especies, como las garzas y los pelícanos, las crías son alimentadas de manera indirecta durante los primeros días o semanas de crianza, y cambian progresivamente a una alimentación directa conforme se desarrolla su capacidad motriz y sensorial. La hipótesis del método de alimentación predice que las crías ajustarán su estrategia competitiva dependiendo del método de alimentación; es decir que competirán de manera no agresiva cuando sean alimentadas indirectamente y de manera agresiva cuando la alimentación sea directa (Mock y Parker 1997). El método de alimentación, según la hipótesis, actúa como un gatillo que dispara el cambio en la estrategia competitiva de las crías, asumiendo que existe la plasticidad fenotípica necesaria (Mock y Parker 1997). Los estudios mencionados previamente en apoyo a la hipótesis del método de alimentación, aunque describieron el cambio en el método de alimentación y cuantificaron la agresión, no analizaron la variación temporal en tasa de agresión ni relacionaron cambios en agresión a cambios en el método de alimentación (Mock 1985; Mock et al. 1987a). El único estudio que ha puesto a prueba esta predicción de la hipótesis del método de alimentación, realizado en el pelícano café (*Pelecanus occidentalis*), no encontró diferencia en la agresión de las crías durante alimentaciones directas comparadas con la agresión de las crías durante las alimentaciones indirectas (Pinsón y Drummond 1993). Otros estudios presentan resultados que también contradicen la hipótesis. Por ejemplo, en ciertas águilas la transición en el método de alimentación es de directa a indirecta, por lo tanto según la hipótesis las crías deberían competir agresivamente al principio del periodo de nidada. Sin embargo, en el gavilán común (*Accipiter nisus*) y en el busardo aliancho (*Buteo platypterus*) las crías son más agresivas durante la alimentación indirecta (Brown y Amadon 1968; Matray 1974, respectivamente).

- *Tamaño de la nidada*

Respecto a si el tamaño de la nidada es un factor que puede influir en la agresión entre crías, se ha sugerido que conforme aumenta el tamaño de la nidada la agresión es más intensa dada la mayor competencia entre crías. Sin embargo, la evidencia disponible es contradictoria (Drummond 2001b). En la garza blanca, por ejemplo, las nidadas de 3 o 4 crías presentaron una mayor tasa de agresión que las nidadas de 2 crías (Mock y Parker 1986); así mismo, la agresión fue mayor en nidadas más grandes en una población de la gran garza azul (David y Berrill 1987), aunque no en otra población de la misma especie (Mock y Parker 1986). Los dos únicos estudios experimentales que han analizado la influencia del tamaño de la nidada obtuvieron resultados contradictorios: la agresión disminuyó en nidadas de la garza garrapatera cuando la cría mayor fue extraída (Mock y Lamey 1991), pero no se observó un cambio en la frecuencia de la agresión después de una reducción experimental de la nidada en el pelícano café (Ploger 1997). La reducción de la agresión entre crías de la garza garrapatera podría deberse a una mayor disponibilidad de alimento para las crías restantes (Drummond 2001b), si asumimos que la cantidad de alimento ingerido influye sobre la agresión en esta especie. La reducción de la nidada en el pelícano café resultó en una reducción en la ingesta de la cría intermedia (menor después de la reducción); la falta de alimento pudo ser la causa de que la frecuencia de agresión no disminuyera aún en nidadas reducidas (Ploger 1997). Esto resalta la necesidad de controlar por posibles efectos de la ingesta sobre la agresión al analizar la influencia del tamaño de la nidada sobre la intensidad de la agresión (Drummond 2001b).

- *Asincronía*

La agresión generalmente se intensifica conforme se reduce la asincronía entre las crías debido a que se incrementa la similitud en la capacidad agresiva de las crías. Por otro lado, una asincronía exagerada parece reducir la probabilidad de supervivencia de la cría menor en ciertas especies. En el cucaburra común las nidadas con menor asincronía presentaron mayor agresión entre las crías y mayor probabilidad de siblicidio como resultado de la agresión (Legge 2000; Nathan et al. 2001). Estudios experimentales en la garza garrapatera (Fujioka 1985a; Mock y Ploger 1987), el bobo de patas azules (Osorno y Drummond 1995), el milano negro (*Milvus migrans*; Viñuela 1999) y el águila pescadora (Machmer e Ydenberg 1998) mostraron mayor intensidad de agresión en nidadas sincrónicas que en nidadas con asincronía natural. La relación de dominancia fue más clara en nidadas asincrónicas que en nidadas sincrónicas en la garza garrapatera (Fujioka 1985a); además, las nidadas dos veces más asincrónicas que las nidadas naturales presentaron mayor número de nidos en los cuales una cría murió, aunque la tasa de agresión fue menor (Mock y Ploger 1987). En el bobo de patas azules las nidadas experimentalmente sincrónicas formaron una jerarquía similar a la que se observa en nidadas naturalmente asincrónicas y las crías subordinadas presentaron una menor tasa de crecimiento y mayor mortalidad. En nidadas con una asincronía exagerada las crías menores fueron más agredidas y crecieron más lentamente que las crías menores en nidadas control (Osorno y Drummond 1995). Por el contrario, en el águila pescadora, las nidadas con asincronía exagerada no presentaron agresión y la distribución del alimento estuvo menos sesgada hacia la cría mayor (Forbes 1991). En especies con siblicidio obligado la asincronía entre las crías parece influir en el tiempo que sobrevive la cría menor, una mayor asincronía entre las crías acelera la muerte de la cría menor (Meyburg 1974, 1978; Evans 1996).

-*Sexo y orden de eclosión*

En las especies con dimorfismo sexual en tamaño (en especies agresivas las hembras son mas grandes que los machos), el sexo de las crías y su orden de eclosión podrían influir sobre la intensidad de la agresión al reducir o exacerbar la diferencia en tamaño causada por la eclosión asincrónica. La agresión en nidadas del cucaburra común fue mayor cuando la segunda o tercera cría eran hembras, además cuando la primera cría era macho y la segunda hembra aumentó la probabilidad de siblicidio temprano en el periodo de nidada, como resultado directo de la agresión entre las crías (Legge 2000; Nathan et al. 2001). Se ha sugerido que en el águila cabeza blanca (*Haliaeetus leucocephalus*) y el águila real (*Aquila chrysaetos*) la interacción entre el sexo y el orden de eclosión también afectaría la probabilidad de siblicidio debido a la diferencia en tamaño y habilidades competitivas entre las crías (Bortolotti 1986), aunque no se llevaron a cabo observaciones conductuales y la inferencia se basa en las tasas de crecimiento de machos y hembras de cada especie. En el bobo de patas azules el sexo de las crías parece tener una influencia mínima en la competencia agresiva dentro de la nidada. Drummond et al. (1991) reportan una sola inversión de la dominancia en 6 nidadas de dos crías en las cuales ambas crías emplumaron y la primera cría era macho y la segunda hembra. Tampoco observaron indicios de una intensificación de la agresión por parte de una cría mayor macho para eliminar a una hermana menor antes de ésta pueda volverse una competidora peligrosa. Los machos que crecieron con una hermana mayor no crecieron más lentamente, ni llegaron a tamaños menores que machos que crecieron con un hermano mayor. En la misma colonia, la proporción de sexos a la eclosión y al emplumado estuvo sesgada hacia machos (55.9% y 56.4% respectivamente; Torres y Drummond 1999), lo cual apoya la hipótesis de Fisher (1930) de mayor inversión en el sexo menos costoso. Finalmente, aunque la probabilidad de supervivencia al emplumado disminuye con el orden de eclosión, el decremento es similar en machos y hembras (Torres y Drummond 1997).

- *Hormonas*

La influencia de las hormonas sobre la conducta de las crías ha sido poco estudiada. Los niveles de corticosterona parecen aumentar en situaciones de estrés, por lo menos en el bobo de patas azules (Ramos-Fernandez 1993; Nuñez-de la Mora et al. 1996; Ramos-Fernandez et al. 2000) y, en el bobo de Nazca, los niveles de testosterona aumentaron durante las interacciones previas al siblicidio (Ferree et al. 2004). En el bobo de patas azules, cuando las crías son privadas de alimento, los niveles de corticosterona aumentan, independientemente del estatus social de la cría (Nuñez-de la Mora et al. 1996). Esto sugiere que el estrés ocasionado por una reducción en la cantidad de alimento provoca un incremento en los niveles de corticosterona, lo que podría explicar los niveles elevados de corticosterona en crías subordinadas, quienes generalmente reciben menos alimento que la cría dominante. Además, se ha visto que al incrementar experimentalmente los niveles de corticosterona circulante en crías subordinadas hay un incremento en el tiempo activo de la cría subordinada y de la sumisión espontánea (no causada por agresión o amenaza;

Vallarino et al. 2006). En el bobo de Nazca, los niveles de testosterona tanto en crías mayores como en segundas crías aumentaron durante las interacciones agonísticas previas al siblicidio. Las crías mayores presentaron niveles de testosterona más elevados durante las interacciones agonísticas que un día después del siblicidio, y las segundas crías presentaron niveles de testosterona más elevados que sus hermanos mayores durante las interacciones agonísticas (Ferree et al. 2004). Estos resultados sugieren que la testosterona podría efectivamente influir sobre la conducta agresiva, y los niveles podrían aumentar únicamente durante las interacciones agresivas. Pero, la causalidad no puede ser inferida y podrían ser las interacciones agonísticas la causa del incremento de los niveles de testosterona. Finalmente, el primer y segundo huevo de puestas de 3 en la garza garrapatera presentaron niveles de testosterona más elevados que los del tercer huevo, aunque los resultados en la conducta de esta diferencia en niveles hormonales no han sido evaluados (Schwabl et al. 1997).

- *Conducta de los padres*

Los padres podrían no ser espectadores pasivos de la competencia agresiva pero tener cierta influencia sobre su desenlace. En el skua polar (*Stercorarius maccormicki*) los padres a veces intervienen en las peleas entre los hermanos. Cuando los padres no intervienen, los ataques de la cría mayor pueden resultar en el desalojo de la cría menor del nido y los padres se ven forzados a empollar y alimentar a las crías por separado (Young y Millar 2003). En el milano negro los padres a veces alimentan preferentemente a la cría menor, lo que se ha sugerido podría retardar el siblicidio (Viñuela 1999). Los padres también parecen intentar moderar la competencia agresiva entre las crías empollándolas (ej. Meyburg 1974; Cash y Evans 1986), emitiendo falsas señales de alarma (Young 1963) o dando un picotazo sobre la cabeza de la cría agresiva (Drummond 1993; Rodríguez Gironés et al. 1996).

Finalmente, también se ha sugerido que la estructura del nido podría facilitar o impedir ciertas conductas siblicidas de la cría mayor (Anderson 1995).

Función de la competencia agresiva

Existe una gran brecha entre la teoría proveniente de modelos sobre el impacto que tiene la competencia entre crías en la adecuación de los padres y de las crías mismas, y la información empírica. Gran parte de la información actual esta basada en inferencias que se han hecho a partir de los resultados de estudios enfocados a analizar los mecanismos que influyen sobre la competencia agresiva (Drummond 2001b).

Bajo ciertas circunstancias, en acuerdo con la teoría de Hamilton (1964), las crías dominantes moderan su egoísmo y comparten los recursos con sus compañeros de nidada. Esto es apoyado por observaciones en el bobo de patas azules, en el cual, durante periodos cortos de escasez de alimento, la cría dominante en nidadas de dos crías no ingiere una mayor porción del alimento entregado, y las alimentaciones poco abundantes son compartidas equitativamente entre ambas crías. La tolerancia de la cría dominante parece depender de su condición a largo plazo y no de la cantidad de alimento entregado durante una alimentación en particular. Cuando la escasez de alimento es crónica la cría dominante se vuelve más agresiva e impide la alimentación de la cría menor (Anderson y Ricklefs 1995). Resultados similares han sido reportados para el águila pescadora (Forbes 1991). En nidadas de tres crías del pelícano café, la cría intermedia sufre una reducción en su ingesta tras la reducción de la nidada, lo cual sugiere que, al menos en esta especie, podría haber un beneficio, para la cría intermedia, asociado con posponer el siblicidio (Ploger 1997). Sin embargo, en águilas se ha sugerido que los padres no ajustan la provisión de alimento después de la reducción de la nidada (Simmons 2002). Adicionalmente, un experimento en el bobo café (*Sula leucogaster*) sugiere que el siblicidio en esta especie podría ser débilmente facultativo y que la cría mayor podría tolerar a la cría menor hasta que el costo de la cohabitación se vuelva inaceptablemente alto (Osorno y Drummond 2003). En conjunto, estos estudios sugieren que la selección podría favorecer la presencia de estrategias condicionales por parte de las crías dominantes permitiéndoles moderar su egoísmo bajo ciertas circunstancias y posiblemente optimizar la disyuntiva (“trade-off”) entre adecuación directa e indirecta.

La eclosión asincrónica puede ser interpretada como un mecanismo que permite un mayor éxito reproductivo a través de una reducción en los costos de la competencia agresiva para los padres así como para las crías. Dicha reducción podría ser resultado de las diferencias en edad y tamaño de las crías, lo cual parece facilitar el establecimiento de una jerarquía estable (Mock y Ploger 1987; Viñuela 1999; Cook et al. 2000). La asincronía también parece facilitar la reducción de la nidada tanto en especies con siblicidio facultativo como en especies con siblicidio obligado (Edwards y Collopy 1983; Meyburg 1987; Osorno y Drummond 1995; Margalida et al. 2004), y podría ser ajustada adaptativamente para incrementar o reducir la longevidad de la cría menor (Edwards y Collopy 1983; Evans 1996). Las nidadas sincrónicas parecen ser más costosas para los padres puesto que requieren mayor inversión parental y resultan en una mayor mortalidad de crías como sucede en la garza garrapatera y el bobo de patas azules (Fujioka 1985a; Osorno y Drummond 1995).

La selección natural parece favorecer el ajuste del sexo y orden de eclosión de las crías en algunas de las especies con dimorfismo sexual, pero no en todas. El cucaburra común presenta ayudantes en el nido y la calidad de la ayuda brindada depende del sexo del ayudante, los machos siendo mejores ayudantes que las hembras (Legge et al. 2001). En esta especie las hembras parecen ajustar la proporción de sexos de su nidada a la proporción de sexos de sus ayudantes, además de ajustar el sexo y orden de eclosión de las crías en función de su condición (y posiblemente la calidad de la ayuda) acentuando o reduciendo la probabilidad de reducción de la nidada (Legge 2000; Legge et al. 2001). En el águila cabeza blanca y en el águila real se ha sugerido que el sexo y orden de eclosión de las crías deberían interactuar para influir sobre la probabilidad de siblicidio debido a las diferencias en las capacidades competitivas de las crías (Bortolotti 1986); sin embargo, no hay estudios conductuales que pongan a prueba esta hipótesis. En el bobo de patas azules parece que la interacción entre el orden de eclosión y sexo de las crías no influye sobre la intensidad de la competencia entre las crías ni sobre la productividad de las nidadas (Drummond et al. 1991). Si las hembras son capaces de controlar el sexo de las crías (en aves las hembras son el sexo heterogamético), esto podría permitirles ajustar la probabilidad del siblicidio a las condiciones ambientales prevalecientes, a su propia condición o a la evaluación de la calidad de su pareja.

El hecho de crecer como cría dominante o subordinada también podría tener un efecto en la adecuación a largo plazo de la cría, un solo estudio ha analizado esto. Drummond et al. (2003) al comparar, en su primer intento de reproducción, a crías dominantes y subordinadas no encontraron diferencias en la probabilidad de reclutamiento, en la edad de primera reproducción, ni en el tamaño de nidada o éxito reproductivo. Al comparar entre el éxito reproductivo durante los primeros 5 o 10 años las crías subordinadas tendieron a superar a las crías dominantes, pero las diferencias no fueron significativas (Drummond et al. 2003). En conclusión, este estudio sugiere que la experiencia social temprana no tiene efectos irreversibles sobre el desempeño futuro de un individuo.

Evolución de la competencia agresiva

Los estudios de la evolución de la competencia agresiva son escasos. Además, los pocos estudios realizados hasta ahora han sido teóricos y no incluyen un componente cuantitativo, excepto por dos estudios realizados por Mock (1984; 1985).

Existen dos hipótesis propuestas por Stinson (1979) para explicar el siblicidio: la del seguro y la del conflicto padre-hijo. La hipótesis del seguro propone que, en especies con siblicidio obligado, el segundo huevo sirve como reemplazo en caso de infertilidad del primer huevo, problemas de desarrollo o mortalidad prematura de la primera cría. Si la primera cría es viable, la agresión resulta en reducción del tamaño de la nidada e incrementa el éxito reproductivo de los padres y de la primera cría. En especies con siblicidio facultativo, en las cuales toda la nidada puede emplumar cuando los recursos son abundantes, propone que la agresión y el siblicidio son resultado del conflicto padre-hijo (Stinson 1979). Bajo la hipótesis del conflicto padre-hijo, el siblicidio es perpetrado por la cría dominante puesto que al matar a su hermano menor puede incrementar la porción de alimento que recibe durante todo el periodo de nidada y por lo tanto incrementar su probabilidad de supervivencia. En años con recursos escasos la agresión y el siblicidio pueden resultar beneficiosos para la cría mayor y los padres, pero en años buenos, en los cuales posiblemente podría salir adelante toda la nidada, el siblicidio puede presentar un costo para los padres (podría también presentar una perdida en adecuación inclusiva para la cría mayor, aunque Stinson [1979] no contempla esto). Por otro lado, Simmons (1988) argumenta que la competencia agresiva y el siblicidio pueden ser seleccionados en especies longevas donde los sitios de anidación son un recurso escaso: una alta mortalidad juvenil e intensa competencia por los sitios de anidación resultaría en una fuerte presión de selección por producir crías de mayor calidad. No obstante, la hipótesis de Simmons (1988) se aplica difícilmente a especies agresivas en las cuales no hay competencia intensa por los sitios de anidación, y no puede aplicarse a especies con siblicidio facultativo.

El método de alimentación ha sido propuesto como un factor que podría explicar la distribución interespecífica de la competencia agresiva (Mock 1985). Según ésta hipótesis la agresión se presenta únicamente en especies en las cuales las crías son alimentadas de manera directa, siempre y cuando las crías tengan la capacidad de competir agresivamente y exista escasez de alimento (Mock 1985; Mock y Parker 1997). La hipótesis se basa en el supuesto de que la agresión brinda mayor beneficio cuando la alimentación es directa, que cuando es indirecta (Drummond 2001a). Los resultados de dos estudios descriptivos y un estudio experimental con dos especies de ardeido parecen apoyar la hipótesis del método de alimentación puesto que las crías alimentadas de manera directa son más agresivas que las crías alimentadas de manera indirecta (Mock 1984, 1985; Mock et al. 1987a). Sin embargo, los resultados de estos estudios han sido cuestionados puesto que, por un lado, no se controló adecuadamente por la cantidad de alimento ingerido por las crías, lo cual también pude influir en la agresión, y por otro lado ciertos resultados van en sentido contrario a lo predicho por la hipótesis (Drummond 2001a). Finalmente, en una población de la gran garza azul, en Ontario, Canadá, la agresión entre crías y el siblicidio fueron frecuentes a pesar de que las crías en dicha población son alimentadas de manera indirecta (David y Berrill 1987).

Mock et al. (1990) describieron cinco caracteres que probablemente favorecen el que se presente competencia agresiva: competencia por recursos, alimentación directa, la posesión de armamento (un pico duro, puntiagudo o filoso) que pueda causar daño a sus competidores, confinamiento espacial limitando la posibilidad de escapar y diferencias competitivas entre las crías. Los primeros 4 son considerados esenciales para que pueda evolucionar la competencia agresiva, mientras que el quinto probablemente no es esencial y podría ser una consecuencia más que una causa. Drummond (2002) discutió la importancia de los 5 factores previamente propuestos y agregó tres más: que la transferencia del alimento se dé en pedazos o bolos grandes permitiendo a las crías obtener una ganancia considerable al intimidar a los competidores, que dicha transferencia sea lenta permitiendo a las crías utilizar la agresión para competir, y que las nidadas sean pequeñas. Drummond (2002) enfatizó la importancia de realizar estudios comparativos controlando por la filogenia (Harvey y Pagel 1991) para identificar los factores que han favorecido la evolución de la competencia agresiva.

En especies con competencia agresiva el tipo de relación que se desarrolla entre pares de crías podría ser resultado del comportamiento de la cría menor (Drummond et al. 2003; Drummond 2006). La probabilidad de supervivencia de la cría menor, ya sea emplumando junto con sus compañeros de nidada o reemplazando a uno de ellos, debería influir sobre el rol que adopta en la relación de dominancia-subordinación, es decir si acepta mas o menos pacíficamente el establecimiento de la dominancia y por lo tanto su rol como subordinada o si combate ferozmente el intento de su compañero mayor de establecerse como dominante (Drummond 2006). Si la probabilidad de supervivencia de la cría menor es relativamente alta en comparación con la de su hermano mayor (es decir el costo de subordinación es bajo) entonces la selección podría favorecer a crías subordinadas no agresivas y sumisas, y los dominantes podrían beneficiarse, en adecuación inclusiva, al convivir con las crías menores, lo que resulta en agresión-sumisión. Si la probabilidad de supervivencia de la cría menor se reduce en relación a la de su hermano mayor, (e.g. porque los padres sean incapaces de proveer suficiente alimento para que emplume toda la nidada), la cría menor podría incrementar su resistencia al establecimiento de la dominancia e invertir más en competir por el alimento, lo que resulta en agresión-resistencia. Finalmente, cuando la probabilidad de emplumar de la cría menor es casi nula el costo de la sumisión se vuelve muy alto y la cría menor tiene poco o nada que perder en responder agresivamente a todos los ataques e inclusivamente iniciar ataques intentando revertir la dominancia, aún si la probabilidad de éxito es mínima, lo que resulta en una relación de agresión-agresión (Drummond 2006).

OBJETIVOS

Los objetivos principales de este estudio son tres. Primero, identificar algunos de los agentes que han facilitado la evolución de la competencia agresiva entre crías de aves alimentadas por los padres. Segundo, describir el desarrollo de la agresión en la garza garrapatera e identificar los agentes que influyen sobre los patrones de variación temporal. Y tercero, identificar los mecanismos que influyen sobre la ontogenia de la competencia agresiva y el establecimiento de la jerarquía en nidadas de tres crías de la garza garrapatera.

Para cumplir el primer objetivo, se realizó un análisis comparativo controlando por los efectos filogenéticos (Harvey y Pagel 1991). Se consideraron cuatro caracteres como posibles agentes que favorecen la evolución de la competencia agresiva: el método de alimentación, la transferencia de pedazos o bolos grandes de alimento, la capacidad agresiva de las crías y el tamaño de la nidada. Estos agentes fueron elegidos debido a que se prestan bien al análisis cuantitativo. Además, se propuso el periodo de nidada largo como un carácter adicional que posiblemente favorece la evolución de la competencia agresiva. Se utilizaron dos medidas cuantitativas de la competencia agresiva: la incidencia y la intensidad. Siete familias de aves en las cuales por lo menos una especie presentaba competencia agresiva entre las crías fueron incluidas en el análisis.

La descripción del desarrollo de la agresión en la garza garrapatera (objetivo dos) se realizó mediante un estudio en campo donde se analizó la influencia última (evolución) y próxima (mecanismo) del método de alimentación sobre la competencia agresiva entre las crías de la garza garrapatera. La hipótesis del método de alimentación se basa en el supuesto, hasta ahora no puesto a prueba, de que la agresión será más eficaz para incrementar la porción de alimento que obtienen las crías dominantes durante la alimentación directa que durante la alimentación indirecta (Mock y Parker 1997, p. 106). La hipótesis propone que en especies que presentan un cambio en el método de alimentación asociado al desarrollo de las crías, estas adoptarán facultativamente una estrategia de competencia no agresiva o agresiva dependiendo de si el alimento es entregado de manera indirecta o directa (Mock y Parker 1997, ver p. 116). El supuesto básico y la predicción de la hipótesis del método de alimentación pueden ser puestos a prueba cuantificando alimentación y agresión durante la transición en el método de alimentación. Cualquier análisis de los factores que influyen sobre la variación temporal en las tasas de agresión de las crías también debe tomar en cuenta otros factores que posiblemente influyan sobre éstas, por ejemplo la cantidad de alimento ingerido y el establecimiento temprano de una jerarquía (Mock et al. 1987a; Pinson y Drummond 1993; Drummond 2001a).

Finalmente, para identificar los mecanismos que influyen sobre la ontogenia de la competencia agresiva y el establecimiento de la jerarquía en nidadas de tres crías de la garza garrapatera (objetivo tres), se llevó a cabo un estudio en campo donde se describieron los patrones de variación temporal de la tasa de agresión y tasa de sumisión de las crías en nidadas de tres de la garza garrapatera y se analizó la influencia de la evaluación del oponente y del entrenamiento para ganar.

ESPECIE DE ESTUDIO

La garza garrapatera anida en colonias mixtas de alta densidad. Tanto machos como hembras participan en la construcción del nido, incubación de los huevos y cuidado y alimentación de las crías (Hancock y Kushlan 1984). El tamaño de la puesta varía de 1 a 5 huevos (moda = 3.5 huevos) de 28 g en promedio (Singh et al. 1988; del Hoyo et al. 1992). La incubación inicia con la puesta del primer huevo, lo que resulta en una eclosión asincrónica, en la cual 2 días separan la eclosión del primer huevo de la eclosión del segundo y así sucesivamente (Ploger y Mock 1986). En promedio eclosionan 3.1 crías altriciales, casi desnudas y con los ojos cerrados (del Hoyo et al. 1992; Hancock y Kushlan 1984). Cuando las crías son pequeñas, los padres las alimentan depositando el bolo alimenticio en el fondo del nido de donde las crías picotean pedazos que pueden ingerir. Conforme las crías crecen, sus capacidades motrices y sensoriales se desarrollan y se incrementa progresivamente la proporción de bolos que atrapan directamente del pico del adulto hasta que ésta alcanza casi el 100%. Las crías son alimentadas 2 – 3 veces al día, y los padres entregan de 3 – 5 bolos por cada alimentación (Ploger y Mock 1986; Mock y

Parker 1997). Dichos bolos generalmente están compuestos por invertebrados, en su mayoría ortópteros, pero en ocasiones los padres también entregan pequeños vertebrados, por ejemplo ranas, lagartijas y pequeñas víboras (del Hoyo et al. 1992; González Voyer obs. per.).

Las crías compiten de manera agresiva por el alimento y establecen una relación de dominancia subordinación durante las primeras 3 semanas de vida (Ploger y Mock 1986; Mock y Lamey 1991). Las crías mayores picotean a sus hermanos menores en cuanto estos eclosionan y las peleas son generalmente más intensas entre las dos últimas crías en una nidada de tres (Ploger y Mock 1987). Durante las primeras semanas de crianza las crías mas jóvenes de una díada a veces responden con agresión al ser atacadas; estas “peleas péndulo” (Milstein et al. 1970) pueden durar varios minutos y la cría menor generalmente pierde la mayoría de los encuentros (Fujioka 1985a). En ocasiones, la cría menor es quien inicia la pelea, picoteando al hermano. En esta especie, en contraste con el bobo de patas azules, no existe una señal de sumisión estereotipada, las crías señalan concesión de una pelea agachándose en el fondo del nido con la cabeza abajo, lo que generalmente frena el ataque (Drummond 2006). Las crías también presentan despliegues agresivos, llamados “enfrentamientos” (face-offs), que a veces resultan en peleas entre las crías cuando son pequeñas, pero mas tarde podrían ser utilizados para mantener las relaciones de dominancia entre ellas sin la necesidad de agresión física (Creighton y Schnell 1996; González Voyer obs. per.). La mortandad de la cría menor en nidadas de 3 varia entre diferentes estudios: 67% en 15 nidadas en Texas (Ploger y Mock 1986), 33% en 100 nidadas en Oklahoma (Mock y Parker 1997) y 85% en una población en Sudáfrica (Siegfried 1972).

La garza garrapatera es una especie ideal para poner a prueba la hipótesis de la cantidad de alimento puesto que presenta una transición en el método de alimentación ligada al desarrollo y porque las crías compiten de manera agresiva (Ploger y Mock 1986). También es un buen modelo para estudiar la ontogenia de la competencia agresiva puesto que ha sido caracterizada como presentando una relación de agresión-resistencia entre las crías, y en el bobo de patas azules, la única especie en la cual se ha estudiado la ontogenia de la competencia agresiva hasta ahora, las crías presentan una relación de agresión-sumisión.

Capitulo 1: En prensa en Evolution.

WHY DO SOME SIBLINGS ATTACK EACH OTHER?
COMPARATIVE ANALYSIS OF AGGRESSION IN AVIAN BROODS

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Abstract.— In many parentally fed species siblings compete for food not only by begging and scrambling, but also by violently attacking each other. This aggressive competition has mostly been studied in birds, where it is often combined with dominance-subordination, aggressive intimidation and siblicide. Previous experimental and theoretical studies proposed several life-history, morphological and behavioral variables that may facilitate the evolution of broodmate aggression, and explain its taxonomic distribution. Here we apply phylogenetic comparative analyses for the first time to test the influence of five hypothesized facilitators of the evolution of broodmate aggression, analyzing 69 species in seven avian families using two quantitative measures of aggression: incidence and intensity. We show that incidence and intensity of aggression increase with long nestling periods and indirect feeding, and small brood size is associated with intense aggression. Large food parcels were not correlated with either the incidence or intensity of aggression. Our study suggests that indirect feeding, long nestling periods and small broods, possibly in combination with other factors, have tended to favor the evolution of aggressive broodmate competition.

Key words.— Sibling aggression, phylogenetic generalized least squares, feeding method, feeding rate, brood size, length of nestling period.

A keystone principle of Darwin's (1859) theory of evolution by natural selection is that individuals compete for limited resources. Such rivalry is not restricted to unrelated individuals (Hamilton 1964), and in species as diverse as insects, mammals and birds, siblings compete for limited parental investment, sometimes even killing opponents and reducing the reproductive success of parents (review in Mock and Parker 1997). Sibling competition has been most studied in birds, which present striking variation in the means by which chicks compete for parental investment. In the majority of species competition is non-violent, involving begging displays and scrambling (Wright and Leonard 2002), but in diverse avian species sibling competition also involves violent attacks (aggressive competition) often combined with dominance-subordination, aggressive intimidation and siblicide (Drummond 2006).

In species with altricial young and aggressive competition, hatching asynchrony confers an age and size advantage to elder broodmates, who establish dominance early in the nestling period through pecking and biting (Drummond et al. 1986). Dominance allows senior chicks to distort the pattern of relative begging and gain feeding priority (Drummond 2002). For instance, in great egrets (*Casmerodius albus*, Mock and Parker 1997), blue-footed boobies (*Sula nebouxii*, Drummond et al. 1986), black eagles (*Aquila verreauxi*, Gargett 1980) and laughing kookaburras (*Dacelo novaeguineae*, Legge 2000) junior chicks have a higher mortality rate than their siblings, due directly (through lesions) or indirectly (forced starvation or expulsion from the nest) to sibling aggression (Mock and Parker 1997; Drummond 2001b). Compared to begging and scrambling, aggression is an especially effective way for elder chicks to control access to food and ensure their own survival and good condition (Drummond 2002).

Why then, do senior chicks of many species limit themselves to begging and scrambling rather than attacking broodmates? Numerous observational and experimental studies involving a diversity of species have analyzed the proximate causes of aggressive competition (e.g. Gargett 1967; Mock 1984; Evans 1996; Drummond and Canales 1998; Machmer and Ydenberg 1998; Legge 2000), yet surprisingly few studies have attempted to identify the ultimate factors favoring the evolution of this behavior (but see Mock 1985; Mock et al. 1987a; Simmons 1988).

Eight traits have been proposed as having facilitated the evolution of aggressive competition: feeding method (monopolizability of food), effective weaponry (pointed or sharp beaks), limited escape possibilities (nest site topography) and differences in age and size of broodmates (hatching asynchrony; Mock et al. 1990); in addition, Drummond (2002) suggested large food parcel size, small brood size, aggressive potential (maturity and body size) and slow food transfer. Here we test four of these hypotheses chosen for their amenability to quantitative analysis, and we propose and test an additional facilitator of the evolution of aggressive competition. First, according to the Feeding method hypothesis (also “Prey size hypothesis”, Mock 1985), selection favors broodmate aggression in species in which food passes directly from the adult’s beak to the chick’s beak (direct feeding), allowing dominants to violently exclude competitors. When food is deposited on the nest floor (indirect feeding) and is accessible to all broodmates, aggression is less effective for monopolizing it than seizing mouthfuls and ingesting them quickly (Mock 1985; Mock and Parker 1997). Many species show a transition in feeding method as sensory and motor capabilities of chicks develop, e. g. from indirect to direct feeding in herons and pelicans, and from direct to indirect feeding in eagles. The feeding method hypothesis predicts greater use of aggression in species where direct feeding predominates throughout the nestling period. The Feeding method hypothesis is supported by descriptive and experimental field studies (Mock 1984, 1985; Mock et al. 1987a, b; but see Drummond 2001a, 2002).

Second, the size of food parcels fed to chicks could affect the profitability of aggressive competition. According to the Food parcel size hypothesis, since aggression is likely to be costlier than mere begging and scrambling, for it to yield a net benefit the food reward for the aggressor has to be high (Drummond 2002). In aggressive species parental food parcels appear to be large and infrequent, and clustered in bouts or meals, resulting in a sizeable payoff for the aggression of dominant chicks (whether they receive food directly or indirectly). Third, brood size probably affects the efficiency of aggression. As brood size increases it may become more difficult and costly to enforce feeding priority by intimidating broodmates and to establish and maintain dominance-subordination relationships (Drummond 2002). Chicks with several broodmates may compete more efficiently by begging and scrambling for parental food deliveries than by trying to intimidate or attack all of them (Brood size hypothesis). Fourth, the aggressive potential of altricial nestlings probably emerges during their physical and behavioral development, and may depend less on the particular weaponry of the species than on body size (Nestling body size hypothesis, Drummond 2002). According to Vogel (1988), striking opponents is a prerogative of large creatures because only they can confer sufficient momentum to the "projectile" to inflict damage. Small nestlings may be unable to compete aggressively simply because their small head (the projectile) and weak neck muscles (which determine the projectile's speed) make them unable to deliver aversive stimuli or inflict damage.

In addition to these four hypotheses, we suggest long nestling periods should favor aggressive competition because the substantial early investment involved in establishing dominance (e. g., Drummond and Osorno 1992) is more likely to be adequately compensated when broodmates cohabit and compete for parentally provided food for a long period. Long nestling periods give more opportunity for serious food scarcity to arise (Nestling period hypothesis).

We use phylogenetic comparative analyses (Martins and Hansen 1997; Freckleton et al. 2002; Blomberg et al. 2003) to test the influence of these five hypothetical facilitators of the evolution of aggressive broodmate competition. Using a maximum-likelihood-based method, we analyze the correlations between two measures of aggressive competition and the five variables: feeding method, food parcel size, brood size, nestling body size at hatching and length of nestling period.

METHODS

Data and phylogeny

We included seven avian families for which sibling aggression has been reported in at least one species, and for which a detailed phylogeny is available: Accipitridae (eagles, hawks and buzzards), Sulidae (boobies), Anhingidae (anhingas), Threskiornithidae (ibises and spoonbills), Ardeidae (egrets and herons), Pelecanidae (pelicans) and Alcedinidae (kingfishers). Only species with brood sizes larger than one were included.

Data on morphometrics (egg size), life history (clutch size, length of nestling period) and behavior (feeding method, feeding rate, incidence of aggression and intensity of aggression) were collected from primary publications and reference books (see Appendix 1/

Supplementary material available online). Brood size at hatching was available for only 19 of the 69 species, so we used modal clutch size as a proxy variable. Brood size and clutch size were highly correlated in those species for which we had data for both variables ($r_S = 0.832$, $P < 0.001$, n = 19 species). We used egg size (egg length x egg breath) as a proxy for nestling body size at hatching, because data on chick mass were not widely available. Egg size and chick mass at hatching were highly correlated in those species for which we had data for both variables ($r_S = 0.946$, $P < 0.001$, n = 25 species). Feeding method was a continuous variable expressed as the proportion of nestling period (from hatching until fledging) during which feeding is direct, ranging from 0 (indirect feeding throughout the nestling period) to 1 (direct feeding throughout the nestling period). For species with a developmental transition in feeding method, we calculated the proportion on the basis of the average age at which chicks switched from one method to the other. Feeding rate was a proxy for Food parcel size, based on the assumption that as the number of meals per day decreases the amount of food per meal will increase and so will parcel size. We did not adjust feeding rate for brood size because the important value, for the evolution of aggression, is the potential payoff for the aggressor, not the expected food amount for the average brood member. Feeding rate was also a continuous variable, calculated as the average daily number of feeding bouts per brood (of average size) divided by the average day length (in hours). Feeding rate varies over the nestling period, so we only used data from studies where observations included the early nestling period, when feeding rates are generally highest (e. g. Fujioka 1985; Drummond et al. 1986) and aggressive competition typically takes place. Average length of the nestling period (days between hatching and fledging) was log_{10} transformed.

We used two response variables: incidence and intensity of broodmate aggression. Incidence of aggression was the percentage of broods in which aggression was reported: 0 for no broods, 1 for 1 - 49% of broods, 2 for 50 - 99% of broods, and 3 for 100% of broods. Intensity of aggression was scored on a 4 point scale by five judges independently, on the basis of qualitative and quantitative descriptions of broodmate aggression in the primary literature: 0 for no aggression observed in any brood, 1 for few fights or few pecks per fight, 2 for an intermediate number of fights or pecks, and 3 for common and/or long fights. The judges were blind in regard to species identity. Scores of the five judges were highly consistent as shown by the pairwise correlations between their scores (r_S range = 0.71 – 0.88, all P values < 0.0001). We used the median of the five judges' scores for each species. The incidence and intensity of broodmate aggression often vary with offspring age (Drummond 2006), but all descriptions of aggressive competition were from studies that included the early nestling period, when most aggression typically takes place. We carried out an extensive search for behavioral studies of the nestling period of each species using primary journals, ornithological books and the reprint collection of the Edward Grey Institute's Library at the University of Oxford, and included only species for which a minimum of 3 broods were observed during at least 5 hours per brood.

Exploratory analyses showed that egg sizes and lengths of nestling period were highly correlated ($r_S = 0.809$, $P < 0.001$, n = 68). To avoid colinearity we excluded one of these variables (egg size). Further analyses (not reported) showed that, when length of nestling period was replaced in the model by egg size, egg size was not correlated with either of our dependent variables.

We constructed a composite phylogeny for the seven families using the most recent and detailed molecular phylogenies available (Fig. 1). For the Anhingidae, Ardeidae, Threskiornithidae, Pelecanidae and Alcedinidae we used Sibley and Ahlquist (1990); for Accipitridae, Wink and Sauer-Gürth (2000) and Lerner and Mindell (2005); for *Buteo*, Riesing et al. (2003); and for Sulidae, Friesen and Anderson (1997).

Comparative analyses

To control for the phylogenetic relationships among species we used Phylogenetic Generalized Least Squares regression (PGLS; Martins and Hansen 1997; Székely et al. 2004), as implemented by COMPARE 4.6b (Martins 2004). PGLS is a linear regression model in which phylogenetic information is incorporated into the error term, thus controlling for the shared evolutionary history among species (Harvey and Pagel 1991; Martins and Hansen 1997). PGLS introduces a single term (alpha; estimated range 0 - 15.5) into the model, which estimates the magnitude of the evolutionary constraint acting on a phenotype (e. g. due to stabilizing selection). Unlike Felsenstein's (1985) Phylogenetic Independent Contrasts (PIC), PGLS does not assume that evolutionary changes follow Brownian motion (Martins and Hansen 1997). For our analyses we set branch lengths to unit values, since we used a composite phylogeny of various sources. Note that the alpha parameter stretches or shrinks branch lengths to fit data at a given phylogeny (Martins and Hansen 1997; Diniz-Filho and Mundim Tôrres 2002; Martins et al. 2002). Zero alpha would indicate unconstrained evolution similar to Brownian motion, thus a PGLS analysis with alpha = zero is tantamount to an analysis undertaken with PIC. An alpha >> 0 (exact value not provided by COMPARE) indicates that there is no phylogenetic signal in the data (star phylogeny). We refrained from using PICs, because our data did not follow Brownian motion (range of alpha = 2.19 – 15.5; see Tables 1 and 2); although values of alpha indicated some phylogenetic component in our variables (Blomberg et al. 2003).

We constructed four PGLS models; two models each for incidence and intensity of aggression. Feeding rate was poorly documented in the avian literature (22 species had a missing value), and since COMPARE cannot deal with missing data we created two datasets. The first dataset included 47 species for which we had data on feeding rates. This dataset included all independent variables. The second dataset included all 69 species and did not include feeding rate. Models 1 and 3 were constructed using the reduced (47 sp) dataset, whereas models 2 and 4 were constructed using the complete dataset.

COMPARE does not calculate the probability of a given partial regression slope (*b*) so we calculated the corresponding *t* value by dividing the regression slope by its standard error (E. Martins pers. com. 2005), and obtained the *P* value using two tailed *t*-distribution with appropriate degrees of freedom (df = n - # of parameters in the model). We report the percentage of variance explained by the model, and the *P*-values of partial regression coefficients. Note that for visualisation purposes, we plot the species-level data in figures, and present the bivariate correlation results as calculated by PGLS.

RESULTS

Incidence of aggression

Model 1 explained 27.18% of the variance (Table 1) and showed that the incidence of aggression decreased with the proportion of direct feeds ($P = 0.006$), contra the Feeding method hypothesis, and increased with length of nestling period ($P = 0.022$; Fig. 2a), as predicted by the Nestling period hypothesis. Furthermore, the incidence of aggression was unrelated to either feeding rate or brood size (Table 1).

The results of Model 2 (19.53% of variance explained) are consistent with those of Model 1: the incidence of aggression decreased with the proportion of direct feeds (although the partial correlation coefficient was only marginally significant, *P* = 0.066), increased with length of nestling period (*P* = 0.013), and was unrelated to brood size (Table 1).

Intensity of aggression

Model 3 explained 34.28 % of the variance (Table 2) and showed that the intensity of aggression decreased with the proportion of direct feeds (*P* = 0.020), contrary to the Feeding method hypothesis, and decreased with brood size (*P* = 0.006, Fig. 3), as predicted by the Brood size hypothesis. Intensity of aggression marginally increased with length of nestling period (*P* = 0.079, Fig. 2b, Table 2), and was unrelated to feeding rate.

The results of Model 4 (25.86% of variance explained, Table 2) were similar to those of Model 3 in that the intensity of aggression decreased with brood size (*P* = 0.030) and increased with length of nestling period (*P* = 0.018). However, the negative relationship between incidence of aggression and feeding method was no longer significant (*P* = 0.10, Table 2).

DISCUSSION

The PGLS models explained a high percentage of the variance (19.5 – 34.3%), especially considering that in this broad phylogenetic study we included seven avian families and the scores for broodmate aggression were based mainly on qualitative descriptions of the behavior since there were only few quantitative studies. Our results confirm that feeding method, length of nestling period and brood size may have influenced the evolution of sibling aggression in the seven families. Aggression was both more common and more intense among species with indirect feeding and long nestling periods, and more intense in species with small broods. Our main results were consistent regardless of which measure of aggressive competition (incidence or intensity) was used.

Feeding rate (a proxy for food parcel size) was not correlated with incidence or intensity of aggression and in preliminary analyses egg size (proxy for nestling body size and not included in our final analyses because of collinearity with nestling period) was not correlated with either measure of aggression. Thus, neither food parcel size nor body size is likely to have influenced the distribution of aggressive competition in the seven families included in the analysis. However, it is possible that our sample did not include species whose food parcels or nestling body size is small enough to make aggression unprofitable or ineffective, respectively. Certainly other avian families include species with considerably smaller food parcels and nestlings. The mildly aggressive common kingfisher (*Alcedo atthis*) was the species with the highest feeding rate included in our analyses, at 3.8 feeding bouts/h (Rivière 1933; Schultz-Waldmann and Dominiak 1971; Hallet-Libois 1986). In comparison, non-aggressive hooded warbler (*Wilsonia citrine*) broods receive 8 feeding visits/ h (Buehler et al. 2002), tree swallow (*Tachycineta bicolor*) broods 15 feeding visits/ h (McCarthy 2002) and starling (*Sturnus vulgaris*) broods 25 feeding visits/ h (Cotton et al. 1996). (Note, however, that House finches (*Carpodacus mexicanus*), which feed chicks with seeds, have particularly low feeding rates among songbirds: 2.68 feeding visits/ h [Hill 2002].) Common kingfishers also have the smallest egg size of all species in our data set (4 g; Schönwetter 1967), compared with 1.6 g for non-aggressive great tits (*Parus major*; Lessells et al. 2002), 1.9 g for barn swallows (*Hirundo rustica*) and 1.9 g for starlings

(Cramp 1998). Hence, it remains possible that aggression is absent from some families of birds not included in this study because food parcels are too small for aggression to be economical or because nestlings are too small for aggression to be effective.

Our results are not consistent with the Feeding method hypothesis: both incidence and intensity of aggression were common in species with indirect feeding. Qualitative descriptions of chick behavior from single-species studies also contradict this hypothesis. It is after the switch from direct to indirect feeding that Eurasian sparrowhawk (*Accipiter nisus*) chicks become more aggressive towards their broodmates (Brown and Amadon 1968), and in broad-winged hawk (*Buteo platypterus*) chicks begin fighting (Matray 1974). There are also three independent reports of aggressive competition during indirect feeding in 3 species of ardeids (Milstein et al. 1970; David and Berrill 1987; Ploger and Medeiros 2004) and, indeed, aggression was common in the indirectly fed great blue herons (*Ardea herodias*) that gave rise to the hypothesis (Mock 1985). Thus, rather than being restricted to species with direct feeding, aggressive competition is increasingly common and intense as species engage in more indirect feeding during the nestling period. Finally, the first empirical test of the Feeding method hypothesis' assumption that aggression is more efficient for securing a large share of food during direct than indirect feeds (Mock and Parker 1997, p. 106) found no support for it in cattle egrets (*Bubulcus ibis*; Gonzalez-Voyer and Drummond in press).

Aggression may be especially effective when chicks compete for food deposited on the nest floor (indirect feeding) because in this location food tends to be simultaneously accessible to all broodmates. Aggression may not enable a single chick to monopolize the deposited prey item, but should be favored if it increases the aggressor's share sufficiently to repay the cost of attacking. By contrast, during direct feeds dominant chicks' usual advantages in body size and motor maturity could often enable them to outreach sibs and seize prey first, reducing the need to resort to aggression. Precocial chicks feeding from the substrate shift progressively from scramble competition to aggressive resource defense as food becomes experimentally concentrated in a smaller patch (Colon Quezada et al. in prep.), and altricial chicks feeding indirectly face a similar situation, competing for a small patch of food on the substrate.

Both incidence and intensity of aggression increased with length of nestling period, supporting the Nestling period hypothesis. Nestling periods of aggressive species ranged from 25 d to 126 d, and 80% of them had nestling periods of >38 d, compared to 50% of non-aggressive species. Aggression is expected to be more common in species with long nestling periods provided aggression is costly to dominant chicks and lengthy cohabitation provides greater opportunity for dominance to yield a benefit. The costs to dominant chicks of establishing dominance include the tissue damage, energy expenditure and foregone feeding opportunities incurred by both the dominant chick and its subordinate sibling throughout the establishment period. Dominance establishment periods can last anywhere from 10 d in laughing kookaburras (Nathan et al. 2001), to 2 - 3 weeks in cattle egrets (Gonzalez-Voyer unpub.) and 3 - 4 weeks in blue-footed boobies (Drummond 2006). However, length of nestling period may not influence the evolution of broodmate aggression in the very small minority of species with obligate siblicide (prompt unconditional elimination of the broodmate), because the period of broodmate cohabitation is very short and the payoff for aggression is guaranteed.

Brood size (our proxy was clutch size) was negatively correlated with both intensity and incidence of aggression, although the latter correlation was not significant. As brood size increases there may be greater risk that while dominant chicks are busy intimidating and excluding broodmates, other broodmates are free to receive the parental feed and thus preempt the dominant chick. Also, hierarchies may be less stable in larger broods if dominant chicks are unable to recognize or gain access to particular individuals and concentrate punishment on them (Drummond 2002). However, our correlations do not allow us to discount the alternative interpretation that causality runs in the other direction and costly sibling conflict selects for parents creating smaller broods (Godfray and Parker 1992).

In our data set, 80% of aggressive species had a modal clutch of 4 eggs or fewer, and 81% of the 21 species with intense aggression (code 3) had a modal clutch of 2 eggs or fewer. The aggressive species with the largest brood size was the common kingfisher, with a modal clutch size of 6.5 eggs and an average brood size of 6.2 chicks (Schultz-Waldmann and Dominiak 1971; Hallet-Libois 1985; Cramp 1998). This may be the species with the largest brood size for which aggressive competition has been reported and its aggression is reportedly atypical: attacks are uncommon and targeted simultaneously by all broodmates on the chick that jumps the feeding queue (Schulz-Waldmann and Dominiak 1971). Aggression may be workable in large broods only in the unlikely circumstance of broodmates coordinating attacks on individuals rather than operating individually.

Reports from field studies indicate that in several species aggression may be more intense in larger broods (e. g. Fujioka 1985; David and Berrill 1987; Mock and Parker 1997), and in cattle egrets aggression decreased when three-chick broods were experimentally reduced by removing the eldest or youngest chick (Mock and Lamey 1991). Such observations appear to indicate that at the proximate level brood size is positively linked with aggression. However, within species, aggression could increase with brood size not as a response to brood size per se but as a result of decreasing per capita food ingestion

(Drummond 2001b). In several species of birds food deprivation elicits increased broodmate aggression (Drummond 2001a), so characterizing the proximate effects of brood size on aggression will require controlling for food ingestion.

It is possible that extra-pair paternity could have influenced the evolution of aggressive competition by reducing relatedness between broodmates and thus indirect costs associated with sibling competition (Hamilton 1964; Briskie et al. 1994). Lack of information on extra-pair paternity for a number of the species included in our analysis prevented us testing this hypothesis.

Although formal reconstruction of ancestral states has not been undertaken, phylogenetic evidence suggests that a parsimonious explanation for the distribution of broodmate aggression involves several independent evolutionary events rather than a single event followed by subsequent loss of aggression in various clades. Sister clades of the eagles, the boobies and anhingas, and the kingfishers are all non aggressive, therefore it is unlikely that all the ancestors of the clades included in our analyses were aggressive. Thus, our correlations suggest traits that favored the evolution of aggressive competition rather than traits that favored its maintenance.

It is probable that, for aggressive competition to evolve, a species must present a combination of factors that make aggression both effective and profitable. Comparison of two sister-clades, the Accipitridae (eagles, hawks and buzzards; excluding species which have single egg clutches, e. g. old world vultures) and the Falconidae (falcons) is informative. Both clades include predatory species with parentally fed altricial chicks. Eighty-one percent of the 58 accipitrids for which information on sibling competition is available are aggressive compared to none of the 52 falconids (Newton 1979). Accipitrids with non-aggressive competition have clutch sizes and nestling periods similar to those of falcons. Sixty percent of falcons and 60% of non-aggressive accipitrids have modal clutches of >2.0 eggs, compared to only 20% of aggressive accipitrids. Only 10% of falcons and 20% of non-aggressive accipitrids have nestling periods of >44 d compared to 60% of aggressive accipitrids (Thiollay 1994; White et al. 1994). In falconids, as in non-aggressive accipitrids, it may be the combination of short nestling periods, large clutches and possibly other factors that has closed the door on the evolution of broodmate aggression. When further data on key traits become available, these sophisticated interactions can be statistically tested.

In conclusion, our study, the first phylogenetic comparative analysis of morphometric, life history and behavioral hypotheses of sibling aggression in any vertebrate, showed that indirect feeding, small broods and long nestling periods are significantly correlated with broodmate aggressive competition. Similar issues have been investigated in parasitoid wasps, although selective forces favoring aggression probably differ between birds and parasitoids (Mayhew 1998; Pexton and Mayhew 2001). We failed to confirm a link between aggression and large food parcels. Because our dataset was limited to families with altricial, parentally fed chicks that include at least one aggressive species, we are reluctant to extrapolate results to avian clades where there are no aggressive species. However, it is possible that direct feeding, short nestling periods and large broods in combination with other factors not included in our analyses may have impeded the evolution of aggressive competition in other clades such as the passerines, falconids and phalacrocoracids (cormorants). Our models explained 19.5 – 34.3 % of variance in use of aggression, even though their explanatory power was probably limited by coarse scale of the behavioral variables. Additional factors, not considered here, combined with indirect feeding, long nestling periods and small broods may improve the predictive power of the models.

Correlational methods such as PGLS cannot identify cause and effect, therefore further comparative studies based on directional phylogenetic methods are needed to identify the sequences of events that ultimately led to sibling rivalry (Pagel 1994).

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Table 1. Multiple regression models of incidence of aggression (response variable) when controlling for phylogeny using PGLS. Partial regression coefficients (β) ± standard errors and their significances are shown. NA indicates variable not included in the model. Statistically significant correlations are underlined.

	Model 1		Model 2	
	β ± SE	*P*	β ± SE	*P*
Explanatory variables				
Clutch size	-0.15 ± 0.17	0.38	-0.13 ± 0.16	0.42
Feeding Method	-1.50 ± 0.52	0.006	-0.88 ± 0.47	0.066
Feeding Rate	0.17 ± 0.19	0.38	NA	NA
Length of nestling period	2.35 ± 0.99	0.022	2.49 ± 0.97	0.013

Notes

Model 1 included 47 species, alpha (see Methods) = 6.85 and explained 27.18 % of variance.

Model 2 included 69 species, alpha = 15.50 and explained 19.53% of variance

Table 2. Multiple regression models of intensity of aggression (response variable) when controlling for phylogeny using PGLS. Partial regression coefficients (β) ± standard errors and their significances are shown. NA indicates variable not included in the model. Statistically significant correlations are underlined.

	Model 3		Model 4	
	β ± SE	*P*	β ± SE	*P*
Explanatory variables				
Clutch size	-0.38 ± 0.13	<u>0.006</u>	-0.31 ± 0.14	<u>0.030</u>
Feeding Method	-1.02 ± 0.42	<u>0.020</u>	-0.68 ± 0.41	0.10
Feeding Rate	0.16 ± 0.15	0.29	NA	NA
Length of nestling period	1.44 ± 0.80	0.079	2.07 ± 0.85	<u>0.018</u>

Notes

Model 3 included 47 species, alpha (see Methods) = 2.19 and explained 34.28 % of variance

Model 4 included 69 species, alpha = 8.06 and explained 25.86% of variance

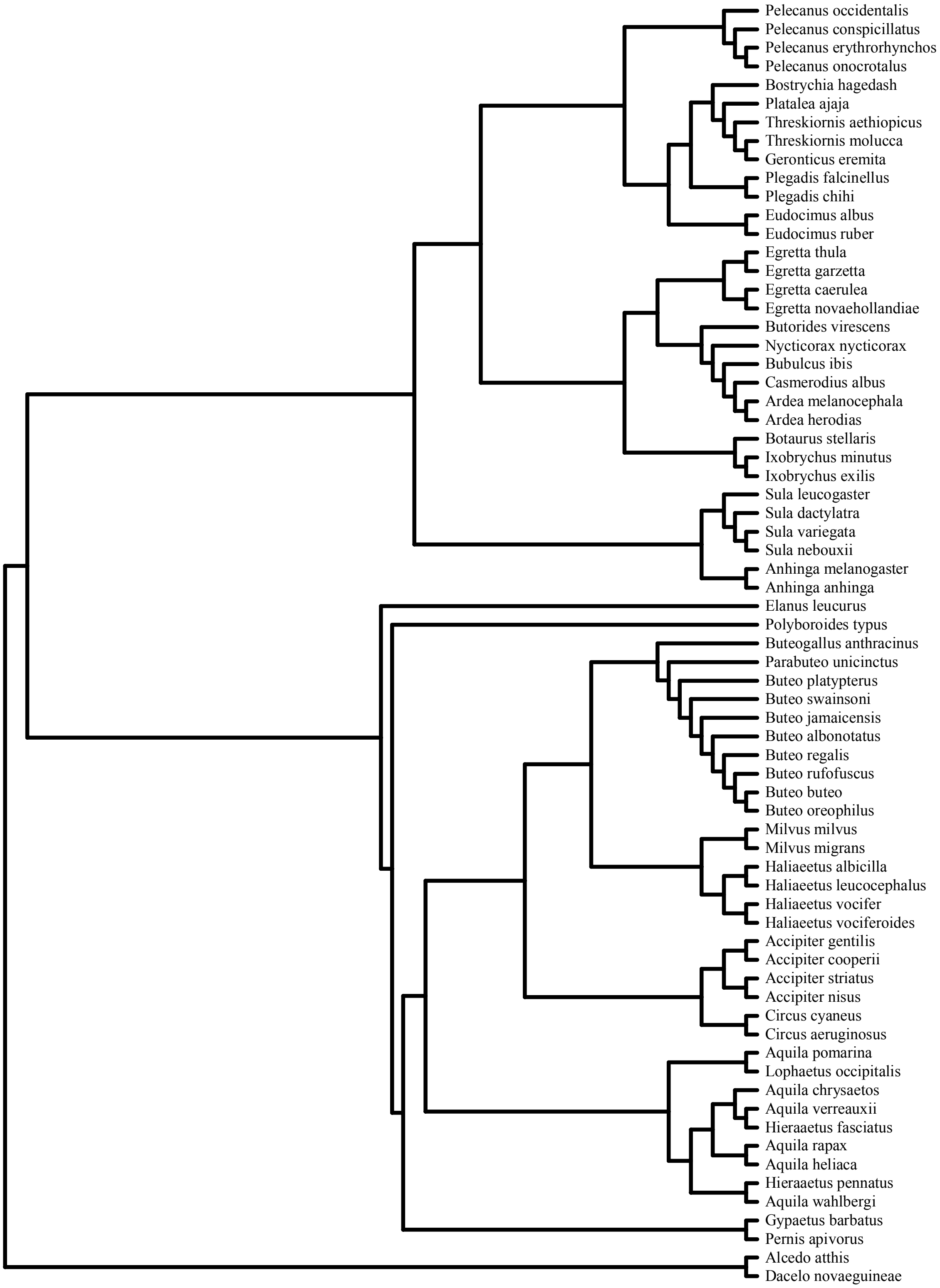

Fig 1. Composite phylogeny of 69 species (7 avian families) used in the comparative analyses.

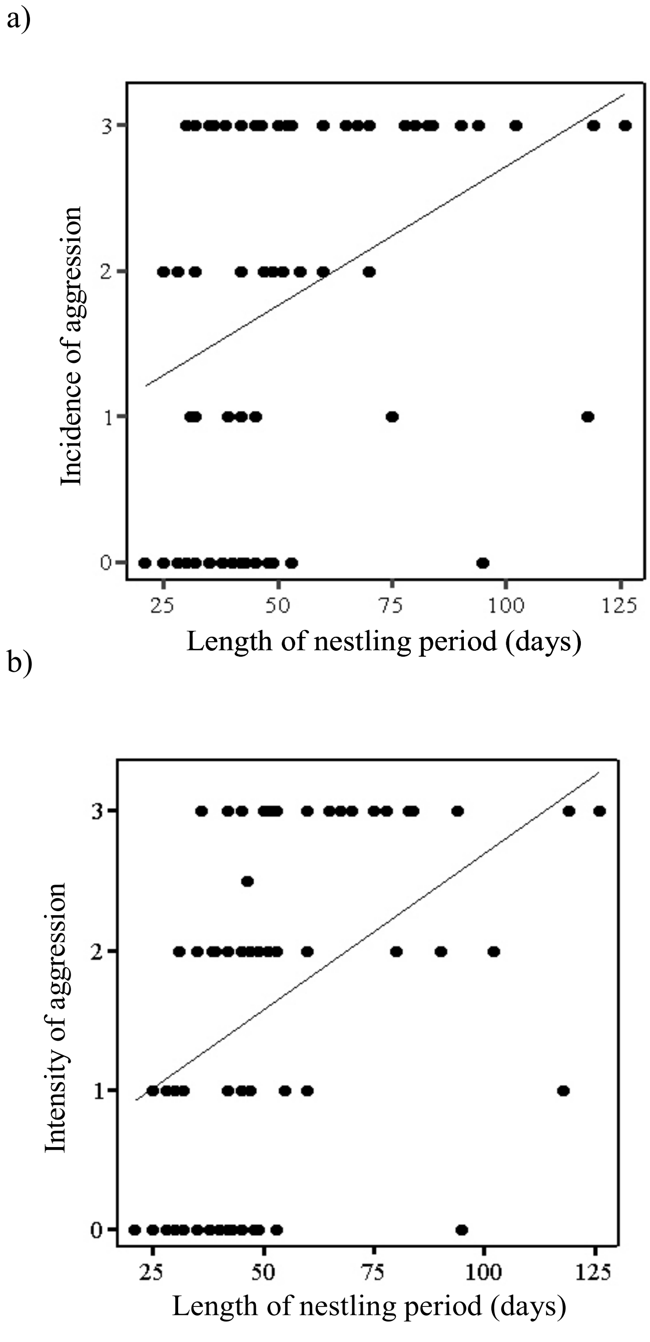

Fig 2. Length of nestling period in relation to (a) incidence of aggression (PGLS: r^2 = 0.150, P = 0.001, n = 69), and (b) intensity of aggression (PGLS: r^2 = 0.175, P = 0.0003, n = 69). Standard least squares regression line fitted, without phylogenetic control, for illustrative purposes.

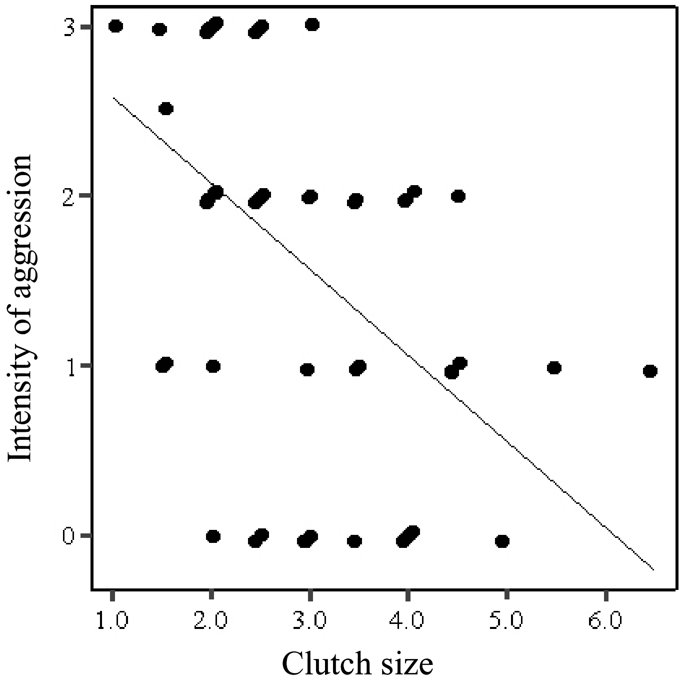

Fig 3. Clutch size (a proxy variable corresponding to brood size at hatching) in relation to the intensity of aggression (PGLS: $r^2 = 0.133$, $P = 0.002$, n = 69). Cloud is jittered because of overlap of data points. Standard least squares regression line fitted, without phylogenetic control, for illustrative purposes.

Capitulo 2: En prensa en Behaviour

Is broodmate aggression really associated with direct feeding?

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Abstract

The Feeding Method hypothesis (FMH) proposes that the way parents transfer food to chicks influences whether broodmates compete for it aggressively or non-aggressively. The FMH assumes that aggression is more efficient for securing a large share of food when prey items pass from bill to bill (direct feeds) than when prey is deposited on the nest floor (indirect feeds). In species with a developmental transition from indirect to direct feeding, the hypothesis predicts more aggression during direct than indirect feeds and an increase in rates of aggression as feeding becomes increasingly direct. We quantified development of aggression and feeding in two-chick cattle egret (*Bubulcus ibis*) broods in order to test the FMH's assumption and its two developmental predictions. We also examined whether changes in rates of aggression early in the nestling period are better predicted by the Feeding Method, Food Amount or Early Dominance Establishment hypotheses. Neither the assumption nor either of the predictions of the Feeding Method hypothesis was supported and, if anything, senior broodmates were more aggressive early in the nestling period when feeding was indirect. These observations cast doubt on the ultimate influence of feeding method on use of aggression and, especially, on the role of direct feeding as a proximate trigger for aggression. Rates of aggression better fitted the temporal patterns predicted by Early Dominance Establishment and Food Amount hypotheses.

Keywords broodmate aggression, feeding method, food amount, dominance, submission, cattle egret.

Introduction

In parentally fed avian species, broodmates generally compete for limited parental food by begging and scrambling (Rydén & Bengtsson, 1980; Royle et al., 2002), but in a diverse minority of species competition also involves pecking and biting (Mock & Parker, 1997; Drummond, 2002). In these aggressive species hatching asynchrony confers a competitive advantage to elder chicks and a dominance hierarchy is established early in the nestling period (Drummond et al., 1986; Mock & Parker, 1997). Senior chicks (first-hatched in a brood) intimidate younger siblings and exclude them from parental feeds, thereby obtaining more than their share of food (Mock, 1985; Ploger & Mock, 1986; Drummond, 2002). Aggression can lead to death of younger siblings through forced starvation, expulsion from the nest or lesions (Mock, 1985; Mock & Parker, 1997; Drummond, 2001a).

Parents transfer food to chicks either indirectly, by depositing whole, pre-digested or dismembered prey items on the nest floor, from where chicks peck or tear pieces they can swallow, or directly, from parental bill to chick's bill. According to the Feeding Method hypothesis (Mock, 1984; Mock, 1985), selection favours the use of aggression by species with direct feeding, provided chicks have the ability to constitute a potential threat to one another and parentally provided food is limiting. Although the hypothesis appeared to propose that the size of the prey transferred to the chick influences aggression (presented as Prey Size hypothesis: Mock, 1985), it is the method of transfer (feeding method) that is the key factor. Hence, the hypothesis is purportedly supported by sibling aggression in some large predatory species, such as boobies, pelicans and raptors, in which parents predigest or dismember large prey and deliver them in small parcels into chicks' beaks (Mock, 1985). For this reason, the Prey Size hypothesis was reassessed and labeled the Feeding Method hypothesis (Drummond, 2001b). According to the hypothesis, at the ultimate level feeding method has determined the distribution of siblicidal aggression among species and at the proximate level feeding method acts as a trigger for use of aggression (Mock, 1984).

The Feeding Method hypothesis hinges on the untested assumption that aggression is more efficient for securing a large share of food during direct feeds than during indirect feeds (e.g., Mock & Parker, 1997, p. 106). Supposedly, when food comes directly from the parent, intimidation of competitors yields exclusive access to the parental bill and bolus; when food is on the floor, it is equally available to all and success depends on handling speed (Mock and Parker, 1997, p. 103). Several species, including some ardeids and pelicanids, show a developmental change in feeding method. Young chicks are initially fed indirectly, then as they grow and mature they switch progressively to catching boluses directly from the parental bill (Mock, 1985; Ploger & Mock, 1986; Pinsón & Drummond, 1993). From this follows the prediction of a proximate effect of feeding method: chicks will facultatively adopt either aggressive or non-aggressive competition according to whether food is provided directly or indirectly. "The logic of the hypothesis also requires that any changes in fighting be accompanied by a switch to the appropriate feeding techniques (and degree of food control). Embedded in this approach is the tacit assumption that the birds possess sufficient developmental flexibility to make such adjustments, that is, to modify their behavioural ontogeny radically as a function of the cue" (Mock & Parker, 1997, p. 116).

Support for the Feeding Method hypothesis comes from two descriptive studies and an experiment comparing aggression of indirectly fed and directly fed broods in two ardeid species (Mock, 1984; Mock, 1985; Mock et al., 1987a). However, the studies have been criticized, among other reasons because they failed to control adequately for food deprivation and because some of their results actually contradict the Feeding Method hypothesis (Drummond, 2001a). To date no study has tested the hypothesis' assumption that aggression is more profitable during direct feeds than during indirect feeds. Furthermore, although the ardeid studies supporting the hypothesis documented temporal changes in feeding method, they did not analyse temporal variation in rates of aggression nor relate changes in aggression to changes in feeding method.

The scarce developmental data available do not appear to support the prediction of a proximate effect of feeding method on use of aggression. Great egret and great blue heron chicks fought vigorously during their first month of life despite being indirectly fed (Drummond, 2001b), and there was no evidence for increased aggression by brown pelican (*Pelecanus occidentalis*) chicks as their feeding switched from indirect to direct (Pinson & Drummond, 1993).

The assumption that aggression is more profitable during direct feeds than during indirect feeds and the developmental prediction that rates of aggression should increase as feeding becomes increasingly direct can both be tested by quantifying feeding and aggression during the developmental change in feeding method. However, any such analysis must also take into account additional potential influences on rates of aggression, such as food amount and establishment of dominance which could provide alternative explanations for changes in the patterns of aggression. The Food Amount hypothesis (Mock et al., 1987a; Drummond, 2001a) predicts that a dominant nestling's aggression will increase as its food ingestion declines. In the majority of bird species, daily food requirements of chicks increase with age to a maximum about midway through growth and then either decline or plateau (Weathers, 1996). When a brood's food requirements are at their maximum and parents probably have most difficulty satisfying them, nestling aggression is likely to be exacerbated by underfeeding (somewhat paradoxically, because ingestion is at its developmental peak). It is unresolved whether food amount has a proximate influence on aggression in ardeid species as it does in some other avian species (Drummond, 2001a; cf. Mock et al., 1987a,b), and only one ardeid study clearly shows that poorly fed individuals are more aggressive (Creighton & Schnell, 1996).

According to the Early Dominance Establishment hypothesis, elder chicks attack their broodmates early in the nestling period to establish the dominance relationships that will ensure their feeding priority later on (Mock, 1985; Pinson & Drummond, 1993; Drummond, 2006). Mock & Lamey (1991) suggested that aggression in ardeid broods declines during the first 3 weeks due to the establishment of dominance relationships. The hypothesis predicts that aggression should first increase sharply as senior hatchlings develop their aggressive potential, then peak and decline to a low level after dominance-subordination is established. It also predicts that rebelliousness of junior chicks (i.e., aggressive resistance of the senior chick's bid for control) should show an early increase, peak and decline. Rebelliousness of junior ardeid chicks could be expressed by: (1) more total pecks per fight (summing pecks of both chicks) if juniors peck back when attacked or require more pecks to respond with submission, (2) junior chicks initiating a greater proportion of fights or (3) a higher proportion of pendulum fights (two chicks facing each other, at close range, pecking in turns, Milstein et al., 1970).

Cattle egret (*Bubulcus ibis*) chicks compete aggressively for parentally provided food and switch progressively from indirect to direct feeding as they develop (Ploger & Mock, 1986). Both parents care for chicks, which fledge on average at 32 days of age (Martínez-

Vilalta & Motis, 1992). Broods in Texas were fed an average 5.2 boluses in each of 3.0 meals per day (Ploger & Mock, 1986). Violent aggression between broodmates involves mainly pecks, but also bites. Mortality of last hatched chicks is common. In three-chick broods, 67% of last-hatched chicks died in 15 broods in Texas (Ploger & Mock, 1986), 33% in 100 broods in Oklahoma (Mock & Parker, 1997) and 85% in a South African population (Siegfried, 1972). In 161 two-chick broods of a South African population, 15.8% of chicks died before fledging and 61% of deaths were attributed to starvation (Siegfried, 1972).

We report the first quantification of developmental variation in rates of aggression in an ardeid. Our study examines the ultimate influence of feeding method on aggressive competition by testing whether aggression secures for chicks a larger proportion of food during direct than indirect feeds. It also examines the proximate influence of feeding method on aggressive competition by testing whether aggression is greater during direct than indirect feeding and whether it increases as feeding becomes increasingly direct. Finally, it examines whether temporal changes in rates of aggression are better predicted by the Feeding Method, Food Amount or Early Dominance Establishment hypotheses.

Methods

From mid-June until the end of July 2003, four observers studied cattle egret broods in a dense, mixed species colony, on a 12 by 15 m mangrove (*Rhizophora mangle*) islet in a coastal brackish lagoon at La Mancha, Veracruz, Mexico (19º 24′ N and 96º 24′ W).

Twenty nine accessible nests were selected and individually marked with numbered plastic tags, mostly between clutch completion and hatching but in two cases after the eggs had hatched. Average clutch size before hatching was 2.71 eggs (range=1-5) and 2.00

chicks hatched per nest on average (range=1-3, *n*=28 nests). In the nests marked before hatching, first and second chicks hatched 2.29 days apart (range=1-7 d, *n*=14 clutches), while second and third chicks hatched 2.00 days apart (range=1-3, *n*=6 clutches). We observed behaviour in nine young and visually accessible two-chick broods of the sample, after marking chicks on the crown and rump with non-toxic acrylic paint: red for first hatched (senior) and black for second hatched (junior) chicks. Color marks have no apparent effect on dominance hierarchies or other behaviour of chicks (Ploger & Mock, 1986).

Observations were made from three floating wooden towers (observation nests were at or below observer eye-level) stationed 16–17 m from the edge of the colony. Egrets were habituated to the daily activities of the fishermen in the lagoon and observers did not appear to affect their behaviour. All nine broods were observed during two 3-hour periods (0730–1030 h and 1600–1900 h) on a daily basis from completion of hatching (mean: 5.6 d of age of the senior chick, range=4–11 d) until the senior chick was 20 d old, except when it rained. Each observer watched a maximum of three broods simultaneously. Preliminary observations showed that egret activity levels varied little between midday, morning and afternoon periods, thus the two three-hour observation periods allowed representative sampling of daily activity.

Observers recorded all feeding bouts and fights, largely following the sampling methods of Mock (1985) and Ploger & Mock (1986). (Those studies focused on larger broods, but the relevant hypotheses and methods are not brood-size specific.) For each food delivery observers noted the size of the bolus (classified from 1 to 4) by comparing it with the length of the adult's beak, the visually estimated proportion (in tenths) of the bolus ingested by each chick and the feeding method of each chick (indirect or direct). We multiplied the proportion of each bolus ingested by a particular chick by the bolus size and summed across all boluses delivered during the bout to obtain the “food amount units” (FAU) ingested by each chick during each bout. A bout began when the adult regurgitated the first bolus and ended when no more boluses were regurgitated during 10 min. We regarded a feeding bout as indirect if at least 70% of boluses touched the nest floor before being ingested by one of the chicks or direct if at least 70% of boluses were taken from the adult’s beak. These criteria are broader than the criteria based on a value of 80% used by Mock (1985) for a different purpose: dividing the nestling period into phases. Using criteria based on 70% rather than 80% enabled us to increase sample sizes for analyzing the assumption of the feeding method hypothesis; it had no influence on the direction of differences found and had little influence on their magnitude.

We registered a peck when a chick forcefully made contact with its beak on any part of a broodmate’s body and a bite when a chick pressed any part of a broodmate’s body between its mandibles. Summed pecks and bites are referred to as attacks. A fight began with the first attack and ended when attacking did not occur for at least 10 s. For each fight, observers noted which chick attacked first and the number of attacks delivered by each chick. Observers also noted whether each fight took place during a feeding bout, that is, if it took place within one min before the first bolus was delivered or within 10 min after the last bolus was delivered.

The three measures of junior chick rebelliousness were calculated for each brood on each day: (1) proportion of fights initiated by the junior chick is the number of fights where the junior attacked first divided by total fights, (2) proportion of pendulum fights is the number of pendulum fights divided by total fights and (3) fight length is the number of attacks per fight.

We tested the assumption that aggression is more efficient for securing large shares of food during direct feeds than during indirect feeds using only senior chicks (the main aggressors). Feeding bouts were classified as "with attacks" when seniors pecked or bit their broodmate at least once during the bout. We calculated the average proportion of FAUs ingested by each senior chick for all of its indirect feeds with and without aggression as well as for all of its direct feeds with and without aggression for each day. However, not all broods presented feeding bouts of all four categories, thus sample sizes (numbers of broods) in our comparisons varied.

All statistical comparisons involved the mean of several behavioural scores for either the junior or the senior chicks of each of several broods, and sample sizes given are the numbers of broods included in each analysis. We present means and standard errors except when non-parametric analyses were used, when we present medians. Averages presented in Results are calculated across broods. For example, the average age when senior chick rate of aggression peaked was based on the average of the nine ages at which each of the nine senior chicks reached its individual peak. On the other hand, graphs show, for each chick age on the X axis, the average of the behavioural scores (e.g., number of attacks) of all seniors or juniors observed at that age, with the exception of Figure 2. Note that the age at which a behavioural peak or inflection occurred for the total sample shown in the figures is not necessarily the same as the mean of the peaks and inflections of the *n* individuals in the sample.

For parametric analyses yielding non-significant results, we present 95% confidence intervals (95% CI) for the difference between means rather than the power of the test, as suggested by Hoenig & Heisey (2001) and Colegrave & Ruxton (2003). If a comparison between two samples is non-significant, the 95% CI includes zero. As the samples become increasingly different the CI becomes wider and more asymmetric around zero.

Results

There was no mortality in any of the 9 observation broods, at least until 20 d of age of the senior chick. In thirty percent of the marked broods at least one chick died: one of 7 single-chick broods, 3 of 17 two-chick broods and all 5 three-chick broods were reduced.

In all 9 observation broods, chicks competed aggressively and both seniors and juniors attacked and initiated fights. We observed 0.48±0.07 fights/h during the nestling periods of the 9 broods (ages 4–20 d), and junior chicks initiated 11.9±2.3% (range=2.7–25.6%, *N*=9) of the fights in their broods. Pendulum fighting occurred in 16.1±3.7% (range=2.3–31.8%, *N*=9) of observed fights, mostly between 8.3 and 12.6 d of senior chick age. Juniors, and on some rare occasions seniors, conceded fights by fleeing or, more often, by crouching in the bottom of the nest, after which attacks stopped. Both senior and junior chicks participated in all feeding bouts, and did so by begging and scissoring the parental bill.

Chicks in all nine broods fed indirectly at first then switched progressively to direct feeding. The transition took about four days, with senior and junior chicks, respectively, starting to switch at ages 7.7±0.42 d and 7.3±0.41 d and feeding predominantly directly (>70% of boluses taken directly) by ages 12.1±0.73 d and 11.4±1.1 d (*N*=9; see Figure 1). From age 5.6 d (range 4–11 d) until age 20.0 d, the nine senior chicks ingested 13.8% more food than their junior broodmates (median senior=1.24 FAU/h, junior=0.94 FAU/h; Wilcoxon matched pairs: *Z*=2.67, *N*=9, *P*=0.008). When we compared seniors and juniors at the same age (from 4 to 18 d of age), thus controlling for the potentially confounding effect of age differences due to asynchronous hatching, senior chicks ingested 17.3% more food than junior broodmates (average senior=1.49 FAU/h, junior=1.05 FAU/h; Paired *t* test: *t*8=3.47, *P*=0.008).

Seniors attacked their junior broodmates 5.8 times more often than *vice versa* (median attacks by senior=0.9 attacks/h, attacks by junior=0.2 attacks/h; Sign test: *P*=0.039, *N*=9). In a single brood this trend was reversed, with the junior chick attacking 1.2 times more often than its senior broodmate, while the senior ingested only 2.7% more food despite being one day older than the junior chick. Average rates of aggression were higher in our population than those reported in previous studies: 0.1 attacks/h by the A-B dyad (eldest and second hatched chicks) and 0.2 attacks/h by the B-C dyad (second and third hatched) in a Texas population observed until the senior was 25 d old (Ploger & Mock, 1986) and 0.02 *fights* per day in two-chick broods of a Japanese population observed until the senior was about 60 d old (Fujioka, 1985).

Feeding Method hypothesis

Contrary to the critical assumption of the Feeding Method hypothesis, seniors did not ingest a larger proportion of food during direct feeding bouts with attacks (mean=58%) than during direct bouts without attacks (mean=60%; *t* test: *t*8=-0.21, *P*=0.84, 95% CI of difference between means: -0.28–0.23; Figure 2). This result was unchanged when we restricted the sample to the period when intimidation of the junior chick presumably was largely established, after age 7d of the senior chick (respective means 62% and 55%; Mann Whitney U= 18.5, *P* = 0.61, *N* = 14). More importantly, seniors did not ingest a larger proportion of food during direct bouts with attacks (mean=58%) than during indirect bouts with attacks (mean=56%; *t* test: *t*6=-0.83, *P*=0.44, 95% CI of difference between means: -0.30–0.15; Figure 2). Finally, senior chicks did not ingest a larger proportion of parentally provided food during indirect feeding bouts with attacks (mean=56%) than during indirect bouts without attacks (mean=61%; *t* test: *t*8=1.02, *P*=0.34, 95% CI of difference between means: -0.75–0.19; Figure 2). Although sample sizes were small for these comparisons, mean values were surprisingly similar for all categories, variance was relatively low and the 95% CI of difference between means were narrow and relatively symmetric around zero. We could not test whether the increase in proportion of food ingested achieved using aggression during indirect feeds was smaller than the increase in proportion achieved through aggression during direct feeds because we had insufficient broods where we had observations of both indirect and direct feeds with and without aggression. In any case, the means shown in Figure 2 hold out little prospect of there being such a difference.

Contrary to the main prediction of the Feeding Method hypothesis, senior chicks were just as aggressive during (predominantly) indirect feeding bouts (median=0.08 pecks/bout) as during (predominantly) direct feeding bouts (median=0.00; Mann-Whitney *U* test: *U*=34.5, *N*=8, *P*=0.89). Furthermore, temporal changes in rates of aggression did not parallel changes in feeding method: aggression increased and peaked before feeding became predominantly direct and by the time feeding was predominantly direct, rates of aggression were close to zero (Figure 3). Finally, when we compared overall senior chick rates of aggression (during and outside feeding bouts) early in the nestling period, when bouts were predominantly indirect (5–8 d of senior chick age), with overall senior chick rates of aggression late in the nestling period, when bouts were predominantly direct (16–19 d of senior chick age), seniors were 28 times more aggressive during the indirect feeding period (1.12±0.49 attacks/h) than during the direct feeding period (0.04±0.03attacks/h), although the difference fell short of significance (Paired *t* test: *t*6=2.16, *P*=0.074, 95% CI of difference between means: - 0.43–6.88).

Other hypotheses

As predicted by the Food Amount hypothesis, the peak in the senior chick's rate of aggression, at 10.6±1.3 d of senior chick age, coincided with the peak in food ingested by the brood, at 9.9±0.7 d, and aggression declined roughly when ingestion declined (see Figure 4). The difference between peak ingestion and peak aggression in each brood did not differ significantly from 0 (One sample *t* test, *t*7 = 1.58, *P* = 0.879, 95% CI of difference between means: -1.74–1.99; one brood excluded because observations initiated at 11d of senior chick age).

As predicted by the Early Dominance Establishment hypothesis, senior and junior chick rates of aggression peaked early in the nestling period, then declined and remained low (Figure 5). The nine senior chicks began attacking their broodmates at age 6.3±0.7 d and their aggression rate peaked at age 10.6±1.3 d, after which it declined and remained at a consistently low level (0.96±0.22 attacks/h from 12 to 20d of age, *N*=9). After dominance was established attacks were mostly unidirectional, juniors rarely being aggressive (pers. obs.). Junior chicks also began attacking at an early age (6.0±0.5 d; *N*= 9), even initiating fights as early as 4 d old in 3 cases, and their rate of aggression peaked at 7.0±0.5 d (*N*= 9). Our three measures of junior chick rebelliousness showed similar temporal patterns: fight length, proportion of pendulum fights and proportion of fights initiated by the junior chick all showed an early increase and peak followed by a decline as chicks got older (Figure 6). The nine brood average peaks for fight length, proportion of pendulum fights and proportion of fights initiated by the junior chick occurred at similar ages of the senior chick (10.5±1.13 d, 10.44±0.73 d and 9.56±1.13 d, respectively, *N*=9). Note that the average age at which our three measures of junior rebelliousness peaked coincides closely with the average age at which senior chick aggression peaked (10.6±1.3 d, *N*=9), and that senior chick aggression decreased to consistently low levels at the same time as junior chick rebelliousness subsided (see Figure 6).

Eight of the nine broods showed similar temporal patterns of change in rate of senior chick aggression, with peaks occurring at similar ages of the senior chick. In the only brood that differed, the pattern of temporal variation in rates of aggression was similar but the increase, peak and decline occurred between the ages 12–16 d of the senior chick. The apparently bimodal pattern of junior chick rebelliousness in Figure 6 results not from individual broods showing a bi-modal pattern but from individual broods peaking at different ages (7–11 d of the senior chick).

Discussion

Senior chicks enjoyed a clear feeding advantage, ingesting 13.8% more food than junior broodmates throughout the nestling period (4–20 d of senior chick age). Even when we controlled for age differences due to hatching asynchrony the difference remained significant. Aggressive superiority throughout the nestling period was demonstrated by senior chicks attacking broodmates nearly six times more than *vice versa*.

Feeding Method hypothesis

The assumption that aggression should be more efficient for increasing the aggressor's share of food during direct feeds than during indirect feeds was not supported. First, senior chicks using aggression did not obtain a greater proportion of food during direct than indirect feeds, even though most direct feeds occurred after the dominance-subordination relationship was established and most indirect feeds occurred before it was established. However, we cannot rule out that the relative inefficiency of scrambling competition might have been obscured by the large competitive asymmetries between chicks at the early ages when such competition occurred. By the time dominance was established, the large disparity in size and maturity of the broodmates may have largely disappeared and *continuation* of senior chick's feeding advantage may have depended on their use of aggression. Second, use of aggression during direct feeding did not secure a greater proportion of food, even when the sample was restricted to ages when intimidation of junior chicks was largely established (after the senior chick's peak in aggression). We can be confident that aggression during feeding bouts had little positive effect on how much food the aggressor obtained because the small non-significant differences between our sample values were in the direction opposite to that assumed by the hypothesis, and because the confidence intervals for difference between means were narrow and symmetrical around zero. However, priority of senior chicks during feeding bouts when no aggression was used may have depended on the intimidation effect of their earlier aggression. Third, the benefits of using aggression could be obscured if senior chicks selectively use aggression during bouts when their expected share of food is low while simply scrambling for food when their expected share is high. In sum, our observations cast doubt on the assumption that aggression is more efficient for achieving feeding priority during direct feeds than during indirect feeds but are insufficient to dismiss it.

Our results also failed to support the Feeding Method hypothesis' developmental prediction that as the proportion of direct feeds increases the frequency of aggression will also increase. Over the range of ages studied, senior chicks were not more aggressive during direct feeding bouts than during indirect bouts and rates of aggression did not increase as feeding became increasingly direct. Indeed, if anything, senior chicks attacked more frequently in the early nestling period when fed indirectly than later on when fed directly, although the difference fell short of significance. This result argues against direct feeding being a proximate cue for increased use of aggression. Even if direct feeding is an ultimate cause of broodmate aggression, it seems that direct feeding has little or no proximate influence on use of aggression. Our results suggest that during the period when altricial chicks undergo profound developmental changes in sensory and motor abilities, and in social relations, use of aggression is largely under the control of factors other than feeding method.

Might this evidence against the feeding method hypothesis have been obtained using broods of a size that the hypothesis does not apply to? Broods of two might tend to be better fed and show less aggression and siblicide than the broods of three originally studied by Ploger & Mock (1986), and aggression might become an effective way of competing for food on the floor when there is only one competitor. The idea that two-chick cattle egret broods are too well fed for serious competition to occur did not hold for a previous study with a tropical population where two-chick broods showed significant starvation mortality (Siegfried, 1972), nor does it apply to our population, where juniors were clearly outcompeted by seniors, receiving 14.7 % less food at the same age. Furthermore, the Feeding Method hypothesis does not require that aggression be severe enough to lead to siblicide, only that aggression enable privileged access to food (see, for example, Mock & Parker's, 1997, p. 115, application of the hypothesis to the magpie goose, *Anseranas semipalmata*). Finally, total attack rates in our broods (2.18 attacks/h) were 14 times higher than those reported for the dyad with most aggression (2nd and 3rd hatched chicks) in the three-chick broods studied by Ploger & Mock (1986; 1.6 attacks/fight x 1.4 fights/14h = 0.16 attacks/h). The idea that the hypothesis does not apply to two-chick broods because aggression becomes an effective way of competing for indirect feeds when the number of competitors falls to one is inconsistent with previous claims. For example, it is usually claimed that aggression in two-chick broods of the (direct-feeding) blue-footed booby (*Sula* *nebouxii*) and some two-chick raptors supports the hypothesis (e.g. Mock et al., 1990). We are not aware of evidence for any species showing that aggression during indirect feeds becomes effective when there is only one competitor.

Our results add to the evidence from studies of pelicans and other ardeids suggesting that aggression is not exclusively associated with direct feeding and not more effective for skewing food allocations during direct than indirect feeding (Milstein et al., 1970; David & Berrill, 1987; Pinson & Drummond, 1993; Ploger & Medeiros 2004; but see Fujioka, 1985). In sum, descriptive studies of five avian species cast doubt on the suggestion that aggressive exclusion is associated with direct feeding and hence raise doubts as to whether feeding method has a proximate influence on the use of aggression in broodmate feeding competition.

Other hypotheses for development of agonism

If food shortage provokes aggression, rates of aggression should be highest at ages when competition for food is expected to be most acute, and indeed senior chick aggression peaked at the age when estimated food ingestion by the brood also reached its maximum (senior ages when aggression and ingestion peaked: 10.6±1.3 d and 9.9±0.7 d, respectively). Other cattle egret populations have also shown a peak and decline in food ingestion during the nestling period, at variable ages of the senior chick: 20-29 d in a Japanese population observed to age 60 d (Fujioka, 1985) and 10-16 d in a US population observed to age 25 d (Creighton & Schnell, 1996). Similar peaks roughly half-way through the nestling period have been reported in little egrets (*Egretta garzetta*), at 7–11 d (Inoue, 1985), white-tailed tropic birds (*Phaethon lepturus*; Ramos & Pacheco, 2003) and shy albatrosses (*Thalassarche cauta*; Hedd et al., 2002).

We assumed that when food ingestion by the brood is maximal parental work load also peaks and underfeeding becomes more likely. This assumption is supported by senior chick aggression in a Japanese cattle egret population which peaked when food provision to the brood was highest, although this did not occur until age 20–29 d (Fujioka, 1985). Although experimental studies with five different species have demonstrated that a food shortage elicits increased broodmate aggression (review in Drummond, 2001b; Osorno & Drummond, 2003), in ardeids the possible influence of food on aggression is unresolved (Mock et al., 1987 a,b; Mock and Lamey, 1991; Creighton and Schnell, 1996; Drummond, 2001b). Our indirect and correlational evidence merely shows that Food Amount is a viable candidate explanation for the observed temporal pattern in aggression.

Dominance was established in all broods by violent pecking and biting, and establishment of dominance could account for the early onset, peak and subsequent decline in agonism. Senior chicks began attacking their broodmates when 6.3 d old and their rate of aggression peaked four days later. Juniors violently resisted the establishment of a dominance-subordination relationship, pecking back when attacked and even initiating fights at ages as young as 4 d (cf., Fujioka, 1985). All three measures of junior chick rebelliousness peaked at average senior chick ages 9.5–10.5 d. Some fights ended when a submissive display by junior chicks (not quantified) appeared to inhibit attacking by seniors: crouching with neck stretched horizontally on the nest floor. When attacks were particularly violent, submissive chicks sometimes flapped their wings while crouching. All of these observations are in accordance with early establishment of a dominance-subordination relationship of the aggression-resistance type (Drummond, 2006), followed by relaxation after successful establishment. In particular, the almost simultaneous decrease in both senior chick rate of aggression and junior rebelliousness at about age 8–10 d, along with the presence of submissive displays, strongly suggests that dominance-subordination relationships were established. This pattern coincides with a previous report of intense aggression in cattle egret broods early in the nestling period, which decreased after the establishment of the hierarchy (Mock & Lamey, 1991).

The Early Dominance Establishment hypothesis may shed light on the surprising result that aggression during feeding did not appear to influence the proportion of food ingested by the senior chick. Early aggression in ardeids seldom increases the proportion of food ingested by the senior chick in the current feeding bout and its main function may well be to establish dominance and secure priority in feeding and survival over the rest of the nestling period (Mock & Parker, 1997; Pinson & Drummond, 1993). After dominance is established, little or no aggression may be necessary to elicit submission or hesitation by juniors during feeding bouts (Mock, 1985; Ploger & Mock, 1986).

Mock (1985) suggested that selection should favour the use of aggression early in the nestling period to establish dominance-subordination relationships, so that seniors can reap the benefits of early aggression when feeding eventually becomes direct. This idea parallels what is proposed by the Early Dominance Establishment hypothesis but it was based on the assumption that aggression is efficient only during competition for direct feeds. According to this view, early aggression would only be adaptive in species with direct feeding or with an eventual switch to direct feeding. However, great blue herons and grey herons that are indirectly fed throughout the nestling period nonetheless present fierce aggression causing wounding or expulsion from the nest (Milstein et al., 1970; Mock, 1985; David & Berrill, 1987), and our analysis of the effects of aggression on competition under direct and indirect feeding suggests that securing priority during direct feeding bouts need not be the main function of nestling aggression.

Our data fail to support the basic assumption that aggression is a more efficient tactic for competing for direct feeds than indirect feeds and they contradict the hypothesis that feeding method has a proximate influence on use of aggression. The cattle egrets' developmental changes in rates of aggression were better predicted by both the Food Amount and Early Dominance Establishment hypotheses. The Food Amount hypothesis is the less plausible of the two hypotheses because it appears unable to explain temporal variation in aggression in blue-footed boobies, where food provisioning continues to increase for at least 10 d after aggression peaks and declines (Guerra & Drummond, 1995; Valderrábano et al. in prep.) and because the applicability of the hypothesis to ardeids is unresolved. It is the Early Dominance Establishment hypothesis that most credibly explains temporal variation in rates of senior chick aggression in both blue-footed boobies and cattle egrets and also the temporary belligerence and eventual subordination of junior chicks.

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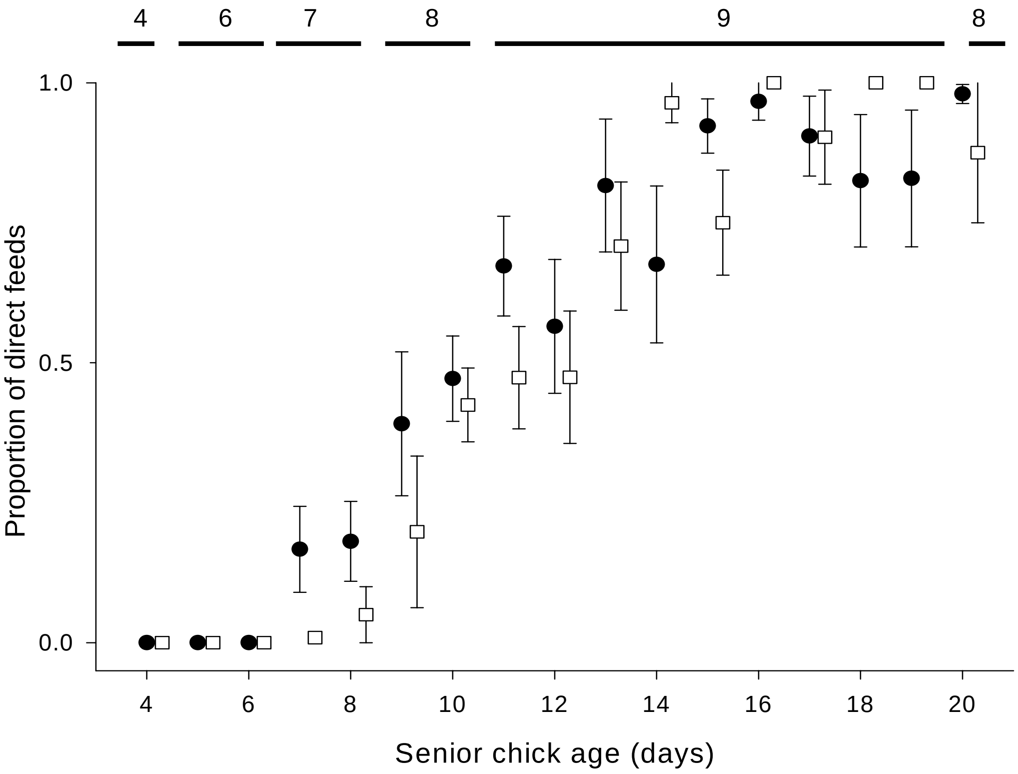

Figure 1. Developmental transition from indirect to direct feeding. Proportion of feeds (X ± se) which were direct for both senior (●) and junior (□) chicks as a function of senior chick age. Numbers along the top indicate number of broods.

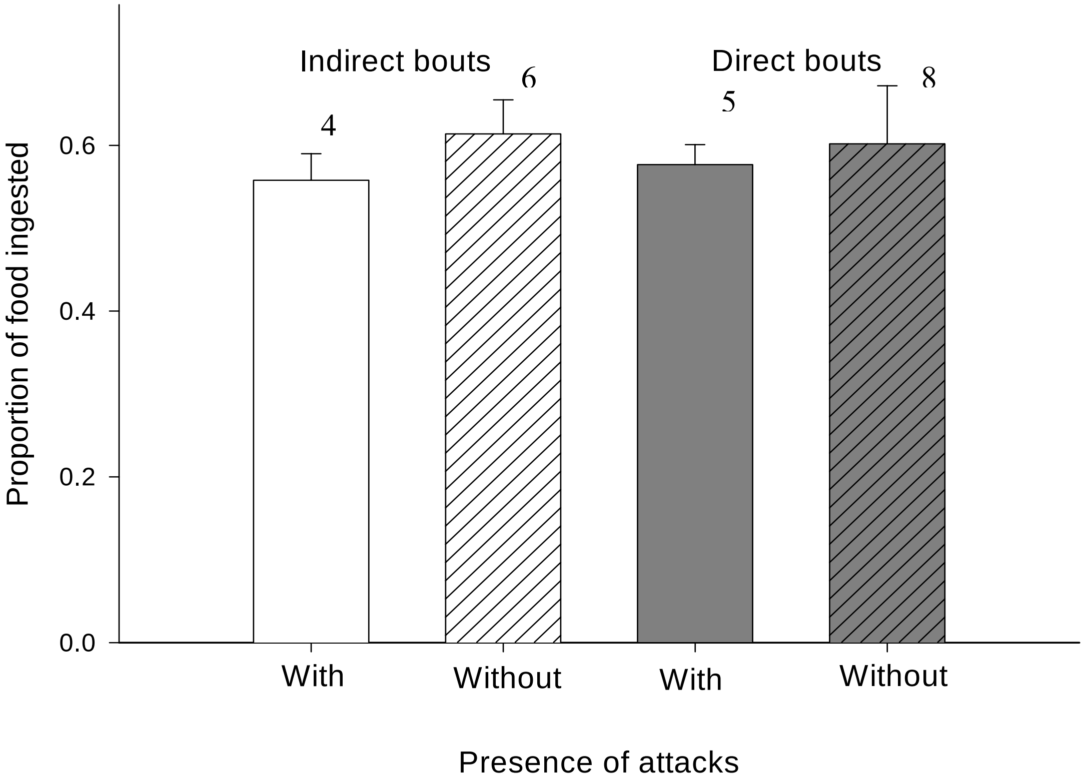

Figure 2. Profitability of senior chick's aggression during indirect and direct bouts. Proportion of food ingested by the senior chick (X±se) during indirect and direct bouts, with and without attacks. Numbers above the bars are the number of broods.

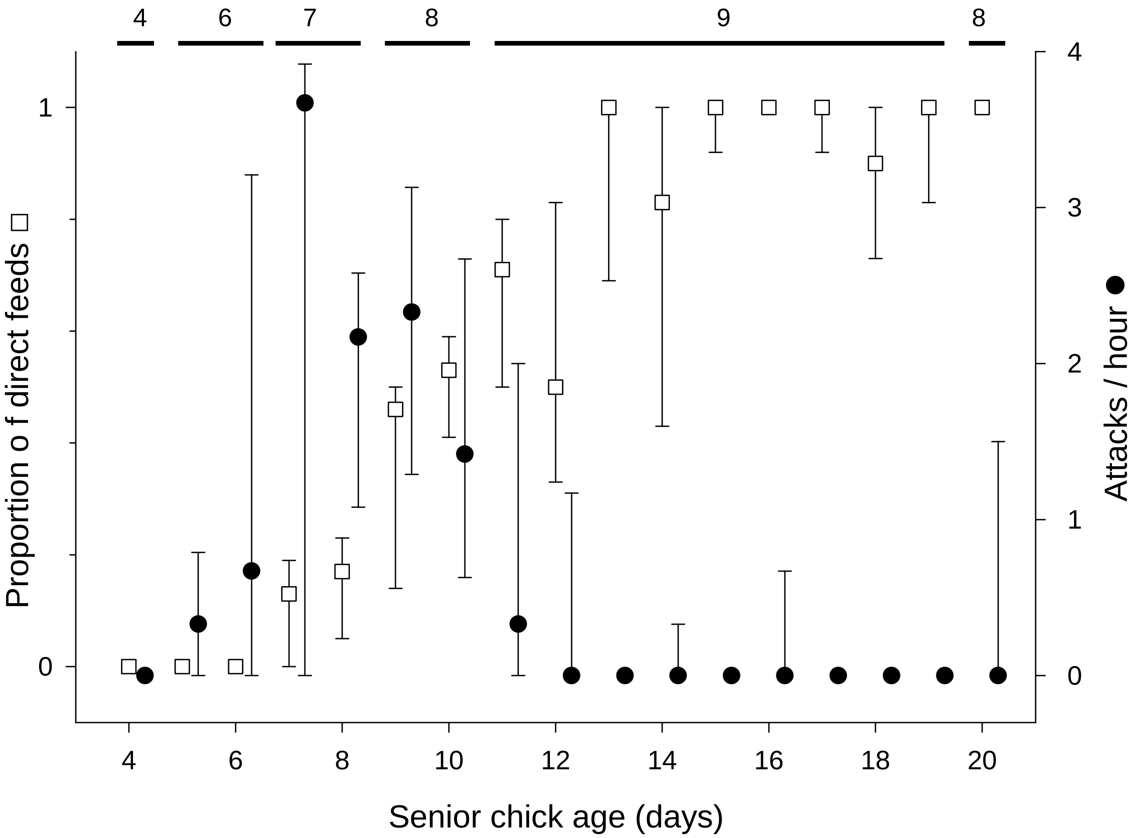

Figure 3. Temporal variation in feeding method and rate of aggression of senior chicks. Symbols represent the median and whiskers the 2nd and 3rd quartiles. Numbers along the top indicate number of broods.

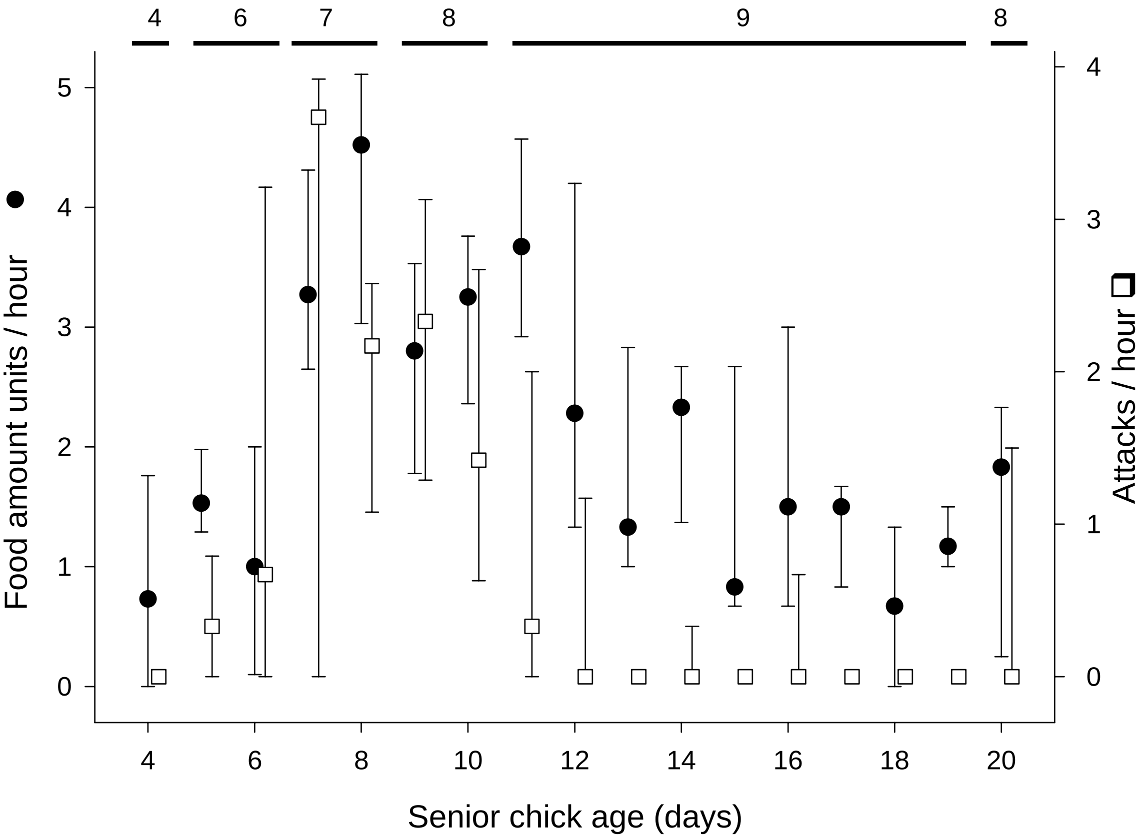

Figure 4. Temporal variation in amount of food ingested by the brood and rate of aggression of senior chicks. Symbols represent medians and whiskers the 2nd and 3rd quartiles, numbers along the top indicate number of broods.

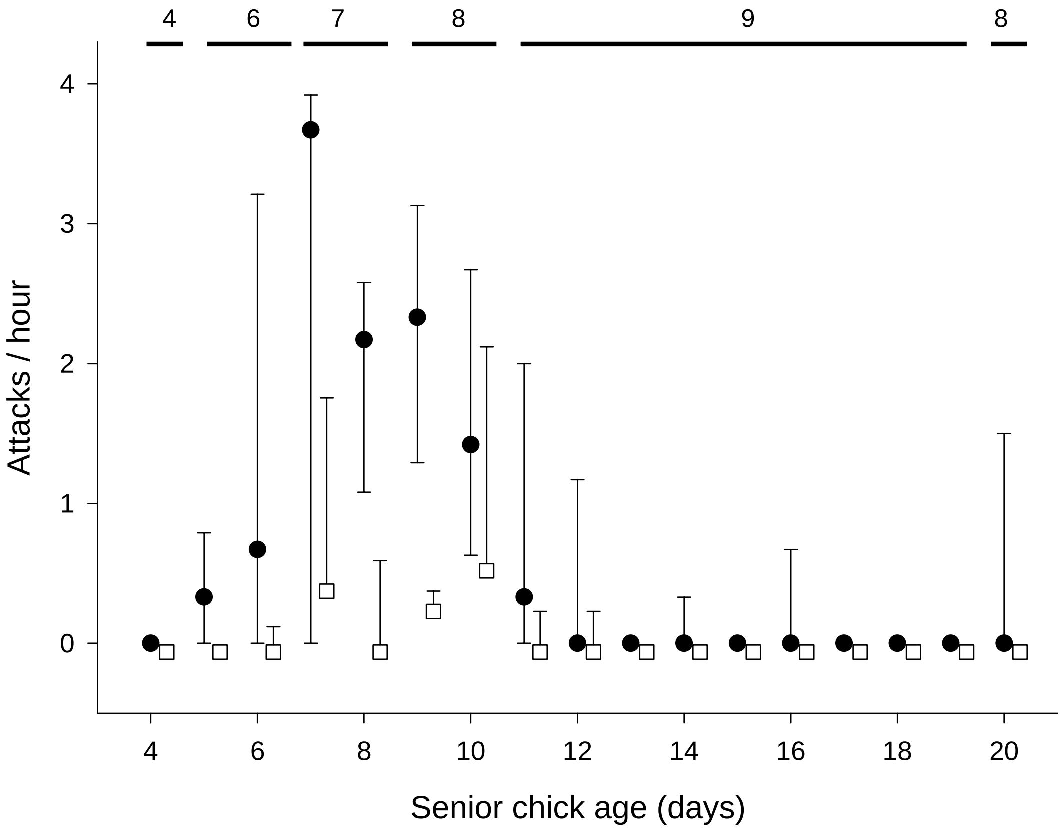

Figure 5. Rate of aggression for senior (●) and junior (□) chicks as a function of senior chick age. Symbols represent medians and whiskers the 2nd and 3rd quartile, numbers along the top indicate number of broods.

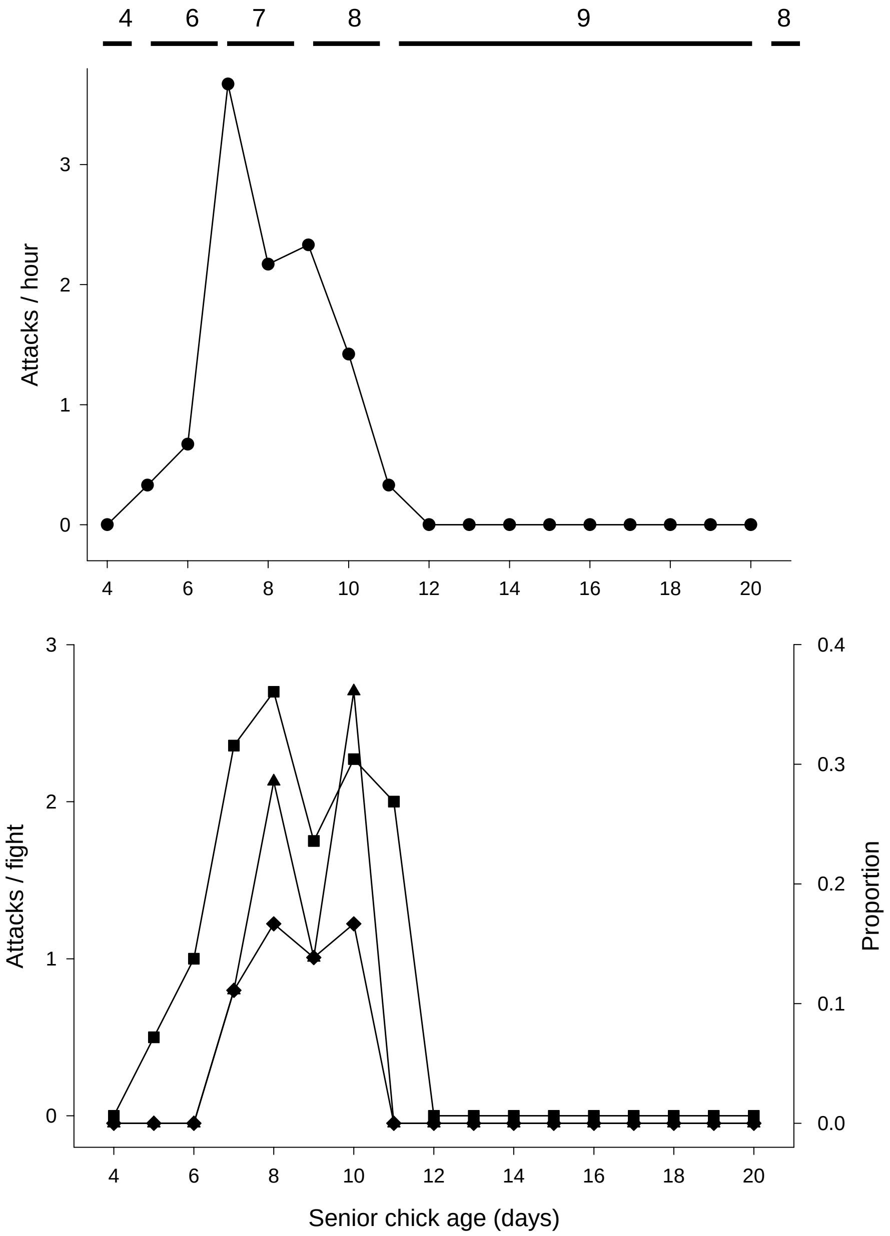

Figure 6. Temporal pattern of aggression by senior chicks and three measures of rebelliousness by junior chicks. Top: senior chick aggression (median) as a function of senior chick age. Bottom: median numbers of attacks by both chicks per fight (■), proportions of pendulum fights (▲) and proportions of fights initiated by the junior chick (♦). Numbers along the top indicate the number of broods.

Capitulo 3.

Trained to win? Establishment of dominance hierarchies in cattle egret broods

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Abstract: Sibling aggressive competition is generally said to involve the establishment of a transitive hierarchy based on dominance-subordination relationships. An individual's rank within such hierarchies may depend on intrinsic aggressive ability, assessment of opponents and cumulative experience based on training as a winner or as a loser. Infant hierarchies show striking differences in the relationships among broodmate pairs which hint at potential interspecific differences in the mechanisms influencing hierarchy establishment and maintenance. We described development of aggression and concession, for the first time, in three-chick cattle egret broods to infer the mechanisms influencing hierarchy establishment and maintenance. Chicks of all age-ranks developed aggressive tendencies and overall patterns of temporal variation in aggressiveness were similar for all ranks, although the magnitude of the changes varied between ranks. At their respective peaks, rates of attack of A and B chicks did not differ, but B chicks attacked more than C chicks. Intermediate and subordinate chicks do not appear to be trained as losers since the proportion of fights which they conceded to the senior decreased with age. Intermediate chicks presented more aggressive resistance the senior's bid at establishing dominance than juniors resisted the intermediate's bid at asserting dominance. The intermediate's resistance gradually eroded with age. Dominant chicks progressively substituted physical aggression with aggressive displays. Results suggest that assessment and trained winning are the two key mechanisms influencing hierarchy establishment and maintenance in cattle egret broods.

Key words: Hierarchy establishment, development, aggressive tendencies, dominance, trained winning, assessment, cattle egrets.

In diverse mammal and bird species siblings compete aggressively, by pecking, biting or scratching, for parentally provided food (Mock and Parker 1997). Aggressive competition is generally described as involving the establishment of a transitive hierarchy based on dominance-subordination relationships between siblings (Smale et al. 1995; Bekoff and Dugatkin 2000; Drummond et al. 1986; review in Drummond 2006). Dominants intimidate competitors, sometimes excluding them from parental feeds, thus biasing food distribution in their favour. When resources are insufficient for the entire litter or brood, dominant individuals may eliminate competitors through aggressively enforced starvation, lesions or eviction (Mock and Parker 1997).

An infant's rank within the hierarchy may be influenced initially by intrinsic fighting ability, i. e. its resource-holding potential (Parker 1974), and later increasingly depend on cumulative experience, defined as the influence of the outcome of prior aggressive interactions on an individual's behaviour in subsequent interactions (Beaugrand 1997; Dugatkin and Earley 2004). Individuals may also asses their opponents' aggressive ability or motivation, based on cues such as body size or displays (Drummond 2006), and respond appropriately during encounters. Two mechanisms have been suggested as having an important influence in the development of cumulative experience: trained winning and trained losing (Chase et al. 1994; Dugatkin 1997). Trained winning can be defined as an increased tendency to behave aggressively during interactions based on having won previous interactions. Conversely, trained losing can be defined as an increased tendency to behave submissively during interactions based on having lost previous interactions

(Beaugrand 1997; Dugatkin 1997). Trained winning and losing are not two sides of the same coin, and hierarchy establishment or maintenance does not necessarily require both to play a role (Beaugrand 1997). Studies with young coyotes (*Canis latrans*) and blue-footed booby (*Sula nebouxii*) chicks have shown an influence of trained winning and losing in hierarchy establishment and maintenance (Drummond and Osorno 1992, Drummond and Canales 1998; Bekoff and Dugatkin 2000). However, analysis of the ontogeny of aggressive and submissive behaviour as well as the mechanisms involved in creating and maintaining hierarchies among infants has been neglected. Most information comes from studies of avian hierarchies, particularly studies with blue-footed boobies (Drummond and Osorno 1992, Drummond and Canales 1998, Valderrabano et al. in press).

Two experiments with blue-footed boobies have shown that trained winning and trained losing, as well as assessment of the opponent's aggressive ability, are involved in channelling chicks into adopting specific roles within a hierarchy (Drummond and Osorno 1992, Drummond and Canales 1998). In singleton chicks (from broods of one) without prior social experience with a broodmate, differences in age and size determined the direction of dominance. In chicks from broods of two, prior social experience in the natal brood determined the behaviour of chicks when pitted against an unfamiliar chick, whatever the prior social experience of the unfamiliar chick. The effects of training as a loser appear to overwhelm age and size advantages as subordinates were unable to dominate a smaller and younger dominant chick (Drummond and Osorno 1992). Social experience early in the nestling period appears to have long-lasting effects. When dominant chicks were paired with slightly larger singletons and subordinates with slightly smaller singletons in 10 d trials, the proportion of dominants that won decreased progressively until only about half were winning by day 6 while subordinates continuously lost encounters.

Trained losing had more persistent effects than trained winning, in part because the experimental design perpetuated subordinate training and counteracted dominant training (Drummond and Canales 1998).

Results of a descriptive study which analyzed development of aggression and submission in blue-footed booby broods suggest that trained winning and trained losing are two largely independent axes of learning since the same individual may simultaneously become more aggressive and more submissive to broodmates. Chicks of all social ranks showed development of aggressive tendencies, although the level of expressed aggression depended on the social rank of the chick and even dominant chicks developed moderate submissiveness (Valderrabano et al. in press). Younger broodmates are progressively trained to respond to attacks with stereotypical submissive postures (“bill down face away”, Nelson 1968), as the proportion of attacks to which juniors submitted increased progressively with age and remained high. Senior chick rates of aggression decreased after juniors responded to 90% of attacks with submission. As they aged, seniors replaced physical violence with threats, which became increasingly effective in causing submission, although never as effective as attacks (Valderrabano et al. in press).

Among species with aggressive competition there are considerable differences in the behaviour of chicks of different status and thus the type of dominance relationships (Drummond 2006). Blue-footed booby hierarchies, for example, are characterized by aggression-submission relationships between broodmates. Rather than fights between chicks, ordinarily there are distinct roles: one chick is generally aggressive and the other responds with stereotypical submissive postures and seldom initiates attacks against its elder broodmate. In contrast cattle egret (*Bubulcus ibis*), great egret (*Casmerodius albus*) and brown pelican (*Pelecanus occidentalis*) hierarchies present aggression-resistance relationships: both chicks are aggressive and initiate attacks, leading to repeated clashes (often called fights) sometimes with both chicks exchanging blows, stereotypical submissive postures are lacking and subordinate chicks rather than passively accepting their role defy dominance of the elder chick (Drummond 2006). Such interspecific variation in the type of dominance relationship and rank-related behaviour of chicks hints at possible differences in the mechanisms involved in hierarchy establishment and maintenance.

Information on hierarchy establishment in cattle egret broods is scarce and the mechanisms involved have not been identified. Dominance hierarchies in three-chick broods are apparently established by three weeks of age, when attacks decrease noticeably (Mock and Lamey 1991). Temporal variation in rates of aggression has only been described in two-chick broods where, as in boobies, aggression increased early in the nestling period, peaked and decreased to permanently low levels. Senior and junior chicks developed aggressive tendencies although the ages at which their rates of aggression peaked and the magnitude of their changes differed (Gonzalez-Voyer and Drummond in press).

Other than the characteristic resistance of younger chicks there is little information on rank specific behaviour of chicks in cattle egret hierarchies. Early in the nestling period younger cattle egret chicks sometimes peck back when attacked, resulting in pendulum fights with both chicks pecking in turns (Milstein et al. 1970). These fights may last for several minutes and junior chicks lose the majority of them (Fujioka 1985a). On occasion, juniors also initiate fights (Gonzalez-Voyer and Drummond in press). In three chick broods attacks are most intense in the youngest dyad (Ploger and Mock 1986). Some attacks end with one of the chicks crouching at the bottom of the nest with the head down, which has been interpreted as a sign of concession (Drummond 2006), since in cattle egrets there are no submissive displays. Joint aggressive displays by two chicks, termed face-offs, sometimes lead to fights early in the nestling period (Creighton and Schnell 1996). Later in the nestling period face-off displays could serve the function of maintaining dominance relationships without the need for overt aggression.

We described development of aggression and concession in three chick cattle egret broods in order to infer the mechanisms influencing hierarchy establishment and maintenance in a species with aggression-resistance. We use the findings of the studies of the blue-footed booby as a basis for comparison. We asked whether, as in boobies, both trained winning and trained losing influence hierarchy establishment and maintenance, and what the role of assessment was. We predicted that (1) if chicks are trained as winners, the tendency of a chick to behave aggressively during an encounter with a broodmate should increase as the number of encounters it wins increases. (2) If chicks are trained as losers, chicks should develop progressively stronger tendencies to respond with concession during fights with broodmates as the number of encounters they lost increases. Finally, (3) if assessment plays a role early in the nestling period chicks should tend to assess opponents through pendulum fights and face-off displays and that this tendency would decrease progressively in subordinate chicks following hierarchy establishment.

Methods

From late May until early July 2004 four observers studied cattle egret broods in a dense, mixed species colony, on a 12 by 15 m mangrove (*Rhizophora mangle*) islet in a brackish coastal lagoon at La Mancha, Veracruz, Mexico (19º 24′ N and 96º 24′ W).

All 65 accessible nests were marked individually with numbered plastic tags, mostly between completion of laying and hatching, but in four cases after hatching of one or two eggs. Average clutch size before hatching was 2.7 eggs (range 1 – 5, *n* = 61), and an average 2.3 chicks hatched per nest (range 1 – 5, *n* = 65). Average hatching interval between first and second hatched chicks (hereafter A and B) in the 54 broods in which we could confidently assign hatching dates for both chicks was 2.3 d (range 1 – 8 d), and average hatching interval between second and third hatched chicks (hereafter C) was 2.3 d (range 1 – 4, *n* = 24). Twenty percent of two-chick broods (7/31 and 70% of three-chick broods (16/24) were reduced. Three brood reductions were attributed to siblicidal aggression. In two cases, B was seen violently attacking C, who mostly cowered at the bottom of the nest or tried unsuccessfully to escape. Siblicide was also witnessed in one two-chick brood, in which A killed B. In most other cases, chicks simply disappeared overnight, probably due to predation by night herons (*Nycticorax nycticorax*), which were seen predating young chicks during observations.

Observers recorded behaviour in thirteen accessible three-chick broods. Chicks were individually marked upon hatching with non-toxic acrylic paint on the crown and rump: red for A, black for B, and green for C chicks. Color marks have no apparent effect on dominance hierarchies or other behaviour of cattle egret chicks (Ploger & Mock 1986).

Observations were made from three floating wooden towers (observation nests were at or below observer eye-level) stationed 16–17 m from the edge of the colony. Egrets were habituated to the daily activities of fishermen in the lagoon and their behaviour did not appear to be affected by the presence of observers. All broods were observed daily during two 3-hour periods (0730–1030 h and 1600–1900 h), except when it rained, from completion of hatching (mean: 6.2 d of age of the senior chick, range 4 – 11 d) until the brood was reduced or the senior chick was 17 d old. Each observer watched 1–3 broods simultaneously. Previous observations have shown that egret activity levels varied little between midday, morning and afternoon periods, thus the two three-hour observation periods allowed representative sampling of daily activity (Gonzalez-Voyer and Drummond in press).

Opportunistically, when broods were visited at the end of the morning observation period to refresh marks on chicks (about once a week), brood members were weighted. We obtained the weight of chicks in 15 broods, although in one of them we were unable to weigh the A chick and in a second were unable to weigh the C chick. Weights were obtained at different ages spanning the observation period, mean = 8.4 d of A chick age (range: 3 – 15 d of age of A).We compared weight differences between the A and B chick to the difference between B and C using a one-way ANOVA with weight differences between chicks nested within each of the broods where data were collected. Including age differences between dyad members as a covariate does not influence results, thus it was omitted from the analysis. In any case, there is no significant difference in asynchrony between A-B and B-C.

Observers recorded all aggressions and face-off displays following the sampling methods of Gonzalez-Voyer and Drummond (in press) and Ploger and Mock (1986). A peck was registered when a chick forcefully made contact with the point of its beak on any part of a broodmate's body, and a bite when a chick grasped any part of a broodmate's body between its mandibles. Summed pecks and bites are referred to as attacks. A fight began with the first attack and ended when attacking did not occur for at least 10 s. Fights involved unilateral attack or exchange of attacks. For each fight, observers noted which chick attacked first, the number of attacks delivered by each chick, and whether the fight ended in concession: one chick crouched at the bottom of the nest and the broodmate stopped attacking. For each chick we calculated the daily proportion of fights conceded to each of its broodmates: number of fights with the broodmate that ended with the chick conceding / total number of fights with that broodmate. We also calculated concession as the proportion of attacks causing concession (calculated as above but using attacks rather than fights) in order to compare with Valderrabano et al.'s (in press) analyses of boobies.

A fight was classified as a pendulum fight when both chicks pecked each other (even if one of the opponents only gave a single peck). For each dyad we calculated the percentage of their fights that were pendulum fights by dividing the number of pendulum fights by the total number of fights and multiplying by 100. The proportion of pendulum fights and number of fights initiated by the junior member of a dyad against its elder sib were assumed to be a measure of a chick's resistance to the elder's bid at enforcing dominance (see Gonzalez-Voyer and Drummond in press).

A face-off display was recorded when one chick faced a broodmate and stretched its neck upward, and the opponent responded also stretching its neck upward, each chick facing the other. The loser of a face-off display was the first chick to lower its head. Observers recorded both the initiator of the display and the winner, when a winner could be determined.

For analysis, we divided the period during which broods were observed into three age-blocks of roughly equal size. As a result of asynchronous hatching, chicks within each brood were observed at different ages therefore blocks for A, B and C chicks do not span exactly the same ages: A chicks: 5-8, 9-12 and 13-17 d; B chicks: 3-6, 7-11 and 12-16 d; C chicks: 0-4, 5-9 and 10-13 d. A previous study in the same population showed that in two chick broods the hierarchy is established between 9 and 12 d of senior chick age (Gonzalez-Voyer and Drummond in press), thus our sample covers the establishment and maintenance of the hierarchy. For each behavioural variable, we calculated an average behavioural rate or proportion, for each chick, for each age-block in which it was observed. Sample sizes represent the number of chicks observed in each block.

Our analyses included comparisons between dyads within each brood, using Wilcoxon matched pairs or sign tests, to determine whether hierarchies were established in all broods and describe general patterns of interaction between chicks within broods. We also tested for age related change in behaviour using planned comparisons between age-blocks. To reduce the number of comparisons and avoid inflating the risk of Type II errors, we only compared the first vs. second, and the second vs. third age blocks for each age rank. Three exceptions were cases where the behaviour changed progressively during the observation period and our interest lay in determining whether the temporal change between the first and third age blocks was significant, thus we compared only these two age-blocks. We used independent samples analyses, rather than paired samples, because not all broods were sampled across the three age blocks. We used non-parametric analyses because data distributions could not be normalized by transformation. Some non-significant comparisons were omitted for brevity. We also omitted from some figures age-ranks that were inadequately sampled because few individuals performed the behaviour (e. g. attacks from C to A or concession from A to attacks from B). We present the mean and standard error throughout.

Results

Comparisons between ranks

Weight differences between B and C were significantly larger than the weight differences between the A and B chicks (One-way nested ANOVA: $F_{1, 26} = 4.34$, $p = 0.05$; Fig. 1).

Chicks of all three age-ranks in all 13 broods attacked their siblings. Within brood comparisons showed that a transitive hierarchy was established in every brood, and that elder chicks concentrated punishment on the next younger broodmate. First, we compared chicks at the same age (range: 4-14 d of age) to control for the influence of development on aggressive capabilities. A chicks attacked B chicks 3.1 times more often than *vice versa* (Wilcoxon matched pairs: Z = 2.37, *P* = 0.02, n = 7) and B chicks attacked C chicks 7.1 times more often than *vice versa* (Z = 2.20, *P* = 0.03, n = 7). Second, we compared chicks within broods, without controlling for age differences, to identify patterns of interaction between age-ranks. From 5 to 17 d of A chick age, A attacked B 5.8 times more than it did C (Wilcoxon matched pairs, Z = 2.28, *P* = 0.02, n = 13), and initiated 3.5 times more fights against B than against C (Z = 2.12, p = 0.03, n = 13). Fights between B and C chicks were 2.3 times more frequent than between A and B chicks (Sign test: *P* = 0.01, *n* = 13), but B and C chicks did not exchange more attacks than A and B chicks (Sign test: *P* = 0.15, *n* = 13). Finally, A chicks won 2.8 times more displays against B chicks than *vice versa* (Sign test: *P* = 0.02, *n* = 13), and B chicks won 6.0 times more displays against C than *vice versa* (Sign test: *P* = 0.02, *n* = 13).

Development of aggressive tendencies

Rates of attack of all age-ranks increased early in the nestling period, peaked and decreased, although the magnitude of the increase differed among ranks. At their respective peaks, attack rates of A and B chicks did not differ significantly (U = 38.0, *P* = 0.57, n = 19). On the other hand, B chicks attacked significantly more than C chicks at their respective peaks (U = 9.0, *P* = 0.002, n = 20). Rates of aggression against both broodmates (pooled) peaked at 5-8 d of age for A chicks, 7-11 d of age for B chicks and 5-9 d of age for C chicks.

A chicks

Age related changes in A chick attacks directed towards B chicks followed similar patterns as above: attacks were maximal at 5-8 d of A chick age, significantly decreased between the first two age blocks (U = 12.5, *P* = 0.01, n = 19) and remained low between the last two age blocks (U = 30.0, *P* = 0.07, n = 16; Fig. 2). On the other hand, A chick attacks on C began low (0.17 ± 0.09 attacks/h at 5-8 d of A chick age) and remained low throughout the observation period (0.18 ± 0.09 at 9-12 d and 0.35 ± 0.20 at 13-17d), showing no significant change.

B chicks

Age related changes in attacks towards the elder and the younger broodmate separately did not follow similar temporal patterns. B chick attacks towards A were maximal when B was only 3-6 d old, significantly decreased between the first two age blocks (U = 23.0, *P* = 0.04, n = 20), and remained low between the last two age blocks (U = 11.5, *P* = 0.21, n = 14). On the other hand, attacks towards C were low when 3-6 d of age and increased, although non-significantly, between the first two age blocks (U = 25.5, *P* = 0.06, n = 20), and decreased, non-significantly, between the last two age blocks (U = 9.0, *P* = 0.12, n = 14; Fig. 2). The high variance in attack rate of B chicks, notable during the second age block, is caused by 4 B chicks that were very aggressive towards the C chick (average range 15 – 28 attacks/h), in three cases these attacks culminated in the death of C.

C chicks

Attacks directed towards each of the older broodmates separately showed similar age related changes. Attacks from C towards A significantly increased between the first two age blocks (U = 23.5, *P* = 0.02, n = 20), then decreased significantly between the last two age blocks (U = 10.0, *P* = 0.05, n = 15). Attacks towards B chicks also increased significantly between the first two age blocks (U = 24.0, *P* = 0.03, n = 20), and did not change between the last two age blocks (Mann-Whitney U: U = 16.5, *P* = 0.28, n = 15; Fig. 2).

Development of concessive tendencies

Tendency to concede increased with the age-rank of the chick. Concession by the A chick to B was only observed during the first age block when out of an average 0.76 fights/h, the A chick conceded only 2.3% of them. In no occasion did A chicks concede a fight with C. On the other hand, B and C chicks conceded, on average, more than half of all their fights with A (57 ± 34 % and 72 ± 22 %, respectively).

Contrary to our prediction, younger chicks did not tend to increasingly concede fights with the senior broodmate as the proportion of fights lost increased. Concession by B and C chicks of fights with A tended to decrease across the observation period (Fig. 3). Concession by B was highest (62 ± 12 %) when A was 5-8 d old, when A's attacks on B were at a peak, then it decreased although non-significantly, to 44 ± 15 % when A was 9-12 d old (when the rate of attacks by A also decreased), and reached a low of 33.2 ± 33.2 % when the A chick was 13-17 d old (Fig. 3). Concession by C was high from the outset at 85.4 ± 8.6 % when A was 5-8 d old, increased slightly, though non-significantly, to a peak of 92.0 ± 7.0 % and then decreased significantly to 17.6 ± 31.9 % when the A chick was 13-17 d old (U = 1.5, *P* = 0.01, n = 11; Fig. 3). Proportion of attacks which caused concession showed similar patterns. Proportion of attacks by A causing concession by B decreased from 37.3 ± 6.6% at 5-8 d of A chick age to 5.8 ± 5.8% at 13-17 d of age. Proportion of attacks by A causing concession by C peaked at 80.3 ± 9.4% when A was 9-12 d old and decreased to 21.7 ± 12.8% when A was 13-17 d.

As A chicks aged, they increasingly replaced physical violence (attacks) with face-off displays, at least against B chicks. Although the number of displays initiated by A *versus* B did not vary significantly during the observation period (U = 26.5, p = 0.95, n = 15; displays initiated/ h at 5-8 d = 0.75 ± 0.33 and at 13-16 d = 0.70 ± 0.30), the proportion of initiated aggressions which were face-offs significantly increased from 17.9 ± 5.6 % when 5-8 d old to 91.1 ± 5.1 % when 13-17 d old (U = 0.0, p = 0.006, n = 12).

The proportion of displays which the B chick conceded to A increased significantly between A's first and second age blocks (Mann-Whitney U: U = 13.0, p = 0.016, n = 18, Fig. 4). There were fewer face-off displays between A and C chicks than between A and B chicks, however when these did occur the C chick conceded the overwhelming majority of them (91% ± 0.05). Thus the average proportion of face-offs conceded by the C chick *versus* A was high throughout the observation period. The increase in proportion of displays won by A may result from the fact that early in the nestling period displays generally lead to fights (and thus for the display there was no winner), while later on one of the chicks, generally the younger one, conceded.

Resistance of subordinates

The proportion of fights between A and B that were pendulum fights significantly decreased from 23.3 ± 5.1% at 5-8 d to 2.5 ± 2.5 % at 13-17 d of A chick age (Mann-Whitney U: U = 5.5, p = 0.008, n = 15). Proportion of fights that were pendulum fights between B and C chicks remained low during the observation period (U = 15.0, p = 0.43, n = 14; means at B age 3-6 d: 4.6 ± 3.3 % and 12-16 d: 19.9 ± 15.9 %). The higher proportion of the last age-block (19.9±15.9% when B was 12-16d old) results from one brood showing an unusually high percentage of pendulum fights (66.6%). Within broods there was a higher proportion of pendulum fights between A and B than between B and C (Wilcoxon matched pairs: Z = 2.29, p = 0.022, n = 13).

The rate of fights initiated by B chicks against A chicks decreased significantly from 0.17 ± 0.04 fights/h at 3-6 d to 0.04 ± 0.01 fights/h at 7-11 d of B age (Mann-Whitney U: U = 24.0, p = 0.044, n = 20) and decreased, although non-significantly so, to 0.0 ± 0.0 fights/h at 12-16 d of age (U = 8.0, p = 0.06, n = 14).

Discussion

A transitive hierarchy was established in all 13 broods and social rank followed the hatching order. We observed no inversions of dominance. Elder members of a dyad attacked the younger members significantly more than vice versa, even when controlling for age differences due to asynchronous hatching. Elder members of a dyad also won a significantly higher proportion of face-off displays against the younger member than vice versa.

Rates of attack of all age-ranks increased at an early age, peaked and subsequently decreased, although the ages at which rates changed and the magnitude of these changes varied among ranks. Even C chicks, that were facing two older and larger broodmates, showed development of aggressive tendencies although to a much lesser degree than A and B chicks. Similar temporal patterns in attack rates have been reported for two-chick broods of this population (Gonzalez-Voyer and Drummond in press). Yet, in those two-chick broods the peak in attack rate for A chicks took place at 10.6 ± 1.3 d of age, and coincided closely with the peak in B chick attack rate, while in our study A chick attack rate peaked at an earlier age (5-8 d) and also occurred earlier than the B chick’s peak. It is possible that in the presence of a third broodmate, with the potential associated risk of increased competition (Mock and Lamey 1991), A chicks accelerate establishment of dominance.

As in boobies, cattle egrets chicks appear to be channelled into adopting specific roles within a hierarchy initially by asynchronous hatching and later by the influence of training. Asynchronous hatching results in age and size differences among chicks which initially determine a chick's fighting ability and thus its rank within the hierarchy, as shown by the fact that social rank followed the hatching order in all broods. There may also be intrinsic differences in aggressive potential associated with age-rank as a result, for example, of differential investment in the eggs (Schwabl et al. 1997). Afterwards, development of aggressiveness of chicks may be influenced by trained winning. The presence of a younger, smaller victim appeared to influence the magnitude of the development of a chick's aggressive tendencies. However, chicks of different social rank within the hierarchy did not appear to be trained to express differential levels of aggressiveness (Benavides and Drummond submitted). Even though B chicks absorbed considerable punishment from the A chick, there was no significant difference between peak rates of aggression of B and A chicks. B chicks simply concentrated their aggression on the C chicks which they attacked significantly more than they attacked A. However, peak rates of aggression of C chicks were significantly lower than peak rates of aggression of B chicks. The development of the C chick's aggressive tendencies may have been stifled, in part, by the absence of a potential victim and thus of any training as a winner. Furthermore, the marked size disadvantage of C chicks relative to its elder broodmates might also negatively influence development of aggressive tendencies. Finally, last-laid eggs in three egg cattle egret clutches contain fewer androgens than first- and second-laid eggs, which could further handicap junior chicks (Schwabl et al. 1997).

Contrary to what has been reported for boobies, where submission by B and C chicks increases with age, plateaus and remains high (Valderrabano et al. in press), in cattle egrets the proportion of fights which B and C chicks conceded to A actually decreased with age. Peak levels of concession by cattle egret B and C chicks are also lower than those for booby B and C chicks. Peak proportion of attacks causing concession to the A chick in our study was 37% for B chicks and 80% for C chicks, compared with peak submission to A chicks of over 80% for booby B chicks and of 100% for booby C chicks (Valderrabano et al. in press). Concession in egrets may serve the purpose of ending a particular attack, but does not appear to involve training of chicks as losers (cf. Valderrabano et al. in press, Drummond and Osorno 1992). This suggestion is supported by the fact that B chicks concede a higher proportion of fights (or attacks) with A chicks when these are attacking them most, when attacks decrease so does the tendency to concede. Finally, A chicks do not appear to develop any tendency to concede as they only conceded a minimal number of fights with B chicks (2.3 %), and only when 5-8 d old, compared with peak submission of booby A chicks to attacks from B chicks of over 40% (Valderrabano et al. in press). Previous studies have shown that a stable transitive hierarchy can be established based solely on winner effects (Beaugrand 1997, Dugatkin and Earley 2004).

Aggressive resistance to the elder chick's bid at establishing dominance was more striking in the intermediate chick than in the junior. The B chick's aggressive resistance may in part result from its training as a winner and the virtual absence of training as a loser. C chicks did not show any significant temporal pattern in proportion of pendulum fights against the B chick, probably as a result of their lack of training as winners. Furthermore, within broods proportion of pendulum fights between A and B was significantly higher than between B and C. The smaller size difference between A and B chicks than between B and C chicks may also enhance the intermediate's tendency to violently resist the elder broodmate's bid at asserting dominance. Descriptive and experimental studies in several species have shown that reduced asynchrony leads to increased aggression between broodmates and in some cases may also diminish the stability of the hierarchy (Fujioka 1985a; Mock and Ploger 1987; Osorno and Drummond 1995; Machmer and Ydenberg 1998; Viñuela 1999; Nathan et al. 2001).

The B chick's resistance to the senior's bid at establishing dominance eroded with age. B chicks probably learn to concentrate aggression on their younger broodmate who to a certain extent gratifyingly responds with concession and seldom attacks back, while avoiding encounters with their more aggressive elder broodmate who generally punishes belligerence with intensified violence (Benavides and Drummond in prep.).

As they aged A chicks progressively replaced physical aggression against the B chick, their principal competitor, with face-off displays. Furthermore, as A chicks aged B chicks also increasingly conceded face-offs against A chicks. Thus, rather than showing a decreased tendency to behave aggressively, A chicks appear to replace potentially costly physical aggression with aggressive displays as the dominance relationships become established. Face-off displays may allow senior chicks to periodically reinforce their dominant status without the need for potentially costly fights. Younger chicks may also take advantage of displays to assess elder broodmates possibly through comparison of relative differences in body size.

Are C chicks trained as losers? C chicks do concede a high proportion of fights with both A and B chicks even at very early ages (Fig. 3), and the proportion of fights that ended with concession against A and B chicks peaked at 92% and 80% respectively. Furthermore, C chicks lose virtually all face-offs against A chicks throughout the observation period. On the other hand, there is a significant decrease in proportion of fights which ended in concession to A chicks between 5-9 and 10-13 d of A chick age and, although not significant, the proportion of fights which ended in concession to B chicks also decreased. The high tendency to concede of C chicks may result from the fact that C chicks are facing two older, larger and potentially dangerous opponents.

Aggression early in the nestling period appears to be aimed at establishing dominance (Pinson and Drummond 1993; Gonzalez-Voyer and Drummond in press). In blue-footed boobies senior chick rate of aggression decreased when younger chicks responded with submission to over 90% of attacks (Valderrabano et al. in press). In cattle egrets, reduction in rate of attacks by senior chicks may be triggered by decreased resistance from younger broodmates. In a previous study of two chick broods, rate of attacks of the senior chick and junior chick resistance (i.e. proportion of pendulum fights, fights initiated by junior and number of pecks per fight) both peaked and decreased at similar ages of the senior chick (Gonzalez-Voyer and Drummond in press).

In sum, our results suggest that assessment and trained winning are the key mechanisms influencing hierarchy establishment in cattle egrets and our inferences must now be confirmed with experiments. The cost of subordination (Drummond 2006) combined with trained winning and the virtual lack of trained losing appears to result in the establishment of an aggression-resistance relationship between cattle egret chicks. Pairwise relationships between broodmates appear to be influenced by the social environment of each chick and develop as a result of the training effects of repeated interactions with particular broodmates. Thus, intermediate chicks may simultaneously learn to behave aggressively with their younger broodmate while decreasing their tendency to respond aggressively to attacks from their elder broodmate, as has been suggested for boobies (Valderrabano et al. in press).

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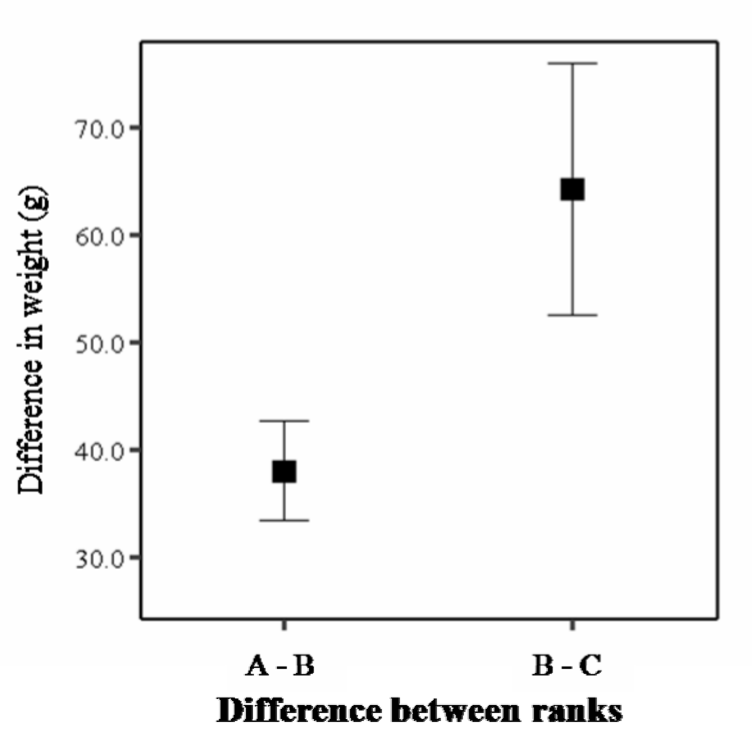

Fig 1. Difference in weight between A and B chicks and between B and C chicks. Shown are average and standard error.

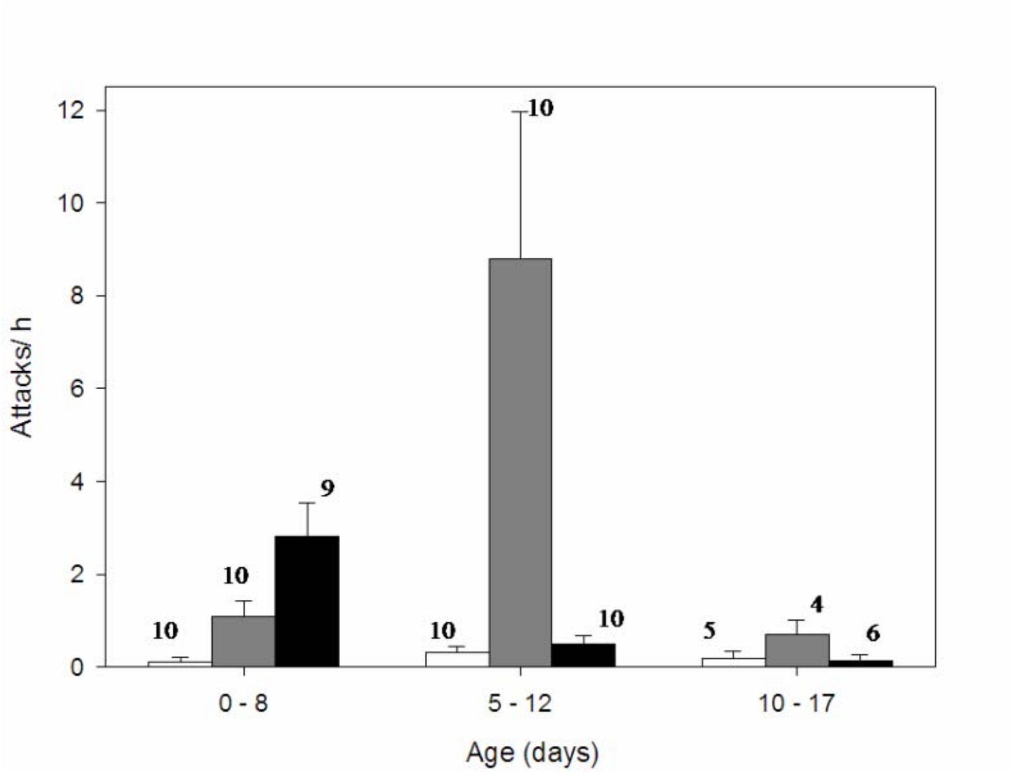

Fig 2. Rate of attack of A to B (black bars), B to C (grey bars) and C to B (white bars) as a function of age. Bars represent averages and whiskers the standard error. The numbers above the bars represent the sample size. The first age-block (0-8 d) spans ages 0-4 d: C, 3-6 d: B, 5-8 d: A; the second block (5-12 d) spans ages: 5-9 d: C, 7-11 d: B, 9-12 d: A; and the third block (10-17 d) ages: 10-13 d: C, 12-16 d: B and 13-17 d: A.

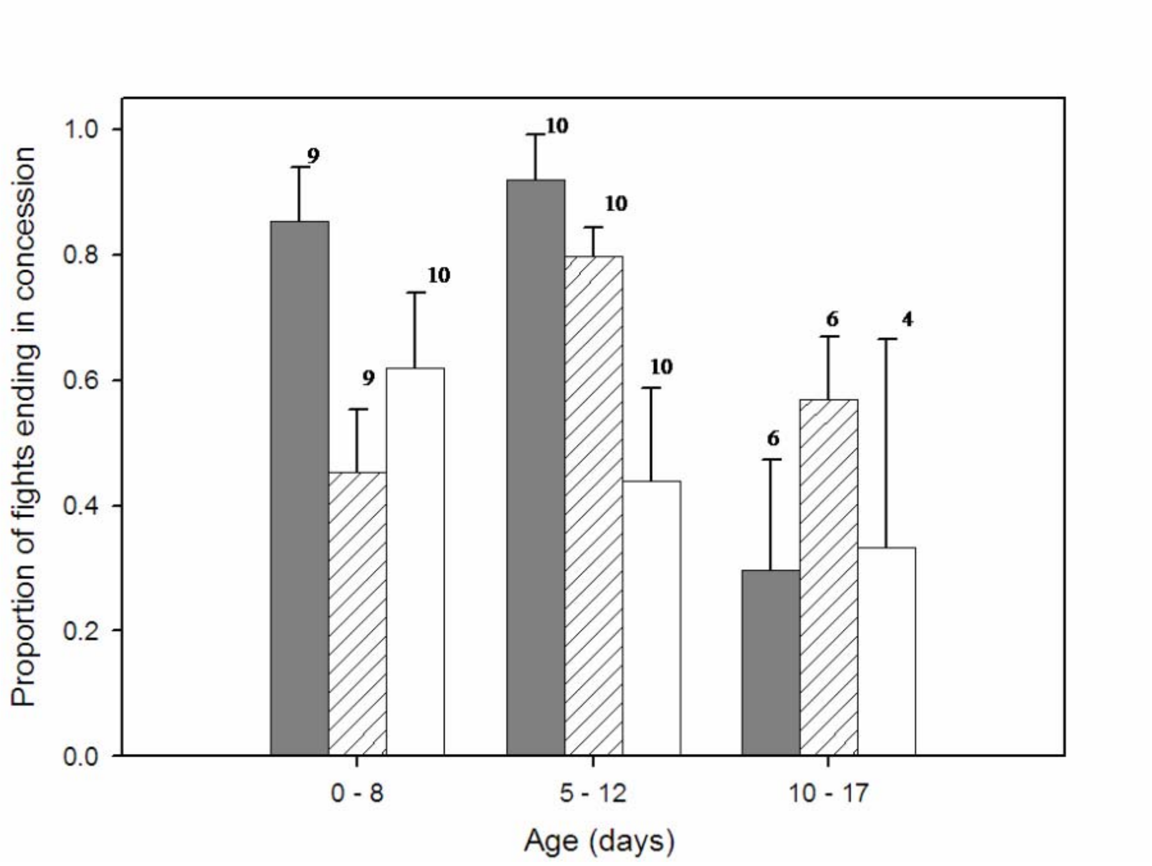

Fig 3. Proportion of fights conceded by C (grey bars) and B (white bars) against A chicks and by C against B chicks (dashed bars) as a function of A and B chick age. Bars represent averages and whiskers the standard error. The numbers above the bars represent the sample size. The first age-block (0-8 d) spans ages 3-6 d: B, 5-8 d: A; the second block (5-12 d) spans ages: 7-11 d: B, 9-12 d: A; and the third block (10-17 d) spans ages: 12-16 d: B and 13-17 d: A.

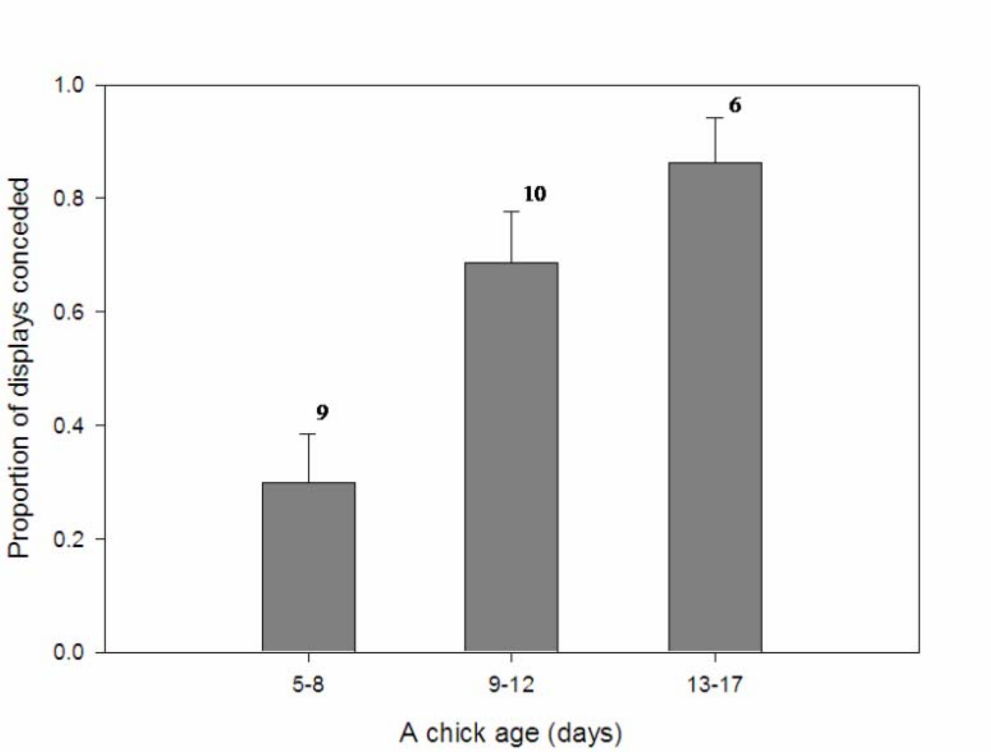

Fig 4. Proportion of face-off displays lost by B chicks *versus* A as a function of A chick age. Bars represent averages and whiskers the standard error. The numbers above the bars represent the sample size.

DISCUSIÓN GENERAL

Los tres objetivos principales de esta tesis se cumplieron exitosamente. El análisis comparativo, que abarcó 69 especies de aves, permitió identificar tres caracteres que posiblemente facilitaron la evolución de la competencia agresiva entre las crías. Los resultados del análisis de los agentes que influyen sobre la variación temporal de la tasa de agresión de las crías, en conjunto con los resultados del estudio comparativo, socavan fuertemente la hipótesis de que la alimentación directa influye sobre la distribución específica y sobre la expresión de la competencia agresiva (Mock 1985; Mock y Parker 1997). Finalmente, los resultados del estudio sobre la ontogenia de la agresión y los mecanismos que influyen sobre el establecimiento de la jerarquía en nidadas de la garza garrapatera sugieren que la evaluación de las capacidades agresivas y el entrenamiento para ganar tienen una influencia importante en el establecimiento de la jerarquía. Así mismo, los resultados sugieren que las crías de esta especie no están entrenadas para perder.

Los resultados del estudio comparativo (capítulo 1) demostraron que los periodos de nidada largos y la alimentación predominantemente indirecta están asociados con una mayor incidencia e intensidad de competencia agresiva. Además, las nidadas pequeñas están asociadas con una mayor intensidad de agresión. Por otro lado, los resultados del estudio comparativo ponen en duda una influencia última de la entrega de pedazos o bolos grandes de alimento, puesto que éste rasgo no presentó una correlación significativa con la incidencia ni la intensidad de la agresión. Así mismo, los análisis preliminares sugieren que el tamaño corporal de las crías tampoco influye sobre la evolución de la competencia agresiva.

Puesto que el análisis comparativo solo incluyó familias en las cuales por lo menos una especie presentaba competencia agresiva, la extrapolación de los resultados a familias en las cuales ninguna especie es agresiva no es aconsejable, ya que los resultados podrían explicarse tanto debido a patrones evolutivos particulares a familias que incluyen a especies agresivas (es decir que presentan un cierto potencial agresivo) como a patrones evolutivos que influyen en familias con especies agresivas y también en familias en las cuales ninguna especie es agresiva. Se ha sugerido que las características que han potencialmente favorecido la evolución de la competencia agresiva pueden ser clasificadas como aquellas que permiten el uso de la agresión (relacionadas con el potencial agresivo) y aquellas que afectan el beneficio obtenido por el uso de la agresión (su rentabilidad; Drummond 2002). Es posible que las familias incluidas en el análisis comparativo, al incluir por lo menos a una especie agresiva, presentaban un cierto potencial para la evolución de la agresión. La subsiguiente evolución de la agresividad podría estar condicionada por las características que afectan la rentabilidad de la agresión. Por otro lado en las familias en las cuales ninguna especie es agresiva tanto características relacionadas con el potencial agresivo como aquellas relacionadas con la rentabilidad de la agresión podrían estar restringiendo la evolución de este comportamiento. En estas familias no agresivas, es probable que los periodos de nidada cortos, la alimentación directa y las nidadas grandes hayan impedido la evolución de la competencia agresiva en combinación con otros caracteres no incluidos en nuestro análisis.

Los periodos de nidada largos y las nidadas pequeñas posiblemente influyen sobre la rentabilidad de la competencia agresiva (Drummond 2002). El defender agresivamente un recurso es favorecido por la selección natural cuando los costos relacionados con la defensa son contrarrestados por los beneficios que obtiene el individuo que defiende el recurso

(Brown 1964). Los periodos de nidada largos posiblemente permitan a los individuos dominantes colectar el beneficio de la jerarquía impuesta temprano en el periodo de nidada obteniendo prioridad alimenticia y posiblemente reduciendo el costo de la competencia por los recursos con los hermanos durante un largo periodo de cohabitación. Las nidadas pequeñas reducen el número de competidores y por lo tanto el número de interacciones agonísticas. Además se ha propuesto que las jerarquías posiblemente sean más estables en nidadas pequeñas que en nidadas grandes (Drummond 2002).

Puesto que los resultados del estudio comparativo son correlativos no es posible inferir causalidad. Por lo tanto es necesario realizar análisis direccionales que sí permiten determinar la causalidad (Pagel 1994). También, para identificar el número de eventos independientes de evolución de la competencia agresiva, es necesario realizar análisis de reconstrucción de estados ancestrales basados en una filogenia que incluya tanto clados en los cuales ciertas especies son agresivas como clados en los cuales ninguna especie es agresiva. Estos análisis permitirían también realizar inferencias sobre las condiciones ancestrales que favorecieron la evolución de la competencia agresiva.

Tanto los resultados del estudio comparativo como los resultados del estudio empírico de campo (capítulo 2) no apoyaron la hipótesis del método de alimentación (Mock 1985; Drummond 2001a). Los resultados de estos estudios ponen en duda tanto una influencia última (función) como una influencia próxima (mecanismo) del método de alimentación sobre la competencia agresiva. Los resultados del estudio comparativo mostraron que tanto la incidencia como la intensidad de la competencia agresiva decrecieron con la alimentación directa, lo que contradice la hipótesis del método de alimentación (Mock 1985). El estudio empírico, primero en haber puesto a prueba el supuesto básico de la hipótesis de que la competencia agresiva es más beneficiosa durante alimentaciones directas que durante alimentaciones indirectas, no encontró apoyo alguno para ésta. Las crías dominantes ingieren una proporción similar de alimento al utilizar agresión durante alimentaciones indirectas que al ser agresivas durante alimentaciones directas. Además, se ha reportado de manera independiente competencia agresiva, e inclusive siblicidio, durante la alimentación indirecta en seis especies de aves (Brown y Amadon 1968; Matray 1974; Milstein et al. 1970; Mock 1985; David y Berrill 1987; Ploger y Medeiros 2004).

El estudio empírico tampoco encontró evidencia en apoyo a la influencia próxima del método de alimentación. Las crías de la garza garrapatera no parecen ajustar su estrategia competitiva al método de alimentación, pues compitieron de manera agresiva tanto durante alimentaciones indirectas que durante alimentaciones directas, en contra de lo que predice la hipótesis (Mock y Parker 1997). Además la competencia agresiva no incrementó en frecuencia conforme aumentó la proporción de las alimentaciones directas (Mock y Parker 1997). Al contrario, las crías dominantes presentaron una tendencia, casi significativa, a agredir más durante el periodo en el cual la alimentación fue predominantemente indirecta que durante el periodo en el cual la alimentación fue predominantemente directa. En un estudio previo con pelícano café, que también puso a prueba esta predicción ligada al desarrollo, tampoco se encontró el incremento en agresión asociado al incremento en proporción de alimentaciones directas predicho por la hipótesis (Pinsón y Drummond 1993).

Los resultados de estos dos estudios de la tesis (capítulos 1 y 2) agregan a la evidencia de estudios previos (Brown y Amadon 1968; Matray 1974; Milstein et al. 1970; David y Berrill 1987; Pinsón y Drummond 1993; Drummond 2001a; Ploger y Medeiros 2004) la cual pone en duda una influencia del método de alimentación sobre la evolución y expresión de la competencia agresiva. Es probable que la concentración espacio-temporal del alimento, y no el método de alimentación, sea el factor determinante en la efectividad y rentabilidad de la agresión para competir por el alimento. En apoyo a esta hipótesis, las crías precoces de dos especies de aves, quienes obtienen el alimento del substrato, cambian de competencia por rebatiña hacia una defensa agresiva del recurso conforme el alimento es experimentalmente concentrado en el sustrato (Colón-Quesada et al. en preparación).

Los resultados de los dos estudios empíricos de campo (capítulos 2 y 3) muestran que los patrones de variación temporal de la tasa agresión están en acuerdo con las predicciones de la hipótesis del establecimiento temprano de la jerarquía (Pinsón y Drummond 1993; Gonzalez-Voyer y Drummond en prensa). En ambos estudios la tasa de agresión de las crías, de todos los rangos de edad, incrementa temprano en el periodo de nidada hasta un nivel máximo, que depende del rango de la cría, y decrece generalmente a niveles bajos constantes. En nidadas de dos crías, el pico en la tasa de agresión de la cría dominante coincidió con el pico de las tres medidas de rebelión de la cría menor (capítulo 2). Los resultados de ambos estudios sugieren que la agresión temprano en el periodo de nidada sirve para establecer las relaciones de dominancia-subordinación que, en un futuro, resultarán en una ventaja alimenticia para la cría dominante. Estudios previos en el bobo de patas azules y el cucaburra común mostraron patrones temporales de la tasa de agresión de las crías similares a los reportados en la garza garrapatera (Nathan et al. 2000; Valderrábano et al. en prensa). Es posible que en las especies con siblicidio facultativo la agresión temprano en el periodo de nidada sirva para el establecimiento de la jerarquía y por lo tanto se esperaría que los patrones de variación temporal en diferentes especies sean similares a los que se ha reportado en el bobo de patas azules y la garza garrapatera. Si esta sugerencia es cierta, la variación interespecífica podría limitarse a la edad a la cual se presentan los puntos de inflexión en la variación temporal de la tasa de agresión y en la manera por la cual las crías menores señalan su subordinación a la cría mayor. Por ejemplo, en el bobo de patas azules la tasa de agresión de la cría dominante decrece después de que la cría menor responda con la postura estereotipada de sumisión a más de 90% de los ataques (Valderrábano et al. en prensa). En la garza garrapatera los resultados del segundo estudio de campo sugieren que las crías menores señalan su subordinación reduciendo la resistencia, es decir al reducir el número de peleas que inician y la proporción de peleas en las cuales responden agresivamente a los ataques de la cría mayor.

Finalmente, los resultados del estudio descriptivo del establecimiento de la jerarquía en nidadas de la garza garrapatera (capítulo 3) sugieren que los dos mecanismos clave que influyen sobre el establecimiento y mantenimiento de la jerarquía son la evaluación de las capacidades competitivas y el entrenamiento para ganar. Las crías subordinadas de la garza garrapatera no parecen estar entrenadas para perder puesto que no mostraron una tendencia a conceder una mayor proporción de peleas con sus hermanos dominantes conforme aumentaba el número de interacciones que habían perdido. Al contrario en el bobo de patas azules, donde se ha demostrado una influencia del entrenamiento para perder, la proporción de ataques que causan sumisión aumenta progresivamente con la edad de la cría hasta llegar a un nivel máximo constante (Valderrábano et al. en prensa). La cría mayor y la cría intermedia en nidadas de tres crías mostraron indicios de un entrenamiento para ganar al atacar a sus hermanos menores más frecuentemente que vise versa. La cría dominante remplaza progresivamente la agresión física con despliegues agresivos que aparentemente le permiten reforzar su estatus como dominante sin tener recurrir a interacciones agresivas potencialmente costosas y riesgosas. Es posible que la mayor resistencia hacia la dominancia del hermano mayor expresada por la cría intermedia en comparación con la cría menor se deba en parte al entrenamiento para ganar de la cría intermedia y la virtual ausencia de dicho entrenamiento en la cría menor. Ahora es necesario realizar experimentos para comprobar las inferencias de este estudio descriptivo.

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