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**PROPORCION DE SEXOS E INVERSION
PARENTAL DIFERENCIAL EN HIJOS E
HIJAS EN EL BOBO DE PATAS AZULES**

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Esta tesis se compone de tres artículos que son referidos por los numerales I-III.

RESUMEN

De acuerdo con la hipótesis de Fisher, la proporción de sexos a la independencia debería estar sesgada hacia el sexo más barato cuando machos y hembras representan costos diferentes para los padres. Las hembras del bobo de patas azules (*Sula nebouxi*) son más grandes y en promedio 32% más pesadas que los machos, por lo tanto podrían representar mayores costos para los padres. Se registraron las proporciones sexuales a la eclosión y el emplumado durante 1989, y las proporciones sexuales al emplumado durante los siguientes cuatro años. Para evaluar si las hijas representan mayores costos que los hijos, se comparó el crecimiento de crías hembras y machos cuando experimentalmente recibieron la misma cantidad de alimento y se registró la frecuencia de alimentaciones parentales a emplumados marcados. En 1989 se encontró un sesgo hacia machos a la eclosión (56%) y el emplumado (56%). Globalmente las crías de ambos sexos tuvieron una mortalidad similar, sin embargo, al avanzar la temporada reproductiva, las hembras sufrieron un mayor aumento en mortalidad que los machos. Las proporciones sexuales al emplumado durante las siguientes cuatro temporadas reproductivas presentaron un sesgo consistente hacia machos y una relación positiva con la temperatura promedio del mar: el sesgo hacia machos aumentó en los años en que la disponibilidad de alimento fue presumiblemente menor. No se encontró relación entre las proporciones de sexos y la fecha de eclosión, el orden de eclosión y la experiencia reproductiva de los padres. Tampoco se encontró evidencia de que las hijas reciban una mayor inversión en alimento que los hijos. Por lo tanto, los datos no apoyan la idea de que el sesgo hacia machos en esta especie sea una adaptación a costos diferenciales entre machos y hembras, resultado del dimorfismo sexual en tamaño.



INTRODUCCION GENERAL

Desde el siglo pasado Darwin (1859) reconoció que la proporción de sexos de las crías es una característica posiblemente sujeta a selección natural, ya que podría afectar el éxito reproductivo de los padres. Desde entonces se han realizado un gran número de estudios teóricos y empíricos sobre las proporciones sexuales de la progenie en diversas especies de plantas y animales. El objetivo principal de este proyecto es estudiar las proporciones sexuales en el bobo de patas azules *Sula nebouxii*, un ave marina colonial que presenta dimorfismo sexual en tamaño. En particular se pusieron a prueba predicciones sobre (1) la teoría general de Fisher (1930) sobre la proporción de sexos, (2) los posibles ajustes facultativos de la proporción de sexos en función de las condiciones ecológicas para la reproducción, el orden de eclosión de la progenie y la experiencia reproductiva de los padres, (3) el supuesto de que en especies que presentan dimorfismo sexual en tamaño las crías del sexo más grande representan mayores costos para los padres, y (4) mortalidad diferencial de crías hembra y macho.

Teoría general de la proporción de sexos

Fisher (1930) propuso que cuando la producción de hijos e hijas representa costos similares, la selección natural favorecerá a los padres que inviertan igual en las crías de ambos sexos. Si



uno de los sexos es más costoso, una inversión similar en cada sexo resultaría en un mayor número de crías del sexo más barato (Williams 1979, Charnov 1982). En especies que presentan dimorfismo sexual en tamaño, comúnmente se supone que el sexo más grande representa mayores costos para los padres, por lo que se esperaría una proporción sexual sesgada hacia el sexo menos costoso (Trivers 1985, Gowaty 1991, Weatherhead y Teather 1991).

La propuesta de Fisher (1930) se refiere a la inversión total en machos y hembras a nivel poblacional. Sin embargo, a nivel individual, cuando criar machos y hembras representan costos diferentes, los padres podrían estar ajustando la proporción de sexos que producen de acuerdo a sus propias condiciones o a las condiciones ecológicas prevalecientes (Williams 1979, Charnov 1982, Gowaty 1991). Si los padres pueden predecir las condiciones que afrontarán durante la crianza, se esperaría que la proporción de sexos de su progenie al nacer anticipara sus capacidades de inversión. En cambio, si las condiciones para la crianza son impredecibles al inicio de la temporada reproductiva, la proporción de sexos podría ajustarse, a través de mortalidad diferencial durante el periodo de cuidado paterno (Trivers y Willard 1973, Howe 1976). En aves se ha encontrado que la proporción de sexos de la progenie puede variar a lo largo de una misma temporada reproductiva (Howe 1977, Meathrel y Ryder 1987), en función del orden de puesta (Howe 1977, Ankney 1982, Ryder 1983, Bortolotti 1986, Weatherhead 1985,

Edmunds y Ankey 1987, Dijkstra et al. 1990) y con la edad de los padres (Blank y Nolan 1983).

Dimorfismo sexual de tamaño

La idea de que en especies que presentan dimorfismo sexual en tamaño el sexo más grande tiene mayores requerimientos alimenticios, y por lo tanto representa mayores costos para los padres ha sido ampliamente aceptada. Sin embargo, en aves la evidencia empírica no es muy clara (Stamps 1990). Sólo cuando los machos son el sexo más grande se han reportado mayores demandas energéticas y de consumo de alimento (e.g. Fiala 1981, Slagsvold et al. 1986). Cuando las hembras son el sexo más grande, ambos sexos parecen consumir cantidades similares de alimento (Newton 1978, Collopy 1986, Frumkin 1988).

Richter (1983) propuso que a pesar del dimorfismo sexual en tamaño, diferencias en la asignación de recursos durante el crecimiento y desarrollo de las crías podrían estar igualando los costos (requerimientos alimenticios) de machos y hembras. Por ejemplo, las crías del sexo más grande podrían estar asignando más recursos a crecimiento en masa y tamaño, mientras que las crías del sexo de menor talla podrían estar asignando más recursos al desarrollo del plumaje o al desarrollo psicomotriz (Richter 1983, Stamps 1990).

Para evaluar si las crías del sexo de mayor tamaño son más costosas, es necesario saber si el sexo más grande recibe una mayor inversión parental que el sexo más pequeño, y si esto

disminuye cualquier componente de la adecuación de los padres (Trivers 1972, Clutton-Brock 1991). Se considera inversión parental a todas las acciones que realizan los padres que aumentan la adecuación de una cría a expensas de una disminución en el éxito reproductivo o sobrevivencia de los padres (Trivers 1972). En este trabajo sólo se consideró la inversión parental en términos de alimentación.

Mortalidad de machos y hembras

La mortalidad diferencial de crías macho y hembra se ha interpretado, dentro del contexto del modelo de Fisher, como un factor que puede afectar los costos relativos de producir crías de cada sexo (Trivers 1985). Entre los modelos que predicen variaciones en las proporciones sexuales que producen los individuos, la mortalidad diferencial se ha propuesto como un mecanismo de ajuste facultativo de la proporción de sexos por parte de los padres (Trivers y Willard 1973).

Alternativamente, existen otras hipótesis no relacionadas con la teoría de la proporción de sexos para explicar la mortalidad de machos y hembras (Mittwoch 1971 y 1993, Clutton-Brock et al. 1985, Weatherhead y Teather 1991). Por ejemplo, la mortalidad diferencial se ha explicado como el resultado de la expresión de efectos deletereos en el sexo heterogamético (Myers 1978, Clutton-Brock et al. 1985), o como el resultado de una mayor vulnerabilidad a escasez de alimento por parte del sexo con

tasas de crecimiento y/o requerimientos nutricionales mayores (Clutton-Brock et al. 1985).

Otros modelos sobre las proporciones sexuales

A partir del modelo de Fisher sobre las proporciones sexuales se generaron nuevos modelos que incluyeron otros aspectos poblacionales (e.g. poblaciones subdivididas) y genéticos (e.g. tipo de control de la asignación sexual) que se observan en diferentes especies (Charnov 1982, Karlin y Lessard 1986, Frank 1990, Antolin 1993). En general, los modelos sobre las proporciones sexuales han utilizado dos aproximaciones, en la primera se enfatizan las funciones de optimización y adaptativas de la asignación sexual, desde el punto de vista de las estrategias evolutivamente estables, en la segunda, se enfatizan las consecuencias de los mecanismos genéticos de la determinación del sexo (Karlin y Lessard 1986). Estas dos aproximaciones no son excluyentes, y de hecho ambos aspectos, los mecanismos de determinación del sexo y los factores genéticos y ambientales, además de aspectos filogenéticos, son necesarios para tener una visión más completa de la evolución de las proporciones sexuales (Karlin y Lessard 1986, Frank 1990).

En aves y mamíferos se consideraba hasta hace algunos años, que las proporciones sexuales a la fecundación eran siempre 1:1 (Charnov 1982). Esto se explicaba como resultado de restricciones del sistema cromosómico de determinación del sexo (XX:XY en mamíferos y ZZ:ZW en aves), que como consecuencia de

las reglas de segregación Mendeliana mantendrían una proporción sexual de 1:1. Sin embargo, cada vez hay más estudios empíricos en estos grupos taxonómicos que reportan sesgos en las proporciones sexuales. En términos teóricos se esperarían proporciones de sexos sesgadas, por ejemplo, cuando la condición de la madre afecta diferencialmente el éxito reproductivo de los críos de un sexo (Trivers y Willard 1973), cuando hay conflictos padre-hijo, competencia local por parejas (Hamilton 1967), o competencia local por recursos (Clark 1978).

Sólo mencionaré las ideas que subyacen los dos modelos que tienen que ver con diferencias en la dispersión natal de machos (competencia por parejas) y hembras (competencia por recursos), por ser los que me parece podrían ponerse a prueba en los bobos de patas azules.

En el modelo de competencia local por parejas, se predice que en especies en que los hermanos compiten por las parejas, la selección natural favorecería a los padres que inviertan más recursos en hijas que en hijos (Hamilton 1967). Es decir, cuando el pago genético para los padres por aumentar la asignación de recursos a machos crece a una tasa menor que el pago por aumentar la asignación a hembras se esperaría una proporción de sesgos sesgada a hembras (Hamilton 1967, Charnov 1982, Frank 1990).

Basandose en el modelo de competencia local por parejas, Clark (1978) sugirió que en especies en donde la dispersión natal está sesgada a machos, la competencia entre hermanas por recursos limitados predice una proporción de la progenie sesgada a machos.

A diferencia del modelo de Hamilton en el que hay competencia por parejas y apareamientos entre hermanos (i.e. endogamia), el modelo de competencia local por recursos sólo considera la competencia entre hermanas pero no la endogamia (Frank 1990).

La competencia local por recursos parece ser una presión de selección importante en las variaciones de las proporciones sexuales de la progenie en aves. Por ejemplo, la dispersión natal está sesgada hacia hembras en los *Passerinos*, y hacia machos en los *Anseriformes* (Gowaty 1993). De acuerdo con lo esperado según la hipótesis de competencia local por recursos las proporciones sexuales estuvieron predominantemente sesgadas a hembras en *Passerinos* y a machos en *Anseriformes* (Gowaty 1993).

Posibles mecanismos de variación de las proporciones sexuales

En aves la determinación del sexo está controlada por un mecanismo cromosómico ZZ:ZW, en donde las hembras son el sexo heterogamético (ZW). Es difícil estimar las proporciones sexuales a la fecundación, aunque la evidencia disponible sugiere que hay poca variación genética (Charnov 1982, Frank 1990). Sin embargo, en aves la mayor parte de la inversión parental ocurre después de la fecundación, por lo tanto aún cuando las proporciones a la fecundación fueran 1:1, los padres podrían modificar las proporciones sexuales mediante mecanismos conductuales y fisiológicos (Frank 1990, Krackow 1995).

Uno de los mecanismos que se ha sugerido para el control de la determinación del sexo es la segregación no aleatoria de los

cromosomas sexuales y el crecimiento diferencial de folículos que produzcan un sexo en particular (Howe 1977, Ankney 1982, Krackow 1995). Esto implicaría que la secuencia de ovulación es controlada por la madre, es decir que los ovulos portadores de los cromosomas W y Z no se segregan aleatoriamente (Krackow 1995). Este mecanismo podría explicar la correlación entre el sexo de la cría y el orden de eclosión en la nidada que se ha reportado en varios estudios (e.g. *Haliaeetus leucocephalus*, Bortolotti 1986; *Falco peregrinus*, Olsen y Cockborn 1991; *Larus delawarensis*, Ryder 1983). Por otro lado, mecanismos humorales podrían explicar los cambios a lo largo de la temporada reproductiva en la dirección de las correlaciones entre sexo y orden de eclosión, ya que los niveles de hormonas esteroides varían considerablemente con la temporada reproductiva (Krackow 1995). Sin embargo, hasta ahora no hay datos publicados sobre el efecto de los niveles hormonales de los padres y la proporción sexual de su progenie (Krackow 1995).

Otro mecanismo que podría producir sesgos en la proporción de sexos a la eclosión es la mortalidad diferencial de embriones macho y hembra (Myers 1978). Una revisión de estudios que reportan sobrevivencia de embriones en pollos de granja (*Gallus domesticus*) mostró que globalmente los embriones hembras sufren una mayor mortalidad, especialmente cuando hay retrasos en el inicio de la incubación o cuando son huevos producidos por hembras en condiciones de alimentación inadecuadas (Landauer 1967 en Myers 1978).

Historia natural del bobo de patas azules

El bobo de patas azules *Sula nebouxii* es un ave marina colonial que presenta dimorfismo sexual de tamaño: las hembras adultas son aproximadamente 32% más pesadas que los machos (Nelson 1978, Castillo y Chavez-Peón 1983). Aunque al nacer machos y hembras no difieren significativamente en peso y tamaño, las hembras crecen más rápido, y a la edad de 79 días, son ya 27% más pesadas y 8% y 10% más grandes en pico y ulna, respectivamente, que los machos (Drummond et al. 1991). Estas aves tienen de una a tres crías, que eclosionan con una diferencia de 4 días en promedio (Drummond et al. 1986). La eclosión asincrónica facilita el establecimiento de una relación de dominancia-subordinación en favor de la cría que eclosiona en primera posición (Drummond et al. 1986). Cuando el alimento es escaso, ocurre reducción de la nidada, típicamente a través de agresión entre hermanos, y es la cría que eclosiona al último la que muere con mayor frecuencia (Drummond et al. 1986, Drummond y García Chavelas 1989).

Los bobos de patas azules son filopátricos, aparentemente monógamos y pueden reproducirse con la misma pareja durante varias temporadas (Nelson 1978, Osorio-Beristain y Drummond 1993). Ambos sexos anidan en su primer intento reproductivo cerca y a una distancia promedio similar de su sitio natal: los machos a 24.1 m y las hembras a 28.3 m (Osorio-Beristain y Drummond 1993).

Machos y hembras participan en la incubación y cuidado de las crías, que se prolonga hasta unas semanas después del emplumado, es decir cuando el desarrollo del plumaje está completo (en promedio, 86 días para machos y 90.5 días para hembras; Drummond et al. 1991).

OBJETIVOS Y PREDICCIONES

De acuerdo con la teoría de Fisher, si las hijas del bobo de patas azules representan costos mayores para los padres que los hijos, esperaríamos (1) una proporción de sexos (proporción de machos entre el total) al momento de emplumado sesgada hacia machos a nivel de la población. Esto podría ser el resultado de un sesgo hacia machos desde la eclosión, o de mayor mortalidad de hijas que de hijos durante el periodo de cuidado parental.

El costo relativo de producir crías macho y hembra podría variar de acuerdo a las condiciones reproductivas y entre individuos. Cuando las condiciones reproductivas se deterioran, el costo de producir crías del sexo más grande, y presumiblemente más costoso, podría aumentar. Por lo tanto, en condiciones de baja disponibilidad de alimento esperaríamos (2) un aumento en la proporción de machos a través de la temporada reproductiva, suponiendo que las condiciones para la reproducción se deterioran al avanzar la temporada, y (3) un aumento en el sesgo hacia machos durante años de escasez de alimento.

Por otra parte, se exploró la posibilidad de ajustes de la proporción sexual en función del orden de eclosión en la nidada. En el bobo de patas azules las crías que eclosionan en última posición tienen un mayor riesgo de morir que sus hermanos mayores (Drummond et al. 1991), por lo tanto los padres podrían igualar la inversión en crías de ambos sexos produciendo más hijas en última posición, lo que asegura mayor mortalidad de hembras. Si lo anterior ocurre, en nidadas de dos y tres crías esperaríamos que (4) la proporción de hembras que eclosiona en última posición fuera mayor que la proporción de hembras que eclosiona en primeras posiciones en la nidada, y (5) que la proporción de hembras que empluma en últimas posiciones fuera menor que en la proporción de hembras que empluma en primeras posiciones en la nidada.

A nivel de individuos buscamos evidencia de ajustes facultativos de la proporción de sexos de acuerdo a la experiencia reproductiva de los padres. Si la experiencia reproductiva afecta la capacidad de los padres para la crianza, esperaríamos que (6) los padres con mayor experiencia produzcan una proporción de sexos más baja (i.e. más hembras) que los padres con menor experiencia.

Asimismo, se evaluó el supuesto de que las hijas representan mayores costos que los hijos en términos de inversión en alimento. Si para mantener tasas de crecimiento mayores y alcanzar un mayor tamaño final las hijas requieren de una mayor cantidad de alimento que los hijos, esperaríamos que (7) hembras

y machos tengan tasas de crecimiento similares cuando reciben la misma cantidad de alimento, y/o (8) la frecuencia de alimentaciones y la duración del periodo de cuidado parental sea mayor para las hijas que para los hijos.

Finalmente se puso a prueba la idea de que las hembras, por ser de mayor tamaño, son más vulnerables a disminuciones en la cantidad de alimento. Las predicciones se basan en los supuestos de que las crías que eclosionan al último tienen una mayor probabilidad de sufrir escasez de alimento y que las condiciones reproductivas se deterioran al avanzar la temporada de crianza. Bajo estos supuestos, se espera (9) mayor mortalidad de hembras que de machos, en crías que eclosionan en las últimas posiciones de la nidada, y (10) un aumento mayor a lo largo de la temporada en la mortalidad de las hembras últimas comparada con la de machos últimos.

MÉTODOS GENERALES

Este estudio se realizó de 1989-1994 en la colonia del bobo de patas azules que anida en la Isla Isabel, frente a las costas del estado de Nayarit, México. Para determinar la proporción de sexos a la eclosión y el emplumado en 1989 se realizó un registro intensivo que cubrió la mayor parte del periodo de crianza durante una temporada reproductiva (febrero-julio) y aproximadamente el 80% de los individuos de la colonia,

incluyendo todo el gradiente de densidad de nidos. Todos los nidos en la zona de estudio se marcaron con banderolas numeradas y diariamente se registró la sobrevivencia de las crías hasta que alcanzaron la edad de emplumado. En cada nido se registró la fecha de eclosión de las crías, así como la identidad de los padres cuando se trataba de adultos anillados. Para mantener la identidad de las crías todos los individuos se anillaron durante sus primeros 3 días de vida con alambre de colores (para identificar su orden de eclosión), y con anillos de plástico numerados cuando cumplieron 7 días de edad. Se anillaron un total de 751 crías de 400 nidos donde se determinó el sexo de todas las crías que eclosionaron. Las crías que sobrevivieron hasta la edad de emplumado (575) fueron anilladas permanentemente y sexadas con base en el tamaño asintótico de sus ulnas (Drummond et al. 1991). Las crías que murieron antes de emplumar fueron sexadas en el campo a partir de las diferencias morfológicas de las gónadas, y posteriormente en el laboratorio, a partir del análisis del tejido gonadal bajo el microscopio, identificando la presencia de tubos seminíferos en el caso de los machos, o folículos y/o ovocitos en el caso de las hembras (Drummond et al. 1991).

Para evaluar la variación en la proporción de sexos entre años, durante 1990-1994 se registró el sexo de todas las crías que emplumaron en la zona de estudio. Como un indicador de la disponibilidad de alimento, se utilizó la temperatura (C°) promedio superficial del mar aproximadamente 9 km alrededor de la

Isla Isabel, durante los meses que incluyen la temporada reproductiva para cada año. La temperatura está inversamente correlacionada con la productividad del mar y ha sido utilizado como un indicador de la disponibilidad de alimento para las aves marinas (Schreiber y Schreiber 1984, Hodder y Graybill 1985). Los datos de temperaturas provienen de una combinación de registros directos desde barcos y registros vía satélite (datos obtenidos vía internet publicados por la Universidad de Columbia, benno@Ideo.columbia.edu).

Para poner a prueba el supuesto de que las hembras, por ser de mayor tamaño, requieren más alimento que los machos, durante 1994 comparamos las tasas de crecimiento de crías hembra y macho cuando experimentalmente recibieron la misma cantidad de alimento. Las crías fueron alimentadas en sus nidos durante 9 días, y se les colocó cinta micropore alrededor del cuello para evitar las alimentaciones provenientes de los padres. Se utilizaron 74 crías de 22 d de edad provenientes de nidadas de una cría. Estas crías fueron asignadas aleatoriamente a 3 grupos experimentales: crías subalimentadas, crías sobrealimentadas y crías no manipuladas (grupo de referencia).

Las crías de los grupos subalimentadas y sobrealimentadas recibieron diariamente 150 g y 200 g de pescado fresco, respectivamente, más un aumento del 5% cada 2 días en ambos grupos. Durante el experimento las crías de los 3 grupos se pesaron (± 1 g) y se les midió el largo de la ulna y el pico (± 1 mm). La sobrevivencia de las crías se registró diariamente hasta

la edad de emplumado. El sexo de las crías experimentales se determinó con base en el tamaño de la ulna cuando las crías llegaron a la edad de emplumado, o por diferencias morfológicas de las gónadas, en el caso de las crías que murieron antes de emplumar.

Para evaluar si existen diferencias en la inversión parental a hijos en comparación de hijas después del emplumado, en 1994 se registraron alimentaciones a crías anilladas mayores a los 80 d de edad. Diariamente, de las 1400-1900 h, se realizaron recorridos a través de la zona de estudio. Los recorridos se hicieron siguiendo una ruta establecida sobre la cual se caminaba lentamente haciendose paradas de observación de aproximadamente 30 min. cada 30 m.

RESUMEN DE RESULTADOS

Proporción de sexos

De acuerdo con lo esperado según la propuesta de Fisher, se encontró que la proporción de sexos de la población al momento del emplumado está sesgada hacia los machos (56%; artículo I). El sesgo hacia los machos se presentó desde la eclosión, y globalmente la mortalidad durante el periodo de crianza de los 420 machos y 331 hembras de nuestra muestra fue similar: 23% y 24%, respectivamente (artículo I).

Variación de la proporción de sexos con las condiciones reproductivas

Durante 1989, el año en que se realizó un registro intensivo de la colonia, la proporción de sexos no aumentó al avanzar la temporada reproductiva (artículo I). Sin embargo, la predicción de un aumento en la proporción de machos durante años pobres para la reproducción fue apoyada por los datos. Durante 1989-1994 las proporciones sexuales al emplumado estuvieron significativamente sesgadas hacia machos, excepto en 1993 (artículo I). La proporción de machos que emplumaron fue diferente en cada año, variando desde 52% hasta 72%. Esta variación interanual estuvo relacionada con la temperatura promedio superficial del mar: el sesgo hacia machos aumentó cuando la temperatura del agua aumentó y presumiblemente la disponibilidad de alimento fue menor (artículo I).

Ajustes de la proporción de sexos

No se encontró evidencia de que las proporciones sexuales a la eclosión o al emplumado sean ajustadas de acuerdo al orden de eclosión o a la experiencia reproductiva de los padres. En puestas de dos y tres huevos, la proporción de machos que eclosionó y emplumó en la primera y última posición dentro de la nidada fue similar (artículo I). Sólo en puestas de tres huevos una proporción menor de hembras eclosionó en segunda posición que en tercera posición (artículo I).

La experiencia reproductiva de los padres no afectó la proporción de sexos que produjeron en una temporada. La proporción de machos que produjeron padres anillados fue independiente del número de intentos reproductivos o del éxito reproductivo (crías emplumadas) previos a la temporada de 1989 (artículo I).

Inversión alimenticia en hembras y machos

No se encontró evidencia de que las hijas reciban una mayor inversión alimenticia que los hijos. Las hembras mantuvieron tasas de crecimiento (incremento en peso y ulna) mayores que las de los machos cuando ambos sexos recibieron la misma cantidad de alimento (artículo II). La frecuencia de alimentaciones parentales a emplumados, y posiblemente la duración del cuidado parental fueron similares para hembras y machos (artículo II).

Mortalidad

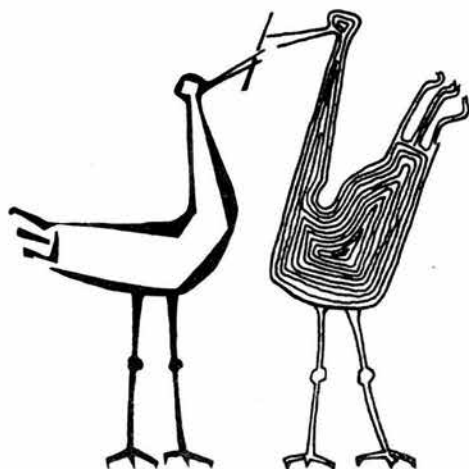
Durante 1989 la mortalidad global de crías hembra y macho no fue diferente. Sin embargo, cuando se analizaron los cambios en la mortalidad a través de la temporada reproductiva, el aumento en la mortalidad de hembras al avanzar la temporada fue mayor que el aumento en machos, llegando a ser 25% y 26% más alto en crías que eclosionaron en segunda y tercera posición, respectivamente, en nidadas tardías (artículo III). Aún en años muy buenos, como fue el caso de 1989, las condiciones para la reproducción en esta colonia se deterioran al avanzar la temporada reproductiva

(García-Cerecedo y Saavedra-Sordo, en prep.). Los resultados indican que las crías hembra parecen ser más vulnerables a disminuciones en la cantidad de alimento, y bajo condiciones de escasez tuvieron una probabilidad de morir más alta que la de los machos.





I



Running Head: Sex ratio in a dimorphic bird

VARIABLY MALE-BIASED SEX RATIO IN A MARINE BIRD WITH
REVERSED SIZE DIMORPHISM

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Abstract

According to Fisher's hypothesis, progeny sex ratios should be biased toward the less expensive sex when the costs of rearing males and females differ. Blue-footed booby (*Sula nebouxii*) females are larger and roughly 32% heavier than males, thus presumably more costly to rear. We recorded hatching and fledging sex ratios in 1989, and fledging sex ratios during the next four years. In 1989, the sample of 751 chicks showed male bias at hatching (56%) and at fledging (56% at ~90 d). Fledging sex ratios during the four subsequent reproductive seasons were consistently male-biased, varying from 52% to 72%. These variations were positively related to mean sea surface temperature: male bias was greater during years when water was warmer and food was presumably in short supply. No evidence of sex ratio adjustment with laying date, hatching sequence, or parent's reproductive experience was found. Thus, male-biased sex ratio and the increased male bias during poor years supports the idea that daughters may be more costly than sons.

Key words: sex ratio, size dimorphism, interannual variation, *Sula nebouxii*.

Key phrases: Progeny sex ratio in a size dimorphic bird; Sex ratio variation among years vs. food supply; Sex ratio adjustments with laying sequence and reproductive experience.



INTRODUCTION

Fisher (1930) suggested that the total investment by parents in offspring of each sex should be equal at the end of parental care. This argument is based on the premise that the minority sex enjoys a mating advantage. When members of one sex are scarce in a population, parents that invest more in offspring of the less represented sex can expect, on average, more grandchildren, so a skewed population sex ratio will tend to unity in a few generations (Williams 1979, Charnov 1982). If some selective pressure results in one sex being more costly than the other, then equal investment implies overproducing offspring of the less expensive sex (Maynard Smith 1980, Charnov 1982, Trivers 1985, Gowaty 1991).

A sex ratio close to unity could simply be the result of Mendelian segregation; thus, species where daughters and sons represent different costs are especially relevant for testing predictions from sex ratio theory. Here, we report a male-biased sex ratio at hatching and at fledging, and interannual variation of the sex ratios at fledging in the blue-footed booby (*Sula nebouxii*), a species with reversed sexual size dimorphism (females larger than males). Evidence of parental adjustment of the sex ratio was also sought by testing predictions related to sex ratio variation with breeding conditions, laying sequence and parent's reproductive experience.



In dimorphic species, production of the larger sex is presumed more costly because of its higher food requirements (Fiala 1981, Teather 1987, Teather and Weatherhead 1988); hence, according to Fisher's hypothesis a biased sex ratio is expected. However in bird species, the influence of size dimorphism on the relative costs of raising sons and daughters is not clear. Although differential provisioning of sons and daughters has rarely been found in sexually size-dimorphic birds (Slagsvold et al. 1986, Teather and Weatherhead 1988, review in Stamps 1990), laboratory evidence suggests that the larger sex has greater energetic needs (Fiala 1981, Fiala and Congdon 1983, Teather and Weatherhead 1988) or food consumption (Teather 1987, Frumkin 1988 but see Newton 1978, Newton and Marquiss 1979). Also, expected variations in sex ratios of avian species with size dimorphism have rarely been found (Table 1). In fact, when females are the larger sex just one study shows a male-biased ratio and the only other study shows a female-biased ratio (Table 1).

Richter (1983) proposed that differences in the developmental patterns of male and female nestlings may balance the cost of producing offspring of each sex, which could explain the unbiased sex ratios of some dimorphic birds (table 1; Clutton-Brock 1986). However, a review of the growth of 16 dimorphic avian species suggests that the larger sex may indeed require greater parental investment; the larger sex had faster growth rates with respect to mass and tarsus length, while growth

of feathers and age at fledging were similar for both sexes (Richner 1991).

Differential mortality by sex during the period of parental care may also affect the relative costs of sons and daughters and potentially acts as a selective pressure for modification of the sex ratio (Maynard Smith 1980, Trivers 1985). If one sex suffers greater mortality, investment in that sex will end earlier, on average, than investment in the other sex, making the former sex cheaper. Differential mortality has been associated with sexual differences in growth patterns, with the larger sex possibly being intrinsically more susceptible to starvation mortality because of its faster growth rate (Clutton-Brock 1985). Alternatively, it has been suggested that greater mortality of the larger sex in dimorphic species may function to equalize investment in sons and daughters (Slagsvold 1990).

Fisher's arguments apply to total investment in sons and daughters within a population. At the individual level, sex ratio adjustment may occur in response to prevailing individual or ecological circumstances (Trivers and Willard 1973, Williams 1979, Charnov 1982, Gowaty 1991). When sons and daughters represent different costs, individuals may need to adjust their progeny sex ratio according to such variables as availability of resources essential to reproduction (Howe 1977, Meathrel and Ryder 1987) or their own age or reproductive experience (Blank and Nolan 1983). For example, in a population of red-winged blackbirds (*Agelaius phoeniceus*), Blank and Nolan (1983) showed

that, although the overall sex ratio of fledglings was 1:1, fewer sons were produced as the season advanced. Sex ratio decrease was associated with maternal age: older mothers tended to overproduce sons (the larger sex) and bred early in the season.

Further evidence for sex ratio adjustment comes from populations in which sex varied with egg-laying sequence (Howe 1977, Ankney 1982 but see Cook and Harmsen 1983, Meathrel and Ryder 1987), and in populations in which sex variation with egg-laying sequence was associated with laying date (Howe 1977, Edmunds and Ankey 1987, Dijkstra et al. 1990).

The blue-footed booby

Females of the blue-footed booby are roughly 32% heavier than males: mass of adults is 1654 ± 127.5 g (mean \pm standard deviation) for females and 1250 ± 113.9 g for males (Castillo and Chavez-Peón 1983). These altricial birds raise from one to three chicks, which hatch at intervals of roughly 4 d (Drummond et al. 1986). Blue-footed boobies are apparently monogamous and highly philopatric (Nelson 1978, Osorio-Beristain and Drummond 1993).

At hatching, nestlings of both sexes are similar in size and mass (ulna: 23.1 ± 0.8 mm for males and 23.3 ± 0.7 mm for females, $t = 0.19$, $df = 20$, $P = 0.84$; mass: 45.5 ± 5.64 g for males and 42.7 ± 5.4 g for females, $t = 1.01$, $df = 15$, $P = 0.32$; unpub. data). However, females grow faster and reach a higher asymptotic mass and size (length of ulna and culmen) than males, although they take on average 4.5 d longer to complete plumage development (Drummond et al. 1991).

Facultative brood reduction through siblicidal aggression occurs when food is scarce, and typically the younger chick is more likely to die (Drummond *et al.* 1986, Drummond *et al.* 1991). Soon after the brood is completed, a dominant-submissive relationship is established between siblings, facilitated by the initially superior size and maturity of first-hatched chicks (Drummond and Osorno 1992). The dominance of the first-hatched chick is seldom reversed, even in broods where a female hatches after a male and as a result of sexual size dimorphism eventually outgrows her elder brother (Drummond *et al.* 1991, Drummond and Osorno 1992).

We derived predictions from Fisher's theory, on the assumption that female blue-footed booby chicks cost more to produce than male chicks, because of their greater size. (1) The overall progeny sex ratio of the population should be male-biased at fledging. This could be achieved through a male-biased sex ratio at hatching or greater mortality of female nestlings.

For the booby colony on Isla Isabel, food availability and breeding conditions deteriorate over the reproductive season and vary among years. Sea surface temperature (an indicator of sea productivity) increases as the reproductive season advances, and it is negatively associated with the number of chicks that fledge (García-Cerecedo and Saavedra-Sordo, *in prep.*). There is considerable variation in reproductive success among years; for example, not a single chick was produced during the El Niño event of 1992, compared with 688 fledglings produced in 1994 (García-

Cerecedo and Saavedra-Sordo, in prep.). Thus, under poor breeding conditions the greater cost of the larger sex may increase and consequently, (2) the sex ratio should increase (more males) as the season advances and (3) the sex ratio bias toward males should increase during years of food shortage.

In the blue-footed booby last-hatched chicks suffer greater mortality than their siblings (Drummond et al. 1991). Hence, to equalize investment in sons and daughters parents could bias mortality toward (costly) females by hatching females last. This parental manipulation should be evidenced at hatching by (4) a higher proportion of females in final position than in earlier positions in the hatching sequence, and at fledging by (5) a lower proportion of females in final position than in earlier positions in the hatching sequence.

We looked for evidence of adjustment of sex ratios at hatching and fledging at the individual level. Since reproductive experience (number of reproductive attempts and previous reproductive success) is likely to enhance parents' ability to invest (e.g. Ollason and Dunnet 1978), (6) experienced parents should produce lower sex ratios (fewer males) than inexperienced parents.

METHODS

This study was conducted on Isla Isabel, Mexico, during 1989-1994. The intensive recording in 1989 covered most of the breeding season (February 12 to July 23), and approximately 80% of the nests in the colony, including dense and sparse nesting areas. The data were collected in two sites, Las Monas and Costa Fragatas (roughly 200 m apart), located at the E and SE of the island respectively (map in Osorio-Beristain and Drummond 1993). All nests (scrapes with eggs and/or recently hatched chicks) found on our arrival or appearing subsequently were marked with numbered flags. Chicks were banded within 3 d of hatching using colored wire to differentiate hatching order, and with individually numbered plastic bands when they were 7 d old. Survival of chicks was recorded every three days until fledging (when a chick's head turned completely black at the end of plumage development; \bar{X} = 86 d for males, and 90.5 d for females, Drummond *et al.* 1991). Additionally, all marked nests were also inspected daily at 1600-1800 h to recover any recently dead chicks for sexing. Ulna and culmen length were measured at fledging, when these structures approximate adult sizes (Drummond *et al.* 1991), and fledglings were permanently marked with individually numbered steel bands.

Of the 751 chicks used in analyses, the 574 fledglings were sexed by the length of the ulna at fledging, when males and

females have reached a non overlapping bimodal asymptote (Fig. 1; Drummond et al. 1991). Additionally, 207 banded chicks from our sample were sexed again by their voice (males whistle and females grunt, Nelson 1978) when they bred in the colony four years later, and only 1 case (0.5%) did not agree with morphometric determination at fledging.

The 176 chicks that died before fledging and whose bodies were recovered were sexed in the field by inspection of gonadal morphology. To test the reliability of the field sexing, gonads were preserved in karnovsky (pH 7.3) when chicks were younger than 30 d, and in 10% formalin when chicks were older. Tissue differentiation of gonads of a random sample of 100 chicks of all ages (1-90 d) was examined under the microscope. Males were identified by the presence of seminiferous cords and scattered Leyding cells; females showed sex cords and/or follicles containing germ cells undergoing the prophase of the first meiotic division (Drummond et al. 1991). Sex identification by two independent observers ignorant of the field identification agreed in every case, and sexing by morphology and tissue differentiation agreed in 99 of 100 cases.

The sex of all the hatched chicks was determined in a total of 400 broods (751 chicks). A further 116 broods were eliminated from our analyses (243 chicks) because we were unable to sex all members of each brood (Table 2). Excluded broods were considered to be an unbiased sample with respect to sex. We are not aware of any likely sources of bias. The 76 dead chicks whose bodies

were not found (representing 50.8% of excluded broods), were probably victims of predation, and were on average 9.52 d old (\pm 9.68 d, $N = 61$; 15 chicks were of unknown age). If mass and size are important determinants of predation risk, then it seems likely that males and females have similar probabilities of being preyed-on during their first 10 d of life. Male and female mass and size during the first 11 d of life are not significantly different (mass: 164.5 ± 35.1 g for males and 169.0 ± 35.4 g for females, $t = 0.41$, $df = 43$, $P = 0.68$; ulna 37.0 ± 3.9 mm for males and 37.9 ± 3.5 mm for females $t = 0.68$, $df = 44$, $P = 0.49$). Of the 76 chicks that were not found, 30 disappeared during the first 6 d of life, probably due to milk snake (*Lampropeltis triangulum*) predation (Drummond et al. 1991). The 46 chicks that disappeared when older than 6 d were probably scavenged by feral cats, crabs, gulls or great-blue herons (occasionally seen in the booby colony), or died away from their nests. Furthermore, overall, there were no sexual differences in mortality or age of death in the chicks that died and were sexed (see Results). Finally, the sex ratios of the excluded chicks at hatching and fledging were similar to unity: 51.5% ($N = 98$, $G = 0.08$, $df = 1$, $P = 0.77$) and 55.3% ($N = 65$, $G = 0.74$, $df = 1$, $P = 0.38$) males, respectively.

Since data recording began some time after the start of incubation, original clutch size of some broods is unknown. Eggs are sometimes lost, mainly to predation by gulls (*Larus heermanii*). However, there is no reason to expect that egg loss

to predation might affect one sex more than the other, and eggs of this species are similar in mass and size regardless of their position in the laying sequence (Castillo and Chavez-Peón 1983).

Hatching failure in our sample was high. Of the 230 two-egg clutches, 32.6% failed to hatch one egg; and of 135 three-egg clutches, 32.6% and 11.8% failed to hatch one and two eggs respectively. Differential mortality of the sexes during incubation could not be detected, because a nondestructive method for sexing an egg is not available (Fiala 1981, Griffiths 1992, Griffiths *et al.* 1992), so analyses of sex allocation and hatching order used only broods where all the eggs hatched.

Estimates of the ages of the 440 chicks included in the analyses that had already hatched at the beginning of the study, were based on (1) the average hatching interval of 4 d (Drummond *et al.* 1986), when we knew the hatching date of any chick in the brood, or (2) the average age of fledging, when we knew the fledging date. The estimated age was 13.4 ± 9.4 d (range, 1-54 d).

For the analyses of effects of reproductive experience, banded parents were classified by their previous (1) number of reproductive attempts, and (2) reproductive success (total number of chicks fledged). For both classifications we used data from 1982 to 1988.

To evaluate fledgling sex ratio variation between years, we used the data base from the long-term study of the blue-footed booby colony on Isla Isabel. These data were collected using a

similar protocol described above for 1989, except that survival was recorded every 3 days until most of the chicks on the colony were > 30 d old, and thereafter every 6 d until all chicks fledged. As an indicator of food availability, we used the mean sea surface temperature (C°) at roughly 9 km off Isla Isabel from January to July (the blue-footed booby reproductive season) of every year (satellite data from the University of Columbia in García-Cerecedo and Saavedra-Sordo, in prep.). Higher sea temperatures are associated with lower productivity and food shortage for marine birds (Schreiber and Schreiber 1989).

To test for an association between sex ratio and hatching date, and between sex ratio and parents' reproductive experience a logistic regression model was used. For this purpose we used a Generalized Linear Model with a logit link function and binomial distribution of error (Crawley 1993). The fit of this model is measured as a G statistic, which is distributed as χ^2 .

Williams' correction was used for all the G -tests of goodness of fit and independence (Sokal and Rohlf 1981), and all t -tests were two-tailed.

RESULTS

Overall Sex Ratio

No differences between the sex ratios of 299 broods from Las Monas and 101 broods from Costa Fragatas were found, so data from both sites were pooled for analyses. The two sites did not differ in the sex ratio at hatching ($N = 751$, $G = 1.31$, $df = 1$, $P = 0.25$) or at fledging ($N = 577$, $G = 1.24$, $df = 1$, $P = 0.26$).

The expected bias at fledging, under the assumption that females are more costly to rear than males, was confirmed. The sex ratio was significantly biased towards males both at hatching (55.9%, $N = 751$, $G = 10.57$, $df = 1$, $P = 0.001$), and at fledging (56.4%, $N = 574$, $G = 9.57$, $df = 1$, $P = 0.002$). Greater production of males was evident in broods from all clutch sizes, but was significantly different from unity only in broods of clutch size 3 (table 3).

The proportion of pre-fledging mortality was similar for 420 males (22.8%) and 331 females (24.4%, $G = 0.26$, $df = 1$, $P = 0.61$). Furthermore, the ages at which males (23.55 ± 1.936 d, $N = 77$) and females (25.60 ± 1.744 d, $N = 61$) died were similar ($t = -0.64$, $P = 0.52$).

Sex Ratio and Hatching Date

The expected increase in the sex ratio over the season was not supported. The proportion of males produced was independent of the breeding date. Pooling across all clutch sizes, sex ratio

did not vary significantly with date, either at hatching ($G = 0.15$, $df = 1$, $P = 0.69$) or at fledging ($G = 2.47$, $df = 1$, $P = 0.12$). Likewise, when clutch size was considered there was no association with date in the proportion of males that were produced, either at hatching ($G = 1.01$, $df = 2$, $P = 0.31$; Fig. 2a) or at fledging ($G = 1.30$, $df = 2$, $P = 0.25$; Fig. 2b).

Sex Ratio Variation Between Years

Sex ratios at fledging varied between years. From 1989 to 1994, excluding 1992 (an El Niño year when no chicks fledged), the sex ratios at fledging were significantly male-biased in all years except one (table 4), and the proportion of males varied significantly between years ($G = 23.60$, $df = 4$, $P < 0.0001$).

The prediction of increased male bias during warmer years was supported. The proportion of male fledglings each year showed a positive linear trend with the increase of mean sea temperature ($X^2 = 9.20$, $df = 1$, $P = 0.002$; Fig. 3).

Sex Ratio and Hatching Order

The relationship between sex ratio and hatching order within a brood was determined only in 1989 broods of two and three chicks where all the eggs of the clutch hatched. There was no clear evidence of a relationship between sex and hatching order: in 2-egg broods the sex ratio at hatching within each hatching position was not significantly different from 0.5 (Fig. 4a), although in 3-egg broods there was a significant male-bias in second position (Fig. 4b). The expected greater proportion of females hatched in final position within the brood was not

supported. In 2-egg broods, equal proportions of females were produced in first (43.3%) and second (43.3%) positions in the hatching sequence ($N = 310$, $G = 0.00$, $df = 1$, $P = 1.0$; Fig. 4a). In 3-egg broods, the proportions of females hatched in first (48.7%) and third (50.0%) positions were similar ($N = 152$, $G = 0.02$, $df = 1$, $P = 0.87$); however, a significantly smaller proportion of females hatched in second position (32.9%) than in final position (50.0%) within these broods ($N = 152$, $G = 4.60$, $df = 1$, $P = 0.03$; Fig. 4b).

At fledging, the expected lower proportion of females in final position than in earlier positions was not found. In 2-egg broods, similar proportions of females fledged in first and second positions ($N = 243$, $G = 0.19$, $df = 1$, $P = 0.66$; Fig. 4a). In 3-egg broods the proportion of females fledglings in final position (41.6%) was not significantly different from the proportion of female fledglings in first ($N = 111$, $G = 0.91$, $df = 1$, $P = 0.34$; Fig. 4b) and second positions ($N = 107$, $G = 0.68$, $df = 1$, $P = 0.40$; Fig. 4b). The fact that fewer females fledged in second position was the result of the greater proportion of males at hatching (Fig. 4b).

Sex Ratio and Reproductive Experience

There was no significant association between parents' reproductive experience and progeny sex ratio in 1989. The proportion of males produced was independent of the number of reproductive attempts before the year of our study, both at

hatching ($G = 0.53$, $df = 1$, $P = 0.46$; Fig. 5a) and at fledging ($G = 0.69$, $df = 1$, $P = 0.40$; Fig. 5b).

Similarly, previous reproductive success (number of fledglings) was independent of the proportion of males that banded parents produced in the year of our study, both at hatching ($G = 0.70$, $df = 1$, $P = 0.40$; Fig. 5c) and at fledging ($G = 0.45$, $df = 1$, $P = 0.50$; Fig. 5d).

DISCUSSION

The male-biased sex ratio found in the blue-footed booby seems to support Fisher's hypothesis, under the assumption that females are more expensive to produce than males because of their larger size. In 1989 this male-biased sex ratio was evident at hatching, and no further adjustment through differential mortality of male and female nestlings was found overall. There are very few reports of biased avian sex ratios at hatching (Gowaty and Lennartz 1985, review in Clutton-Brock 1986), and it is usually argued that hatching sex ratios of birds are fixed at unity (Clutton-Brock 1986, Weatherhead and Teather 1991). The scarcity of evidence for biased avian sex ratios at hatching is partly due to the difficulty of sexing newly hatched birds.

Mechanisms for biasing the sex ratio at conception have not been identified for birds, but plausible suggestions include non-random segregation of sex chromosomes, and earlier or faster

growth of ovarian follicles that will produce one sex (Howe 1977, Ankney 1982, Ryder 1983, Dijkstra et al. 1990, Gowaty 1991, Krackow 1995). However, even if the sex ratio at conception is close to unity, differential mortality during incubation could produce a biased sex ratio at hatching. In fact, in poultry chickens (*Gallus domesticus*), sex ratio variation of embryos seems to be related to length of incubation, with female chicks showing greater mortality under pre-hatching stress (Landauer 1967 in Myers 1978). At the moment, we have no data to evaluate how blue-footed boobies are biasing the sex ratio at hatching, and there are virtually no data for other undomesticated bird species.

The lack of variation of the sex ratio with laying date may be related to the apparently high food availability during 1989. The mean sea temperature in 1989 was 0.7°C lower than the mean temperature for the same period in all the years during 1982-1994, and lower sea temperatures are usually associated with higher productivity (Schreiber and Schreiber 1989). Accordingly, the number of fledglings in 1989 was 148% greater than the average number of fledglings produced during 1982-1993 in the same nesting area ($\bar{X} = 68 \pm 59.6$ fledglings per year, range 0 - 169; García-Cerecedo and Saavedra-Sordo, in prep.). If food was abundant during most of the 1989 breeding season, the differential cost of producing females may not have increased as the season advanced.

Assuming 1989-1994 is a representative period, this population overproduces males overall. Furthermore, increased male bias during years of poor breeding conditions is evidence that daughters may be more costly to produce than sons: in response to food shortage parents may hatch fewer daughters or relative mortality of daughters may increase. In fact, under poor conditions (last-hatched chicks from late broods) females suffer greater mortality than males (Torres and Drummond submitted). We do not know the sex ratios at hatching during 1990-1994, but the data from 1989 show that blue-footed boobies can produce a male-biased sex ratio at hatching and that under food stress females may die more often than males (Torres and Drummond submitted).

Blue-footed boobies did not show any clear association between sex and laying sequence that might further balance the parental investment in each sex. However, even if an equal proportion of daughters and sons is produced in the last position of the laying sequence, parental investment may be equalized through differential mortality of the larger sex when last hatched (Slagsvold 1990).

Likewise, abundant food in 1989 may account for the similarity in nestling sex ratios of parents with different reproductive experience; superior breeding capacity of experienced parents may simply not have been expressed in 1989. We need to compare the breeding performance of experienced and inexperienced parents in poor years to evaluate whether

inexperienced parents produce fewer females than experienced parents during food shortages.

Because most of the biased sex ratios observed hitherto in dimorphic birds are the result of differential mortality of male and female nestlings, it has been argued that these biased ratios may simply be the result of non adaptive greater mortality of the larger sex (Clutton-Brock 1986, Weatherhead and Teather 1991, Griffiths 1992). In the blue-footed booby, male-bias at hatching suggests that sex ratio in this size dimorphic bird may have been adjusted by natural selection; however, we cannot exclude the possibility of non adaptive differential mortality before hatching.

Although for dimorphic species, explanations for sex ratio variation have usually focused on the assumption that the larger sex is more expensive to rear and/or suffers greater mortality, alternative explanations (not necessarily mutually exclusive) are available (Frank 1990, Gowaty 1993). For example, Gowaty (1993) suggests that because of differences in natal dispersal by sex, local resource competition between relatives (Clark 1978) may be an important selective force for adjusting the sex ratio. A male-biased sex ratio at hatching and the increased male bias during poor years supports the idea that daughters are more costly than sons. We need to measure differences between sons and daughters in their food requirements and post-fledging interactions with parents, as well as looking for differential effects of sons and daughters on parental survival and future

reproduction, to clarify if the observed male-biased sex ratio in the blue-footed booby is an adaptive parental strategy.



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LITERATURE CITED

- Ankney, C.D. (1982) Sex ratio varies with egg sequence in lesser snow geese. *Auk* **99**, 662-666.
- Bancroft, G.T. (1986) Nesting success and mortality of the boat-tailed grackle. *Auk* **103**, 86-99.
- Bednarz, J.C. and Hayden, T.J. (1991) Skewed sex ratio and sex-biased hatching sequence in Harries's Hawks. *Am. Nat.* **137**, 116-132.
- Blank, J.L. and Nolan, V. (1983) Offspring sex ratio in red winged blackbirds is dependent on maternal age. *Proc. Nat. Acad. Sci. USA* **80**, 6141-6145.
- Bortolotti, G.R. (1986) Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *Am. Nat.* **127**, 495-507.
- Castillo, A. and Chavez-Peón, A. (1983) Ecología reproductiva e influencia del comportamiento en el control del número de crías en el bobo de patas azules, *Sula nebouxii* en la Isla Isabel, Nayarit. Unpublished thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México.
- Charnov, E. (1982) *The theory of sex allocation*. Princeton University Press, Princeton, N.J.
- Clark, A. (1978) Sex ratio and local resource competition in a prosimian primate. *Science* **201**, 163-165.

- Clutton-Brock, T.H., Albon, S.D. and Guinness, F.E. (1985) Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* **313**, 131-133.
- Clutton-Brock, T.H. (1986) Sex ratio variation in birds. *Ibis* **120**, 317-329.
- Cooke, F. and Harmsen, R. (1983) Does sex ratio vary with egg sequence in lesser snow geese? *Auk* **100**, 215-217.
- Crawley, M.J. (1993) *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.
- Dhondt, A.A. (1970) The sex ratio of nestling Great Tits. *Bird Study* **17**, 282-286.
- Dijkstra C., Daan, S. and Buker, J.B. (1990) Adaptive seasonal variation in the sex ratio of kestrel broods. *Functional Ecology* **4**, 143-147.
- Drummond, H., Gonzalez, E. and Osorno, J.L. (1986) Parent-offspring cooperation in the blue-footed booby (*Sula nebouxii*): social roles in infanticidal brood reduction. *Behav. Ecol. Sociobiol.* **19**, 365-372.
- Drummond, H., Osorno, J.L., Torres, R., García-Chavelas, C. and Merchant Larios, H. (1991) Sexual size dimorphism and sibling competition: implications for avian sex ratios. *Am. Nat.* **138**, 623-641.
- Drummond, H. and Osorno, J.L. (1992) Training siblings to be submissive losers: dominance between booby nestlings. *Anim. Behav.* **44**, 881-893.

- Edmunds, S.R. and Ankney, C.D. (1987) Sex ratios of hatchlings morning doves. *Can. J. Zool.* **65**, 871-874.
- Edwards, T.C., Collopy, M.W., Steenhof, K. and Kochert, M.N. (1988) Sex ratios of fledging golden eagles. *Auk* **105**, 793-796.
- Fiala, K.L. (1981) Reproductive cost and the sex ratio in Red-winged Blackbirds. In *Natural selection and social behavior* (R. D. Alexander and D. W. Tinkle eds.), pp 198-214. Chiron Press, New York.
- Fiala, K.L. and Congdon, L.D. (1983) Energetic consequences of sexual size dimorphism in nestling red-winged blackbirds. *Ecology* **64**, 642-647.
- Fisher, R.A. (1930) *The genetical theory of natural selection*. Clarendon Press, Oxford.
- Frank, S.A. (1990) Sex allocation theory for birds and mammals. *Annu. Rev. Ecol. Syst.* **21**, 13-55.
- Frumkin, R. (1988) Egg quality, nestling development and dispersal in the Sparrowhawk (*Accipiter nisus*). Ph.D. diss. University of Oxford, Oxford.
- García-Cerecedo, M.A. and Saavedra-Sordo, M.T. (in prep.) Variación interanual en el esfuerzo y éxito reproductivo del bobo de patas azules (*Sula nebouxii*) y sus implicaciones en la reducción facultativa de la nidada. Bch thesis, Facultad de Ciencias, Universidad Autónoma de México.
- Gowaty, P.A. (1991) Facultative manipulation of sex ratios in birds, rare or rarely observed? In *Current Ornithology* Vol. 8. pp 141-171.

- Gowaty, P.A. (1993) Differential dispersal, local resource competition and sex ratio variation in birds. *Am. Nat.* **141**, 263-280.
- Gowaty, P.A. and Lennartz, M.R. (1985) Sex ratios of nestling and fledging Red-cockaded woodpeckers (*Picoides borealis*) favor males. *Am. Nat.* **126**, 347-353.
- Griffiths, R. (1992) Sex-biased mortality in the lesser black-backed gull *Larus fuscus* during the nestling stage. *Ibis* **134**, 237-244.
- Griffiths, R., Tiwari, B. and Becher, S.A. (1992) The identification of sex in the starling *Sturnus vulgaris* using a molecular DNA technique. *Molecular Ecology* **1**, 191-194.
- Howe, H.F. (1977) Sex ratio adjustment in the common grackle. *Science* **198**, 744-745.
- Krackow, S. (1995) Potential mechanisms for sex ratio adjustment in mammals and birds. *Biol. Rev.* **70**, 225-241.
- Ligon, J.D. and Ligon, S.H. (1990) Female-biased sex ratio at hatching in the green woodhoopoe. *Auk* **107**, 765-771.
- Maynard Smith, J. (1980) A new theory of sexual investment. *Behav. Ecol. Sociobiol.* **7**, 247-251.
- Meathrel, C.E. and Ryder, J.P. (1987) Sex ratios of ring-billed gulls in relation to egg size, egg sequence and female body condition. *Colonial Waterbirds* **10**, 72-77.
- Myers, J.H. (1978) Sex ratio adjustment under food stress: maximization of quality or numbers of offspring? *Am. Nat.* **112**, 381-388.

- Nelson, J.B. (1978) *The Sulidae: gannets and boobies*. Oxford University Press, London.
- Newton, I. (1978) Feeding and development of Sparrowhawk nestlings. *J. Zoo, London* **184**, 465-487.
- Newton, I. and Marquiss, M. (1979) Sex ratio among nestlings of the European sparrowhawk. *Am. Nat.* **113**, 309-315.
- Ollason, J. and Dunnet, G.M. (1978) Age, experience and other factors affecting the breeding success of the fulmar, *Fulmarus glacialis*, in Orkney. *J. Anim. Ecol.* **47**, 961-976.
- Olsen, P.D. and Cockburn, A. (1991) Female-biased sex allocation in peregrine falcons and other raptors. *Behav. Ecol. Sociobiol.* **28**, 417-423.
- Osorio-Beristain, M. and Drummond, H. (1993) Natal dispersal and deferred breeding in the blue-footed booby. *Auk* **110**, 234-239.
- Picozzi, N. (1980) Food, growth, survival and sex ratio of nestling Hen harriers *Circus c. cyaneus* in Orkney. *Ornis Scand.* **11**, 1-11.
- Richner, H. (1991) The growth dynamics of sexually dimorphic birds and Fisher's sex ratio theory: does sex specific growth contribute to balanced sex ratios? *Functional Ecology* **5**, 19-28.
- Richter, W. (1983) Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics. *Am. Nat.* **121**, 158-171.
- Ryder, J. (1983) Sex ratio and egg sequence in ring-billed gulls. *Auk* **1**, 726-729.

- Sayce, J.R. and Hunt, J.L. (1987) Sex ratio of prefledging western gulls. *Auk* **104**, 33-37.
- Selander, R.K. (1960) Sex ratio of nestlings and clutch size in the bout-tailed grackle. *Condor* **62**, 34-44.
- Slagsvold, T. (1990) Fisher's sex ratio theory may explain hatching patterns in birds. *Evolution* **44**, 1009-1017.
- Slagsvold, T., Roskaft, E. and Engen, S. (1986) Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care: Fisher's theory applied to birds. *Ornis Scand.* **17**, 117-125.
- Sokal, R.R. and Rohlf, F.J. (1981) *Biometry*. 2d ed. W. H. Freeman, San Francisco.
- Stamps, J.A. (1990) When should avian parents differentially provision sons and daughters? *Am. Nat.* **135**, 671-685.
- Teather, K.L. (1987) Intersexual differences in food consumption by hand-reared great-tailed grackle (*Quiscalus mexicanus*) nestlings. *Auk* **104**, 635-639.
- Teather, K.L. and Weatherhead, P.J. (1988) Sex-specific energy requirements of great-tailed grackle (*Quiscalus mexicanus*) nestlings. *J. Anim. Ecol.* **57**, 659-668.
- Teather, K. and Weatherhead, P.J. (1989) Sex-specific mortality in nestling great-tailed grackles. *Ecology* **70**, 1485-1493.
- Torres, R. and Drummond, H. Sex-biased mortality in nestlings of a bird with reversed sexual size dimorphism. In prep.
- Trivers, R.L. (1985) *Social evolution*. Benjamin/Cummings, Menlo Park, California.

- Trivers, R.L. and Willard, D.E. (1973) Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**, 90-92.
- Weatherhead, P.J. (1983) Secondary sex ratio adjustment in red-winged blackbirds (*Agelaius phoeniceus*). *Behav. Ecol. Sociobiol.* **12**, 57-61.
- Weatherhead, P.J. and Teather, K. (1991) Are skewed fledglings sex ratios in sexually dimorphic birds adaptive? *Am. Nat.* **138**, 1159-1172.
- Wiebe, K.L. and Bortolotti, R. (1992) Facultative sex ratio manipulation in American kestrels. *Behav. Ecol. Sociobiol.* **30**, 379-386.
- Williams, G.C. (1979) The question of adaptive sex ratio in outcrossed vertebrates. *Proc. R. Soc. Lond.* **205**, 567-580.

Table 1. Sex ratios (males/males + females) at hatching and fledging in birds with sexual size dimorphism.

SPECIES	SEX RATIO	SEX RATIO	SOURCE OF VARIATION	SOURCE
	AT HATCHING	AT FLEDGING		
MALES LARGER THAN FEMALES				
Common grackle <i>Quiscalus quiscula</i>	0.51	0.37 *	greater male mortality	Howe 1977
Great-tailed grackle <i>Quiscalus mexicanus</i>	no data	0.50	greater male mortality	Teather and Weatherhead 1988
	no data	0.47 *		Teather and Weatherhead 1989
Boat-tailed grackle <i>Quiscalus major</i>	0.50	0.50		Bancroft 1988
	0.50	no data		Selander 1960
Red-winged blackbird <i>Agelaius phoeniceus</i>	0.50	0.50	SR variation with maternal age	Blank & Van Nolan 1983
	0.48	0.48		Field & Congdon 1983
	no data	0.50		Weatherhead 1983
Yellow-headed blackbird <i>Xanthocephalus xanthocephalus</i>	no data	0.50		Richter 1983
Rock <i>Corvus frugilegus</i>	0.50	0.50	greater male mortality	Stagevold et al. 1988
Great tit <i>Parus major</i>	no data	more males	greater female mortality competitive advantage of the larger sex	Dhondt 1970
Green woodhoopoe <i>Phoeniculus porphyrio</i>	no data	0.45	SR variation with date and brood size	Ligon & Ligon 1990
Ring-billed gull <i>Larus delawarensis</i>	no data	1978 0.50 1979 0.40 * 1982 0.50 1983 0.40 * 1984 0.50	SR variation between years	Meehrel & Ryder 1987
Lesser black-backed gull <i>Larus fuscus</i>	0.48	0.39 *	greater male mortality	Griffiths 1992
Western gull <i>Larus occidentalis</i>	0.53	0.47	greater male mortality	Sayce & Hunt 1987
FEMALES LARGER THAN MALES				
European Sparrowhawk <i>Accipiter nisus</i>	no data	0.50		Newton 1978 Newton & Marquis 1979
Harris's hawk <i>Parabuteo unicinctus</i>	no data	more males	SR variation with hatching order	Bednarek & Hayden 1991
Hen harrier <i>Circus c. cyaneus</i>	no data	0.46 *	pooled data from 25 years	Picozzi 1980
Bald eagle <i>Haliaeetus leucocephalus</i>	no data	0.50	SR variation with hatching order	Bortolotti 1986
Golden eagle <i>Aquila chrysaetos</i>	no data	more males	SR variation with food availability and between years	Edwards et al. 1988
European kestrel <i>Falco tinnunculus L.</i>	0.50	0.50	SR variation with laying date and hatching order	Dijkstra et al. 1990
American kestrel <i>Falco sparverius</i>	1988 0.52 1989 0.54 1990 0.56 *	1988 0.51 1989 0.54 * 1990 0.55 *	SR variation between years	Wiebe and Bortolotti 1992
Peregrine falcon <i>Falco peregrinus</i>	no data	0.48	SR variation with laying date	Olsen and Cockburn 1991

* significantly different from 0.5 ($P < 0.05$).
SR = sex ratio.

Table 2. Broods excluded from the analyses from the sample of 1989.

Cause of exclusion	Chicks		Broods
	not sexed	sexed	
Chicks lost their bands	14	15	14
Chicks did not fledge before our departure	7	0	4
Fledglings could not be sexed	6	5	5
Gonads decomposed	42	45	34
Chick disappeared	76	33	59
Total	145	98	116

Table 3. Hatching and fledging sex ratios (proportion of males) according to clutch size in 1989.

Clutch size	Hatchlings				Fledglings			
	M/M+F	N	G	P	M/M+F	N	G	P
1	0.62	35	2.30	0.129	0.65	29	2.79	0.094
2	0.54	385	2.46	0.116	0.54	299	2.06	0.151
3	0.57	331	7.17	0.007	0.58	246	6.41	0.011
Total	0.55	751	10.57	0.001	0.56	574	9.57	0.002

Table 4. Sex ratios (proportion of males) at fledging over five reproductive seasons.

SEX RATIOS AT FLEDGING				
	M/M+F	N	G	P
1989	0.56	574	9.57	0.002
1990	0.72	102	21.40	0.0001
1991	0.55	373	3.67	0.055
1993	0.52	428	0.59	0.44
1994	0.62	688	43.42	0.0001

FIGURE LEGENDS

Fig. 1. Asymptotic ulna lengths of 361 male and 283 female blue-footed booby fledglings, showing mean, *SD* (box) and range. Data from 1989.

Fig. 2. Sex ratios at hatching (a) and at fledging (b) through the 1989 season in broods from clutch size 1 (\blacktriangle), 2 (X), 3 (\blacksquare). Data were grouped in 10-d blocks for visual clarity (but not for statistical analysis). Adjusted regressions for each brood are shown by dashed lines for 32 broods of clutch size 1, solid lines for 213 broods of clutch size 2, and heavy solid lines for 131 broods of clutch size 3.

Fig. 3. Sex ratios at fledging and mean sea temperature ($^{\circ}$ C) in five years, from 1989 to 1994. 1992 was not included because no fledglings were produced that year.

Fig. 4. Sex ratio and laying sequence at hatching and at fledging in (a) 155 broods of two chicks and (b) 76 broods of three chicks; * = deviation from ratios of 0.5 ($P < 0.05$). Only broods from 1989 where all the eggs of the clutch hatched were used.

Fig. 5. Proportion of males produced at hatching (a and c) and at fledging (b and d) during 1989, in relation to parents' previous (1981-1988) reproductive attempts and reproductive success. 32 banded females and 30 banded males were used for the analysis.

Fig. 1

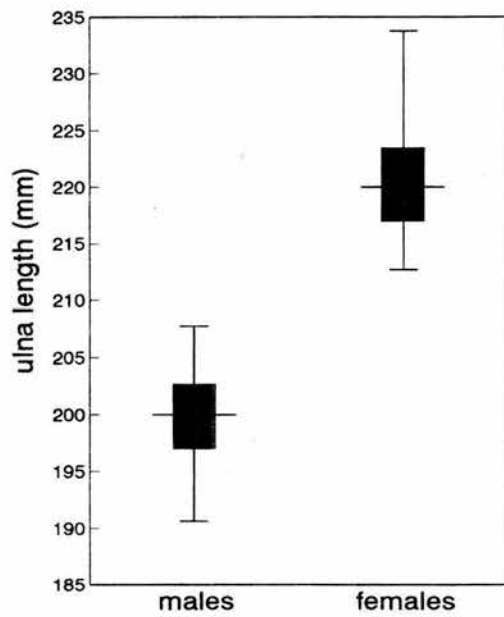


Fig. 2

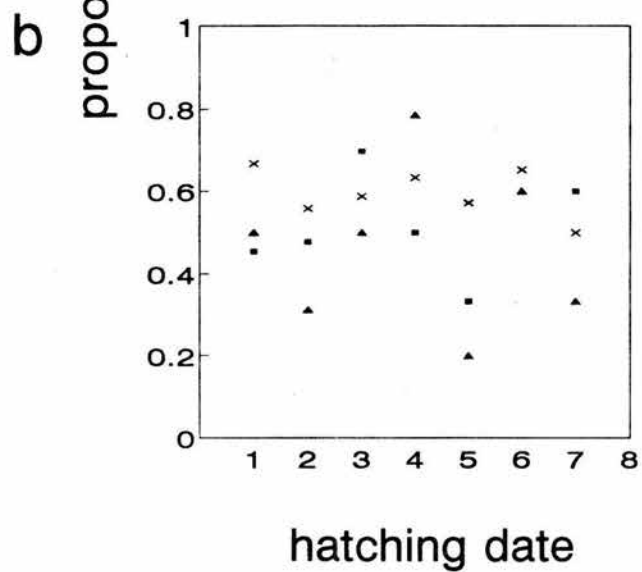
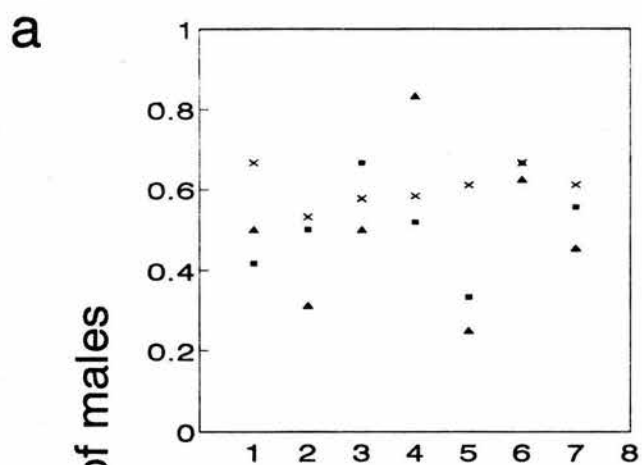


Fig. 3

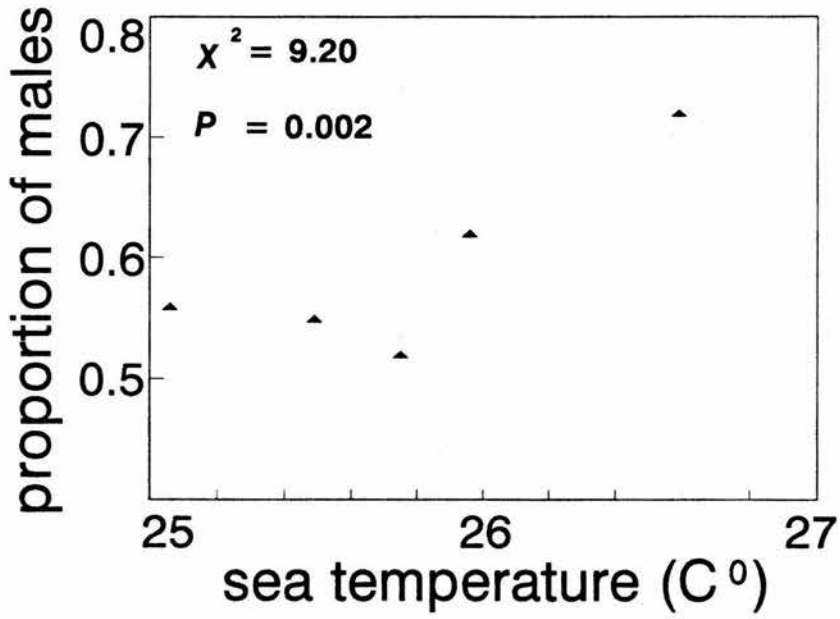
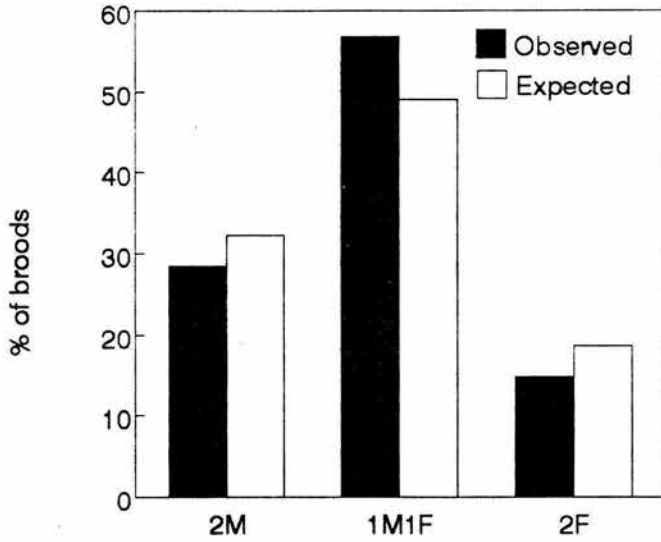


Fig. 4

a



b

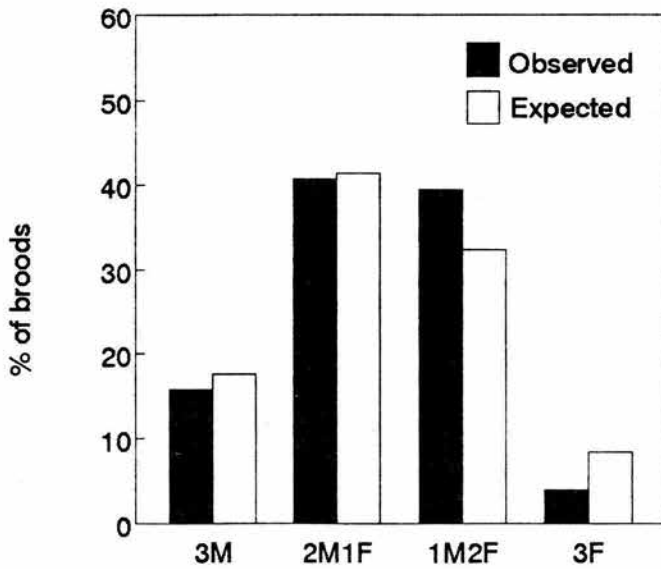
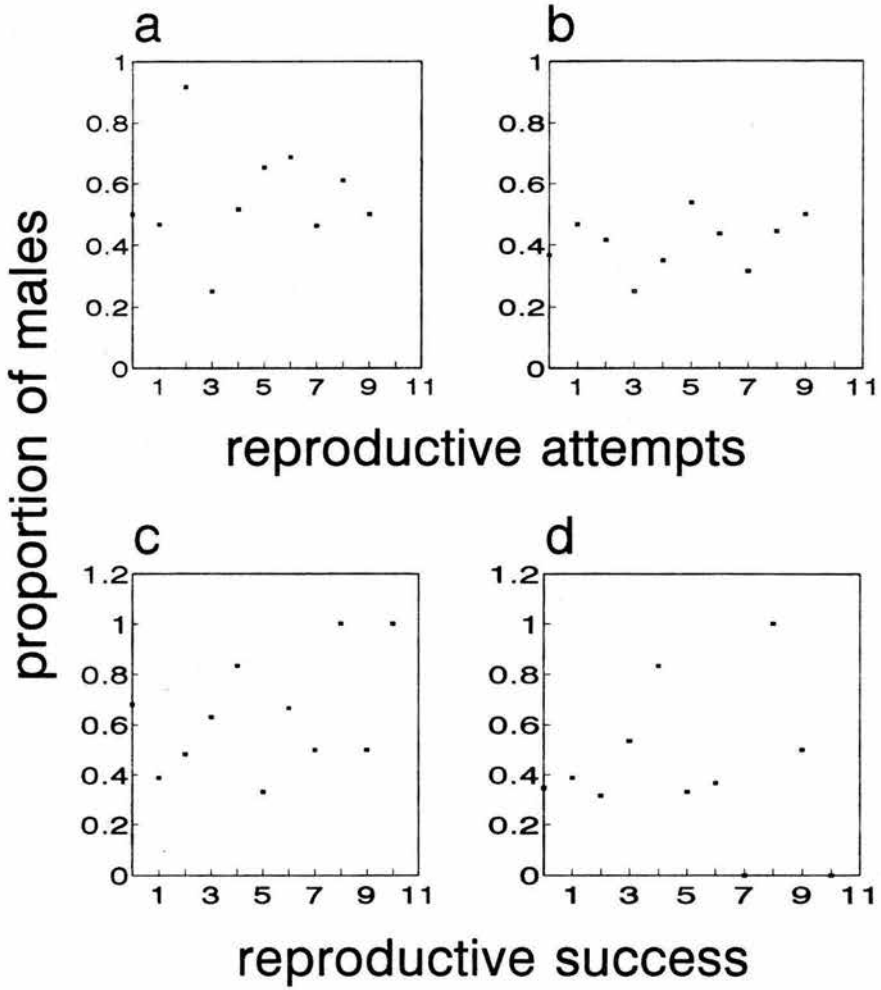
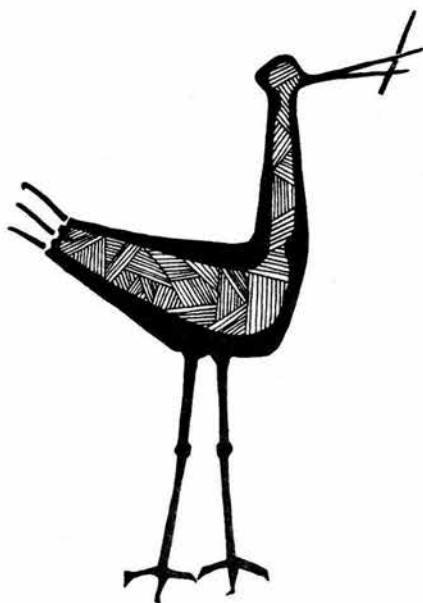


Fig. 5





II





DOES LARGE SIZE MAKE DAUGHTERS OF THE BLUE-FOOTED BOOBY MORE EXPENSIVE THAN SONS? BIBLIOTECA
CENTRO DE ECOLOGIA

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Key words: feeding investment, hand-fed, size dimorphism, *Sula nebouxii*.

Abstract

1. In species with size dimorphism individuals of the larger sex are presumably more expensive to produce than individuals of the smaller sex.
2. We evaluated if females of the blue-footed booby, because of their larger size, require a greater parental feeding expenditure than males.
3. A field experiment compared growth of sons and daughters when fed the same amount of food, and a descriptive field study compared the duration of parental care of sons and daughters.
4. Females maintained greater relative and absolute mass and ulna increases than males when hand-fed the same amount of food.
5. The proportion, and possibly the duration of the period of parental feeds to fledglings were similar for males and females.
6. No evidence that daughters of the blue-footed booby receive a greater feeding expenditure than sons was found. Faster motor development of males in this facultatively siblicidal species may explain how females maintain greater growth rates than males with the same food budget.



Introduction

In animal species where the sexes differ in size, it is generally claimed that members of the larger sex may be more expensive to produce than members of the smaller sex (Clutton-Brock et al. 1981). Individuals of the larger sex have higher growth and metabolic rates (Fiala 1981, Charnov 1982, Teather 1987, Teather and Weatherhead 1988), and presumably require more food during growth than the smaller sex (but see Newton 1978, Richter 1983, Stamps 1990).

Greater parental expenditure on offspring of the larger sex has been reported in several polygynous species of mammals and birds where males are larger than females (Clutton-Brock 1991 for a review). For example, in mammals greater milk intake by male offspring occurs in the red deer (*Cervus elaphus*, Clutton-Brock et al. 1981), the african elephant (*Loxodonta africana*, Lee and Moss 1986) and the american bison (*Bison bison*, Wolff 1988); although equal maternal investment in male and female offspring has been observed in the southern elephant seal (*Mirounga leonina*, MacCann et al. 1989) and the grey seal (*Halichoerus grypus*, Smiseth and Lorentsen 1995).

In birds, greater energy demands and food consumption by the larger sex have been reported in species where male nestlings are larger than females (Fiala 1981, Fiala and Congdon 1983, Slagsvold et al. 1986, Teather 1987 and 1992, Teather and Weatherhead 1988). For example, in red-winged blackbirds



(*Angelaius phoeniceus*), where males are roughly 30% heavier than females, total energy assimilated between hatching and fledging is 27% greater for males than for females (Fiala and Congdon 1983); males were fed 29% more often than females (Teather 1992); and parental feeding rates increased with the proportion of males in the brood (Yasukawa et al. 1990).

When females are the larger sex, parental expenditure on daughters and sons has not been compared in mammals (Clutton-Brock 1991), and the data for birds are scarce and inconclusive. Observations of a small sample of sparrowhawks (*Accipiter nisus*) in captivity suggest that female nestlings, which grow to be roughly 73% heavier than males, may consume more food than males when food is provided ad libitum (Frumkin 1988), although in the field both sexes appeared to consume similar amounts (Newton 1978; Newton and Marquiss 1979). In the golden eagle (*Aquila chrysaetos*), female nestlings grow to be roughly 30% heavier than males, but they did not consume significantly more food than males when the 10-week rearing period was analyzed, either in the field or in captivity (Collopy 1986). However, females in the field consumed on average 39% more food than males during the last 5 weeks of the rearing period, and captive females were capable of consuming more food per meal than were males (Collopy 1986).

Differences in the relative costs of producing sons compared to daughters have implications for the population sex ratio. According to Fisher's (1930) theory, total investment by parents

in offspring of each sex should be equal at the end of parental care. If individuals of one sex are more costly, then equal investment implies producing more offspring of the less expensive sex, and a sex ratio biased towards the cheaper sex is expected at independence.

Females of the blue-footed booby (*Sula nebouxii*) are larger and about 27% heavier than males at 79 d, when the growth curves reach the asymptote (Drummond et al. 1991, Guerra and Drummond 1995), and thus may represent a greater cost to the parents. Although male and female nestlings do not differ in size and mass at hatching (Torres and Drummond submitted), females grow faster and reach a higher asymptotic size and mass (Drummond et al. 1991).

The blue-footed booby raises from one to three chicks, which hatch at intervals of approximately 4 d (Drummond et al. 1986). Both parents incubate the clutch and feed their nestlings by regurgitating sardines and anchovies into their mouths (Nelson 1978). However, although male and female parents feed their brood similarly during the first week, thereafter, and until chicks are at least 60 d old, females provide from two to five times as much mass of food as males (Guerra and Drummond 1995). Parents predigest food before transferring it to very young chicks and transfer whole fishes to older chicks (Guerra and Drummond 1995). Thus, as feeds increase in size with the chick's age, the frequency of feeds declines: diurnal feeds decreased approximately from 10 to 2 feeds per day between ages 10 and 60 d

(Guerra and Drummond 1995). Parental feeding continues for some time after chicks have fledged (when plumage development is completed: \bar{X} = 86.0 d for males and 90.5 d for females; Drummond et al. 1991). Chicks remain near the nest and are attended continuously by at least one parent during the first 8-9 weeks of life (Nelson 1978); thereafter they frequently wander around during the day and return to nests sites to be fed by their parents.

Progeny sex ratios of the blue-footed booby are male-biased, with 59% male fledglings overall across five reproductive seasons (Torres and Drummond submitted). Greater production of sons agrees with Fisherian expectations under the assumption that daughters, because of their larger size, are more costly to rear. To assess whether the observed sex ratio does reflect such an adjustment of expenditure, we evaluated whether daughters do indeed cost more to rear than sons. To do this, we compared the growth of male and female chicks experimentally fed the same amount of food in the natal nest during the age of maximum daily growth rates. If daughters normally sustain their faster growth by consuming more food than sons, we predicted that (1) daughters and sons would have similar growth rates when fed the same amount of food.

Differential investment in daughters and sons may also occur toward the end of parental care. To detect this, we compared natural feeding rates to sons and daughters after fledging. If daughters require a greater investment than sons to reach

independence, we predicted that (2) female fledglings should be provisioned more frequently or for a longer period than male fledglings.

Methods

Field work was conducted from March to July 1994 in the blue-footed booby colony on Isla Isabel, off the Pacific coast of Mexico. All nests in the long-term study area were marked and surveyed every second day, which allowed us to estimate the age of chicks (± 2 d). Nestlings were marked with a colored wire at hatching, and a numbered plastic band from age 7 d. Survival of nestlings was recorded until fledging, and fledglings were permanently banded with individually numbered steel bands. Chicks were sexed by the length of their ulna at fledging, when this structure has reached an asymptotic bimodal size (Drummond et al. 1991, Torres and Drummond submitted). This is a reliable method of sexing blue-footed boobies; in a random sample of 16 fledglings, sex determination by ulna length and later gonadal examination agreed in all cases (Drummond et al. 1991). Additionally, the sex of 207 fledglings determined by ulna length was verified 4 years later by sexing on the basis of the highly distinct adult vocalizations, and in only 1 case did it not agree (Torres and Drummond submitted).

Feeding experiment

SUBJECTS. We used only chicks from single-chick broods to exclude variance due to sibling interactions. Eighty-eight single chicks initially aged 22 d were randomly assigned to three treatment groups: 28 underfed chicks (hereafter, the austere group), 33 abundantly fed chicks (the plentiful group), and 27 unmanipulated chicks (the reference group). To avoid any bias distribution of group assignation, chicks were sorted according to their hatching date in blocks of 7 d, and then randomly assigned to each treatment group. The fact that male and female chicks cannot be distinguished when they are young kept us blind with respect to the sex of the chicks during the feeding experiment.

TREATMENT. To control the amount of food a chick received, we hand-fed the chicks at their nests and placed an adhesive cloth tape around their necks (explained below) to prevent parental feeding between hand-feeding events. Chicks from the austere and plentiful groups were fed during 9 consecutive days, from ages 22 to 30 d. This age interval includes the maximum daily growth rates for ulna length and mass of 13 female and 17 male chicks from natural nests (mean \pm 1 *SD*, ulna: 5.31 ± 0.10 mm/d, range = 0.04 - 5.41 for females, and 5.02 ± 0.07 mm/d, range = 0.02 - 5.11 for males; mass: 46.32 ± 2.39 g/d, range = 0.17 - 48.66 for females, and 38.12 ± 0.84 g/d, range = 0.08 - 39.01 for males;

means and *SD* are for the interval 22 to 30 d, while ranges are for ages 1 to 91 d, unpublished data).

Nestlings were fed beside their home nests by opening their beaks and putting fragments of fresh local fish (skipjack, *Katsuwonus pelamis*, and bonita, *Sarda sarda*) into their mouths. Experimental chicks accepted the new diet and feeding method. The amounts of food for the austere and plentiful groups were based on the estimated baseline food intake of blue-footed booby chicks of similar ages. Guerra and Drummond (1995) reported that between ages 22 and 30 d first-hatched chicks received a total of 1854 g of fish. The amount of food delivered to experimental nestlings in the austere and plentiful groups was 150 and 200 g (± 1 g) of fish per day, respectively, plus a 5% increment every 2 d in both groups. During the 9 days of treatment, chicks from the austere group received a total of 1472 g, which is 21% less than the baseline, while chicks from the plentiful group received a total of 1964 g or 6% above the baseline.

Each chick's daily ration was delivered in three feeding visits, a frequency similar to that performed by parents with chicks of similar ages (\bar{X} = 3.4 feeds in a 12-h period, range = 1 - 12, on Isla Isabel, Mexico, Guerra and Drummond 1995; roughly 3.0 feeds in a 24-h period for two-chick broods, on Isla Española, Galapagos Islands, their figure 7, Anderson and Ricklefs 1992). Feeding visits were performed at roughly 0600, 1100, and 1600 h, providing 40, 20 and 40%, respectively, of the daily ration.

To avoid any ingestion of parental feeds, an adhesive cloth tape (Micropore) was placed around the necks of the experimental nestlings, at the base of the cranium. This method of controlling the amount of food delivered to blue-footed booby chicks has been used for up to 3 d, without any signs of permanent harm (Drummond and Garcia-Chavelas 1989; Nuñez and Drummond in press; Rodríguez-Gironés et al. in press).

Thirteen chicks died during the experiment: six chicks disappeared, possibly victims of predation by feral cats; two chicks died, showing serious injuries which were probably caused by adult neighbors (Drummond et al. 1991); and another five chicks were smaller and looked weaker than the rest of the experimental chicks from the start of the experiment. We could not discount possible association between the experimental treatment and the death of these last five chicks; they were all from the latest 26 broods included in the experiment, and from day 1 their masses were 11% lower and their ulnas were 9% shorter than those of the other experimental chicks. Because four of these five dead chicks belonged to the plentiful group, we decided to remove the tapes from all of the chicks which were still active in this treatment (4 females and 5 males); all nine of them survived until fledging, but neither they nor the five dead chicks of the plentiful group were included in our analyses.

Hand-fed chicks were weighed on an Ohaus electronic balance (0 - 6000 \pm 1 g) before each feeding, and every morning the lengths of their left ulnas were measured (\pm 1 mm). Chicks were

weighed and measured during three additional days after the feeding treatment was over (when tapes were removed at approximately 1800 h), to verify that they were being normally fed by their parents. Chicks from the reference group were simply weighed and measured on the same schedule as hand-fed chicks, but they were not taped or fed by us. Hence, reference chicks were not a strict control, but rather a group illustrating normal growth of chicks comparable to experimental chicks. Daily survival of experimental and reference chicks was recorded until fledging ($X = 86.0$ d for males and 90.5 d for females).

We analyzed growth by calculating the rate of absolute increase of each of the two dependent variables (mass and ulna length) of every chick; we used the slope of the linear regression fitted to its measures over the nine days. Because absolute growth rates could be influenced by the initial size of the chicks, we also compared the rate of relative increase, calculated as the difference between its final and initial measures divided by the initial measure. The rates of absolute and relative ulna and mass increases of male versus female nestlings were compared using Two-way ANOVA's, with treatment (austere, plentiful and reference groups) and sex of the chick as the main factors. Duncans' multiple post hoc comparisons were made using a global significance level of 0.05.

Parental feeding after fledging

Parental feeds to fledglings were recorded daily from 1400 to 1900 h, which includes the peak daylight feeding period (personal observations). Continuous recording of parental feeds to fledglings during one 12-h period from 600 to 1900 h showed that 96% of feeds occurred after 1400 h (N = 28 feeds, personal observations). On Isla Española, Galapagos, 70% of daily parental provisioning to blue-footed booby chicks heavier than 300 g occurred between 1400 and 2200 h, and most feedings were during the 2-h period preceding nightfall or after dark (Anderson and Ricklefs 1992). To register parental feeds to fledglings, an observer walked slowly along a fixed route through the study area, stopping for 30 minutes every 30 m. The direction of the route was alternated every day to avoid any possible bias by systematically passing through the same area at the same time. She recorded all feeds given by parents to fledglings within an estimated 30 m radius of her, noting each fledgling's band number (using 10 X 23 binoculars). Each chick's age and sex determined by the length of their ulna were recovered subsequently from data in our project's routine surveys and measurements of all chicks. Feeding records began on June 16, when roughly 20% of first-hatched chicks from the marked nests in the study area were older than 90 d, and continued until July 15, just before the end of the reproductive season.

Our registration protocol produced a daily sample of the total feedings to marked fledglings in the area surveyed. Assuming that male and female fledglings are fed at the same times of day, the samples allow us to compare feeding frequencies to the two sexes, but they do not yield an estimate of absolute daily frequencies. The statistical analysis was performed using a Generalized Linear Model with a logit link function and binomial distribution of error (Crawley 1993).

Results

Feeding experiment

Feeding treatments produced different patterns of mass and ulna increase (treatment: mass, $F_{2,64} = 5.81$, $P = 0.01$, ulna $F_{2,64} = 10.11$, $P = 0.0002$; Fig. 1). Overall, hand-fed chicks of the austere group showed lower rates of mass increase than chicks of the plentiful and reference groups, while the growth rates of chicks of the plentiful and reference groups were not significantly different (Duncans' multiple comparisons). The mean absolute rates of mass increase (g/d) were 28.07 ± 7.51 for the austere group, 34.34 ± 7.28 for the plentiful group, and 33.75 ± 5.61 for the reference group. The mean absolute rates of ulna length increase (mm/d) were 4.32 ± 0.48 in the austere group, 4.56 ± 0.61 in the plentiful group, and 5.11 ± 0.66 in the

reference group. Ulna growth rates of the austere and plentiful groups did not differ significantly, and both of these groups grew more slowly than the reference group (Duncans' multiple comparisons).

After the 9-d feeding treatment, hand-fed nestlings grew normally or recovered rapidly and no noticeable harm was later found. After the treatments were completed, hand-fed chicks were fed normally by their parents, and three days after tapes were removed, experimental nestlings of the three groups did not differ in their mass or ulna lengths (mass, $F_{2,64} = 0.60$, $P = 0.51$, ulna $F_{2,64} = 0.68$, $P = 0.50$; Fig. 1). Likewise, hand-fed chicks eventually achieved a size (asymptotic ulna length) that was not significantly different from that of unmanipulated chicks (Table 1). Survival to fledging of experimental nestlings was high; only one female died, at the age of 58 d.

The prediction that under a regime of equal food intake female and male chicks should have similar growth rates was not supported. Female rates of absolute mass increase were significantly greater than male rates (sex: $F_{1,64} = 25.55$, $P < 0.0001$; Fig. 2a): 39%, 30% and 15% greater than male rates in the austere, plentiful and reference groups, respectively. There was no significant interaction between treatment and sex ($F_{2,64} = 1.01$, $P = 0.37$; Fig. 2a), suggesting that the growth rates of both sexes varied similarly at different levels of food ingestion.

Similarly, female rates of absolute ulna increase were greater than male rates in the three groups (sex: $F_{1,64} = 12.31$, $P = 0.0008$; Fig. 2b); by 12% in the austere group, 7% in the plentiful group, and 13% in the reference group. There was no significant interaction between treatment and sex ($F_{1,64} = 0.37$, $P = 0.61$; Fig. 2b).

Female relative mass increase was greater than male increase in all three groups: 32% in the austere group, 25% in the plentiful group, and 18% in the reference group (sex: $F_{1,64} = 11.95$, $P = 0.001$; Fig. 3a). The interaction between treatment and sex was not significant ($F_{1,64} = 0.13$, $P = 0.91$; Fig. 3a).

Relative increase of ulna length followed a similar pattern: females showed a greater relative rate of ulna increase than males (sex: $F_{1,64} = 17.42$, $P < 0.0001$; Fig. 3b), and the interaction between treatment and sex was not significant ($F_{1,64} = 0.15$, $P = 0.87$; Fig. 3b). Female relative rates of ulna increase were 9% greater than male rates in the austere group, 12% greater in the plentiful group, and 13% greater in the reference group.

Parental feeding after fledging

Parental feeds to 217 male and 122 female fledglings decreased with the age of chicks ($G = 5.01$, $df = 1$, $P = 0.02$; Fig. 4). The prediction of a greater parental provisioning to daughters than sons was not supported, apparently, male and female offspring are

fed at similar frequencies. Although at the age of 90 d the adjusted feeding curve of males was greater than that of females, male and female feeding curves did not differ either at the intercepts ($G = 2.3$, $df = 1$, $P = 0.12$; Fig. 4) or their slopes (interaction effect, $G = 0.56$, $df = 1$, $P = 0.45$; Fig. 4). Additionally, the maximum age at which an individual chick was observed being fed by its parents was similar for daughters and sons: 142 and 145 d, respectively.

Discussion

Feeding experiment

We found no evidence that singleton daughters, because of their larger size, require a greater feeding investment by parents than sons. When both sexes were fed the same amount of food, females maintained greater absolute and relative rates of mass and ulna increase than males. Also, there was no indication of any interaction between treatment and sex, showing that rates of mass and ulna increase of both sexes are similarly affected by the amount of food delivered to a chick.

Although 9 days represent roughly 13% of the growth period (before asymptote of mass and ulna at approximately 70 d; Drummond et al. 1991), the duration of the feeding experiment was sufficient to detect substantial effects of different levels of

food ingestion on chicks' growth rates. Mass and ulna growth rates varied with treatment, and with the exception of ulna growth in the plentiful group, the magnitude of this variation was commensurate with the variation in food amount. For example, the austere group received 21% less food than the estimated natural intake, and its relative rates of mass and ulna increase were 18% and 17% lower than in the reference group. In contrast, the plentiful group received 6% more food than the estimated natural intake, and its relative rates of mass and ulna increase were 3% and 12% lower than in the reference group. We are unable to explain the different growth patterns of ulna length and body mass.

We cannot discount the possibility that consumption of non-typical food species or frequent handling altered the growth of hand-fed chicks. However, hand-fed chicks that were receiving food amounts similar to the estimated baseline showed rates of mass increase similar to those of chicks fed by their parents. Likewise, a previous study of the blue-footed booby found that even very frequent weighing (12 - 20 times per day) did not prejudice the growth of first-hatched chicks, in terms of mass and ulna length (Guerra and Drummond 1995). There is, as far as we know, no reason to suspect that our manipulations affected the sexes differentially and were responsible for superior growth of females.

Parental feeding after fledging

Greater feeding expenditure on daughters than on sons was not apparent during the period of transition to independence. Contrary to our prediction, males may be fed more frequently than females, and duration of the period of parental feeds is apparently independent of offspring sex. We did not continue observations until all the focal fledglings dispersed, but similar feeding curve slopes and maximum ages for parental feeding suggest that males and females are fed for a similar period of time before independence.

Size dimorphism and patterns of growth and development

We need to explain how one sex can grow to a greater size and mass on the same input of food. It has been argued that avian size dimorphism may be related to different patterns of growth and development, reflecting different strategies of the sexes for using the same quota of resources (Richter 1983, Stamps 1990). However, there is little evidence that the smaller sex adopts potentially costly growth tactics such as accelerated increase in size or plumage development. Growth analysis of dimorphic birds showed that in 13 out of 14 species the larger sex had greater rates of mass and tarsus increase, and in four out of five species males and females developed their plumage at similar rates, although the smaller sex appeared to complete the process

earlier (Richner 1991). The only exception was the hooded crow (*Corvus corone cornix*), where females, the smaller sex, had greater rates of mass, tarsus, and feather length increase than males (Richner 1991). According to Teather and Weatherhead (1994), differences in growth and plumage development in dimorphic species appear to be an allometric effect rather than the result of distinctive intersexual strategies of resource allocation.

In principal, sibling competition could select for faster motor development and increased food consumption of the smaller sex, giving rise to slower growth on the same food budget. In species with size dimorphism more rapid motor development of the smaller sex could potentially compensate for its inferior size in sibling competition for parental investment (Newton 1978 and 1979, Stamps 1990, Drummond et al. 1991, Teather and Weatherhead 1994), particularly if competition involves violent aggressions. Higher energetic demands could result from accelerated neuromotor development and the increased activity accompanying it (Stamps 1990). For example, apparently more rapid motor development of sparrowhawk males might allow them to compete more effectively with their larger sisters (Newton 1978).

In the intense sibling competition of the blue-footed booby, aggressive dominance is established early after hatching, and even in broods where the younger chick is a female and eventually outgrows her older brother, the dominance-subordinance relationship is seldom reversed (Drummond et al. 1991, Drummond

and Osorno 1992). Aggressive dominance depends initially on relative size and maturity among nestlings, but subsequently it is social experience that determines the direction of dominance (Drummond and Osorno 1992). Whether faster motor development of males is partly responsible for their ability to sustain dominance over larger sisters is unknown.

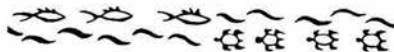
Siblicide and patterns of development

It is intriguing that when females are the larger sex no evidence of greater feeding expenditure in females is available, in contrast to species with larger males, where greater feeding expenditure in males has been reported. This apparent paradox may be explained by the intensity and mode of sibling competition (Newton 1979, Stamps 1990, Anderson et al. 1993). In species that practice facultative brood reduction, aggressive dominance influences the probability of survival, and direction of dominance initially depends on hatching order and relative size/maturity of chicks (Werschkul and Jackson 1979, Collopy 1986, Mock 1984, Drummond and Osorno 1992). Siblings frequently cohabit long enough for sexual size dimorphism to be expressed, and superior competitive abilities of the larger sex could be expected (Newton 1978 and 1979). However, greater competitive superiority of females (the larger sex) over male siblings has been reported only in the american kestrel (*Falco sparverius*), where sibling aggression is apparently absent (Anderson et al.

1993). Thus, faster motor development of the smaller sex may be favored especially or uniquely in facultative siblicidal species (as opposed to species where nestling competition is non-aggressive) to counteract its potentially lethal disadvantage in size (Drummond et al. 1991).

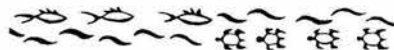
The male-biased progeny sex ratio of the blue-footed booby could in principle be an adaptive response to the relatively higher cost of daughters (Torres and Drummond submitted). Our data show that it is unlikely that daughters are more costly than sons because they consume more food or require longer care. However, biased sex ratios are also expected when the benefits of raising daughters compared to sons differ. For example, local resources competition between relatives may be an important selective force for adjusting the sex ratio when there are sex differences in natal dispersal (Clark 1978, Gowaty 1993).

Thus, we have no evidence that daughters of the blue-footed booby receive a greater feeding expenditure than sons. Faster motor development of males in this facultative siblicidal species may explain the fact that females maintain greater rates of mass and ulna increase than males under the same food amount.



Acknowledgments

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References

- Anderson, D. J. and R. Ricklefs. 1992. Brood size and food provisioning in masked and blue-footed boobies (*Sula* spp.). *Ecology* 73:1363-1374.
- Anderson, D. J., Budde, C., Apanius, V., Martinez Gomez, J. E., Bird, D. and Weathers, W. 1993. Prey size influences female competitive dominance in nestling American kestrels (*Falco sparverius*). *Ecology* 74:367-376.
- Charnov, E. L. 1982. *Sex Allocation*. Princeton University Press, Princeton, New Jersey.
- Clark, A. (1978) Sex ratio and local resource competition in a prosimian primate. *Science* 201, 163-165.
- Clutton-Brock, T. H. 1991. *The evolution of parental care*. Princeton University Press, Princeton N.J.
- Clutton-Brock, T.H., Albon, S.D. and Guinness, F.E. 1981. Parental investment in male and female offspring in polygynous mammals. *Nature* 289:487-489.
- Collopy, M.W. 1986. Food consumption and growth energetics of nestling golden eagles. *Wilson Bull.* 98:445-458.
- Crawley, M. J. 1993. *GLIM for ecologist*. Blackwell Scientific Publications, Oxford.
- Drummond, H., Gonzalez, E. and J.L. Osorno. 1986. Parent-offspring cooperation in the blue-footed booby (*Sula nebouxii*): social roles in infanticidal brood reduction. *Behavioral Ecology and Sociobiology*, 19, 365-372.
- Drummond, H. and C. García Chavelas. 1989. Food shortage influences sibling aggression in the blue-footed booby. *Animal Behaviour*, 37, 806-819.
- Drummond, H., Osorno, J.L., Torres, R., García Chavelas, C. & Merchant Larios, H. 1991. Sexual size dimorphism and sibling competition: implications for avian sex ratios. *American Naturalist*, 138, 623-641.
- Drummond, H., and Osorno, J. L. 1992. Training siblings to be submissive: dominance between booby nestlings. *Animal Behavior* 44:881-893.
- Fiala, K. L. 1981. Reproductive cost and the sex ratio in Red-winged blackbirds. In: *Natural Selection and Social Behaviour* (R. D. Alexander and D. W. Tinkle eds.). Chiron Press, N.Y., pp. 198-214.

- Fiala, K. and Congdon, J. 1983. Energetic consequences of sexual size dimorphism in nestling red-winged blackbirds. *Ecology* 64:642-647.
- Fisher, R. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford.
- Frumkin, R. 1988. Egg quality, nestling development and dispersal in the Sparrowhawk (*Accipiter nisus*). Ph.D. diss. University of Oxford, Oxford.
- Gowaty, P. 1993. Differential dispersal, local resource competition, and sex ratio variation in birds. *American Naturalist* 141:263-280.
- Guerra, M. and Drummond, H. 1995. Reversed sexual size dimorphism and parental care: minimal division of labour in the blue-footed booby. *Behaviour* 132:479-496.
- Lee, P.C. and Moss, C. 1986. Early maternal investment in male and female African elephant calves. *Behavioral Ecology and Sociobiology* 18:353-361.
- McCann, T. S., M. A. Fedak, and J. Hardwood. 1989. parental investment in southern elephant seals *Mirounga leonina*. *Behaviour Ecology and Sociobiology* 25:81-87.
- Mock, D. W. 1984. Infanticide, siblicide, and avian nestling mortality. Pages 3-30 in G. Hausfater and S. B. Hrdy, eds. *Infanticide: comparative and evolutionary perspectives*. Aldine, New York.
- Nelson, J.B. 1978. *The Sulidae: gannets and boobies*. Oxford University Press, London.
- Newton, I. 1978. Feeding and development of Sparrowhawk nestlings. *Journal of Zoology London* 184:465-487.
- Newton, I. 1979. *Population ecology of raptors*. The Pitman Press, Great Britain.
- Newton, I., and M. Marquiss. 1979. Sex ratio among nestlings of the European sparrowhawk. *American Naturalist* 113:309-315.
- Nuñez-de la Mora, A., H. Drummond and J. C. Wingfield. Hormonal correlates of dominance and starvation-induced aggression in chicks of the blue-footed booby. *Ethology*, in press.
- Richner, H. 1991. The growth dynamics of sexually dimorphic birds and Fisher's sex ratio theory: does sex specific growth contribute to balanced sex ratios? *Functional Ecology* 5:19-28.

- Richter, W. 1983. Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics. *American Naturalist* 121:158-171.
- Rodríguez-Gironés, M.A., Drummond, H. and Kacelnik, A. Effect of food deprivation on dominance status in blue-footed booby (*Sula nebouxii*) broods. *Behavioral Ecology*, in press.
- Slagsvold, T., Roskaft, E. and S. Engen. 1986 Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care: Fisher's theory applied to birds. *Ornis Scandinavica*, 17, 117-125.
- Smiseth, T., and S. Lorentsen. 1995. Evidence of equal maternal investment in the sexes in the polygynous and sexually dimorphic grey seal (*Halichoerus grypus*). *Behavioral Ecology and Sociobiol* 36:145-150.
- Stamps, J. A. 1990. When should avian parents differentially provision sons and daughters? *American Naturalist*, 135:671-685.
- Teather, K. 1987. Intersexual differences in food consumption by hand-reared great-tailed grackle (*Quiscalus mexicanus*) nestlings. *Auk* 104:635-639.
- Teather, K. 1992. An experimental study of competition for food between male and female nestlings of the red-winged blackbird. *Behavioral Ecology and Sociobiology* 31:81-87.
- Teather, K. and Weatherhead, P.J. 1988. Sex specific energy requirements of great-tailed grackle (*Quiscalus mexicanus*) nestlings. *J. of Animal Ecology* 57:658-668.
- Teather, K. and Weatherhead, P.J. 1994. Allometry, adaptation, and growth and development of sexually dimorphic birds. *Oikos* 71:515-525.
- Torres, R. and Drummond, H. Variably male-biased sex ratio in a marine bird with reversed size dimorphism. Submitted.
- Werschkul, D. F., and J. A. Jackson. 1979. Sibling competition and avian growth rates. *Ibis* 121:97-102.
- Wolff, J.O. 1988. Maternal investment and sex ratio adjustment in American Bison Calves. *Behav. Ecol. Sociobiol.* 23:127-133.
- Yasukawa, K., McClure, J. L., Boley, R. A. and Zanocco, J. 1990. Provisioning of nestlings by male and female red-winged blackbirds, *Angelanius phoeniceus*. *Animal Behavior* 40:153-166.

Table 1. Asymptotic ulna length (mm) of experimental and unmanipulated chicks of marked nests in the study area.

ULNA LENGTH				
	Females		Males	
	Experimental	Unmanipulated	Experimental	Unmanipulated
	(N = 28)	(N = 257)	(N = 37)	(N = 428)
Mean	216	216	196	196
<i>SD</i>	2.93	3.35	4.15	4.62
Range	210–222	211–226	188–205	181–207
<i>t</i>		1.00		0.08
<i>P</i>		0.32		0.94

Figure Legends

Fig. 1. Mean growth of mass (g) and ulna length (mm) of (a and b) females and (c and d) males in the austere group (12 females and 12 males; dashed line), the plentiful group (7 females and 9 males; solid line), and the reference group (10 females and 16 males; dotted line).

Fig. 2. Mean absolute rates (\pm SE) of (a) mass (g/d) and (b) ulna increase (mm/d) of male (M) and female (F) nestlings in the austere (A), plentiful (P), and reference (R) groups.

Fig. 3. Mean relative rates (\pm SE) of (a) mass and (b) ulna increase of male (M) and female (F) nestlings in the austere (A), plentiful (P), and reference (R) groups.

Fig. 4. Proportion of male (*) and female (Δ) fledglings fed by their parents. Adjusted curves are shown by solid line for males and heavy solid line for females ($r = 0.25$, $df = 105$, $P = 0.01$). Regressions were calculated using a Generalized Linear Model.

Fig. 1

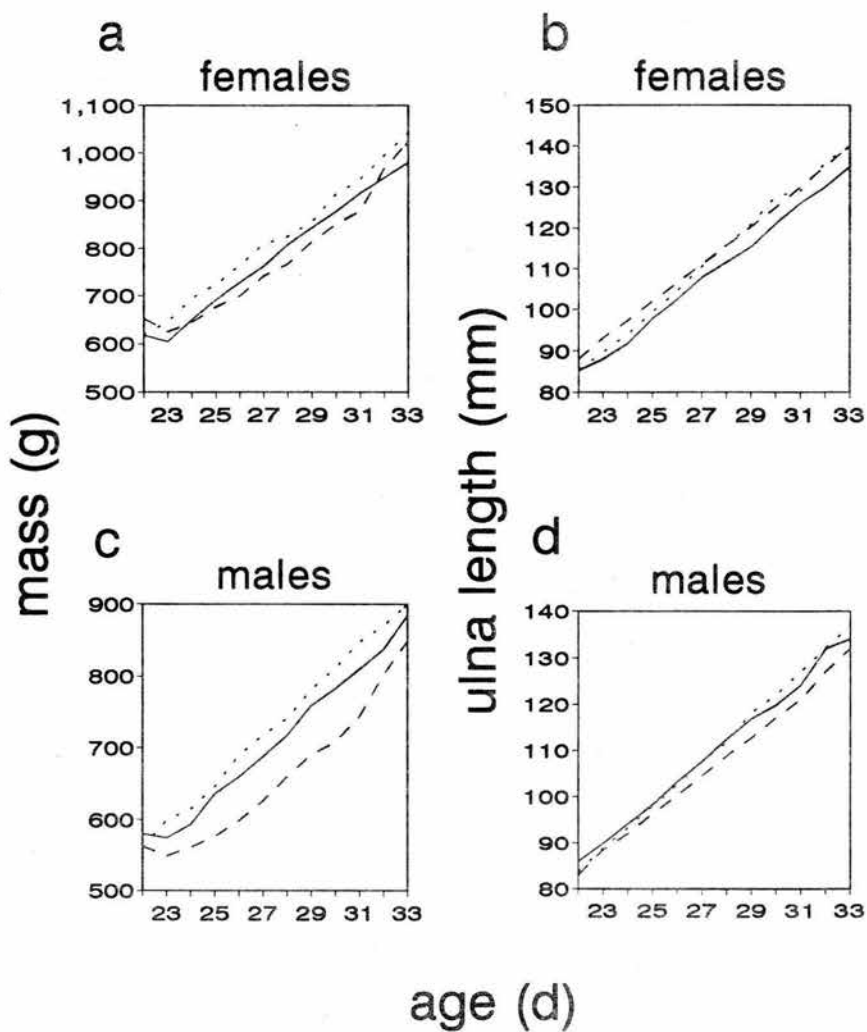


Fig. 2

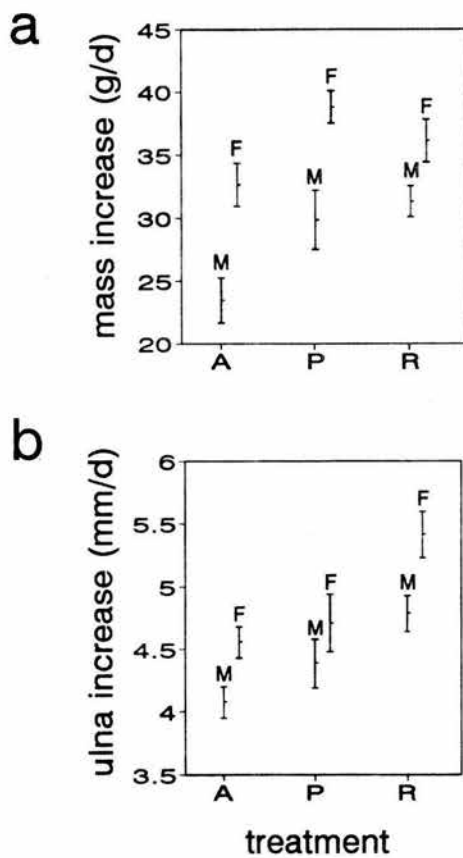


Fig. 3

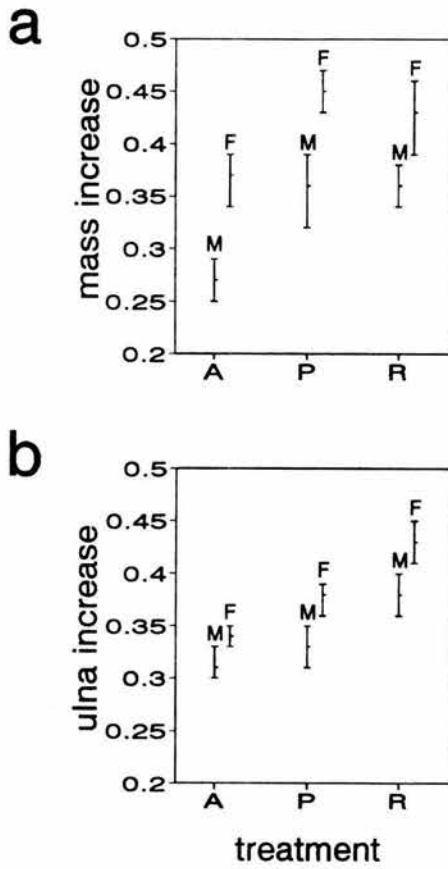
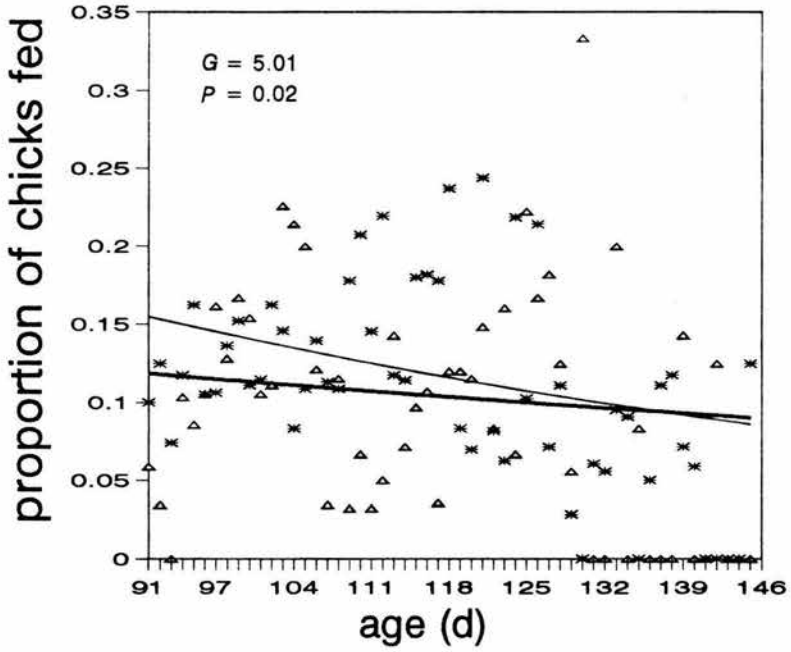
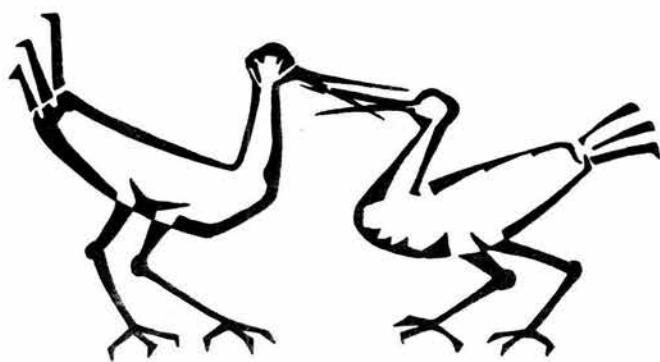


Fig. 4





III



Running headline: SEX-BIASED MORTALITY IN NESTLINGS

**Sex-biased mortality in nestlings of a bird with females
larger than males**

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Key words: dimorphism, food shortage, mortality, sex.

Summary

1. Explanations for sex-biased mortality include higher vulnerability of the heterogametic sex and greater susceptibility of one sex to food shortages.
2. We recorded daily mortality of male and female nestlings in 376 broods of the blue-footed booby *Sula nebouxii*, a species where females are 32% heavier than males. We predicted (1) higher mortality of last-hatched females than last-hatched males, and (2) greater increase of mortality for last-hatched females than last-hatched males through the season.
3. Mortality increased with hatching order, but the differences between male and female chicks were not significant. Male and female mortality were: 15% and 12% in first-hatched chicks, 23% and 24% in second hatched chicks, and 24% and 48% in third-hatched chicks.
4. The risk of death increased substantially as the season advanced, and the increase was different for male and female chicks. Although male and female mortality was similar in early broods, second and third-hatched females showed a greater increase in mortality through the season than males in similar positions in the hatching sequence.
5. These results support the idea that blue-footed booby females are more vulnerable to food-related stress than males because of their larger size.



Introduction

Differential mortality of male and female offspring during the period of parental care has been found in a considerable number of species of birds and mammals (review in Clutton-Brock 1991). A non-functional explanation for sex-biased mortality suggests that higher mortality of the heterogametic sex is a result of the expression of deleterious recessive alleles on the unguarded sex chromosome (Trivers 1972, 1985; Myers 1978; Clutton-Brock, Albon & Guinness 1985). A different explanation argues that reduced food availability has a greater effect on the survival of the sex with the presumed higher food requirements due to its larger size, and/or faster growth rate (Howe 1977; Roskaft & Slagsvold 1985; Slagsvold, Roskaft & Engen 1986; Clutton-Brock 1986; Weatherhead & Teather 1991).

In particular cases, the two hypotheses may generate the same predictions. When the larger sex is also the heterogametic sex, greater mortality is consistent with both hypotheses because deleterious alleles may be expressed only under conditions of stress, such as food shortage.

The evidence for the unguarded sex chromosome hypothesis is unsatisfactory, and the necessary data to evaluate the influence of heterogamety on mortality in organisms are not available (Breitwisch 1989; but see Myers 1978). Male-biased mortality occurs in many species of mammals (e.g. McClure 1981; Clutton-



Brock et al. 1985) in which males are the heterogametic sex, but also in some bird species (e.g. Slagsvold et al. 1986; Teather & Weatherhead 1989; Griffiths 1992), and in birds females are the heterogametic sex. Furthermore, differential mortality by sex in some mammals seems to be related to sexual differentiation due to hormones rather than chromosomal constitution (Trivers 1985).

In birds, differential mortality by sex seems to be more pronounced in species with size dimorphism than in monomorphic species (Clutton-Brock et al. 1985). The evidence comes mostly from species where males are larger than females, and in such species males suffer greater mortality (e.g. *Angelaius phoeniceus*, Cronmiller & Thompson 1981; *Quiscalus mexicanus*, Teather & Weatherhead 1989; *Corvus frugilegus*, Roskaft & Slagsvold 1985; *Larus fuscus*, Griffiths 1992), with the exception of one study where greater mortality for female great tits (*Parus major*) was reported (Dhondt 1970).

So far, the evidence from birds suggests that differential mortality by sex is associated with larger size and faster growth rates rather than heterogamety. To confirm this trend, data are required from species with so-called reversed size dimorphism (females larger than males), but no convincing data have been published.

Most raptor species show a pronounced reversed size dimorphism, but although large data sets are available (e.g. Newton & Marquiss 1979; Dijkstra, Daan & Buker 1990, Wiebe & Bortolotti 1992), the evidence for differential mortality comes

mostly from indirect or incomplete data. For example, Edwards et al. (1988) suggested that male-biased sex ratios of golden eagles (*Aquila chrysaetos*) at fledging are the result of female-biased mortality, but neither the hatching sex ratio, nor death rates of male and female nestlings were recorded.

We present data on mortality of male and female nestlings of the blue-footed booby *Sula nebouxii*, a marine bird with reversed sexual size dimorphism. Blue-footed booby adult females are 32% heavier than males (mean \pm standard deviation, 1654 \pm 127.5 g for females, $N = 28$; 1250 \pm 113.9 g for males, $N = 28$; Castillo & Chavez-Peón 1983; see also Nelson 1978), and female chicks grow faster than male chicks. At 79 d, female nestlings are 27% heavier than males, and their culmens and ulnas are 8.5% and 10.5% longer, respectively (Drummond et al. 1991).

Blue-footed boobies care for one to three chicks (modal clutch size is two), which hatch at intervals of 4 d. Hatching asynchrony produces a competitive feeding disadvantage for last-hatched chicks: for example, in the first week these chicks receive 26% fewer feeds and 20% less mass of food than their older siblings at the same age (Guerra & Drummond 1995). Facultative brood reduction occurs when food is scarce and falls selectively on last-hatched chicks, mainly during the first few weeks of life (18 \pm 17.8 d; Drummond, Gonzalez & Osorno 1986). This mortality is facilitated by sibling aggression, which increases when food intake of nestlings declines (Drummond et al. 1986; Drummond & García Chavelas 1989).

To test the idea that nestlings of the larger sex are more vulnerable to food shortage, we asked whether female boobies suffer greater mortality than males, and whether differential mortality of females increases with food shortage. Parents provide less food to last-hatched chicks, at least in the first few weeks (Guerra & Drummond 1995), and sea surface temperature, a parameter that is negatively correlated with sea productivity, increases with hatching date; thus breeding conditions may deteriorate with hatching date (Garcia-Cerecedo, M. & Saavedra-Sordo, T., unpublished data.). Therefore, we predicted (1) higher mortality of last-hatched females than last-hatched males, and (2) greater increase of mortality for last-hatched females than last-hatched males through the season.

Methods

Data were collected in the colony of the blue-footed boobies on Isla Isabel, Mexico, from February 12 to July 23, 1989. All nests in an area of 20,800 m², which comprises dense and sparse nesting neighborhoods, were included in our study. The surveyed nests represented approximately 80% of the whole reproductive colony. Nests were marked with numbered flags, and chicks were banded within 3 d of hatching using colored wire to differentiate hatching order, and with individually numbered plastic bands when they were 7 d old. Survival was recorded every three days until

chicks were, on average, 119 ± 24 d of age (range, 80-178 d), a period that encompasses fledging (i.e. the end of plumage development; Drummond et al. 1991). At fledging, asymptotic ulna length was measured and chicks were permanently marked with individually numbered steel bands. All marked nests were also inspected daily at 1600-1800 h to recover the bodies of any recently dead chicks.

Blue-footed boobies can be reliably sexed by the length of the ulna at fledging, when males and females have reached a nonoverlapping bimodal asymptote (Drummond et al. 1991). From our sample of 751 chicks, 575 fledglings were sexed by their ulna lengths (males 200 ± 2.65 mm, range 191-207 mm, $N = 361$; females 220 ± 3.43 mm, range 213-233 mm, $N = 277$). To confirm the reliability of this sex determination, in 1993 all banded adults breeding at the colony were sexed on the basis of their markedly different vocalizations (males whistle and females grunt; Nelson 1978). Sex determined by ulna length at fledging, and sex determined by vocalization at breeding, agreed in 206 of 207 cases. Sex of the 176 chicks that died before fledging was assessed in the field by inspection of gonadal morphology, and confirmed by later inspection of tissue differentiation under the microscope (Drummond et al. 1991).

The sample for analyses comprises 712 chicks from 376 complete broods (i.e. all hatched chicks of each brood were sexed and their hatching date was recorded). Twenty-four broods (39 chicks) which were already present at our arrival at the colony,

were eliminated from the analyses because we could not estimate their hatching date. A further 116 whole broods (243 chicks) were eliminated from our analyses because we were unable to sex all the chicks in each brood: in 14 broods 14 chicks lost their bands, in 9 broods 13 chicks did not fledge before our departure, in 34 broods the gonads of 42 chicks were in an advanced state of decomposition when the corpses were recovered, and in 59 broods 76 chicks disappeared, probably to predation by the milk snake *Lampropeltis triangulum* (the average age of chicks that disappeared was $9.52 \text{ d} \pm 9.68$, $N = 61$). Because we have no reason to expect that the causes of brood elimination had a greater effect on one sex, chicks thus excluded from the analyses were considered to be an unbiased sample with respect to sex.

The age of chicks that had already hatched at the beginning of the study was estimated from the average hatching interval between broodmates or the average age at fledging, when we only knew the fledging date.

Mortality of nestlings was analyzed for the period up to fledging (males, $\bar{X} = 86 \text{ d}$; females, $\bar{X} = 92 \text{ d}$, Drummond et al. 1991), unless a different period of time is indicated. No bias in estimates of relative mortality is expected to result from the 6 d difference between male and female fledging ages, because there was no mortality in our sample during this period in the year of our study.

The analysis of mortality was performed using a Generalized Linear Model with binomial error distribution and a logit link

function (Crawley 1993). Brood size, hatching order and sex of offspring were included in the model as categorical factors, and hatching date as a continuous variable. We used a hierarchical model with sex of offspring nested in the factor hatching order. The fit of the model is measured as a χ^2 statistic. To assess the significance of the interaction term, we compared the slopes of the adjusted logistic curves by estimating a coefficient of the difference between two parameters and the standard errors of the differences (Crawley 1993). The significance of this coefficient is measured as a t statistic.

The age at death was analyzed using a Two-way ANOVA with sex of offspring and hatching order as factors.

Results

Prefledging mortality increased with hatching order and hatching date, but did not differ according to the sex of the offspring or the brood size. Although mortality increased with brood size from 15%, to 19% and 23% in 113 one-chick broods, 190 two-chick broods, and 73 three-chick broods, respectively, the differences were not significant ($\chi^2 = 3.61$, $df = 2$, $P = 0.16$). Thus, brood size was excluded from the analysis to build a simplified model.

Mortality and hatching order

Overall mortality of chicks of both sexes did not differ: 19% of 401 male chicks died, and 20% of 311 female chicks died (Table 1, sex of offspring). Mortality increased significantly with hatching order from 14%, to 23% and 34% in 376 first-hatched chicks, 263 second-hatched chicks and 73 third-hatched chicks, respectively (Table 1, hatching order). The prediction of greater mortality of last-hatched females than last-hatched males was not supported. Although third-hatched females suffered 27% greater mortality than third-hatched males, the increase in mortality with hatching order was not significantly different for male and female chicks (Table 1, sex*hatching order interaction). Male versus female mortality was: 15% versus 12% in first-hatched chicks (200 males and 176 females), 23% versus 24% in second-hatched chicks (164 males and 99 females), and 24% versus 48% in third-hatched chicks (37 males and 36 females).

Mortality and hatching date

The risk of death increased substantially as the reproductive season advanced (Table 1, hatching date; Fig. 1). Further, our data supported the prediction of greater increase in mortality through the season for last-hatched females than last-hatched males (Table 1, hatching date*hatching order*sex interaction; Fig. 1). Females showed a greater increase in mortality than males through the season, when they were in second and third position in the hatching sequence (Fig. 1b and c). Thus, even

though mortality in early broods was similar for both sexes, female mortality in late broods increased to become roughly 25% and 26% greater than male mortality in second and third-hatched chicks, respectively (Fig. 1b and c).

In first-hatched chicks the reverse pattern was observed. Although mortality of both sexes was similar at the beginning of the season, male mortality showed a greater increase through the season than female mortality (Fig. 1a).

Comparisons of the slopes of the adjusted curves showed that the risk of death increased with hatching order for females but did not for males. The slope of the third-hatched female curve was significantly greater than the slopes of first and second-hatched females, though first and second-hatched females did not differ significantly in their slopes (F1 vs F2, $t = -0.22$, $df = 376$, $P = 0.82$; F1 vs F3, $t = -2.27$, $df = 376$, $P = 0.02$; F2 vs F3, $t = -2.32$, $df = 376$, $P = 0.02$; F = females, 1 - 3 indicate hatching order; Fig. 1). In contrast, the slopes of the curves of first, second and third-hatched males were not significantly different (M1 vs M2, $t = -0.52$, $df = 376$, $P = 0.60$; M1 vs M3, $t = -0.09$, $df = 376$, $P = 0.92$; M2 vs M3, $t = -0.29$, $df = 376$, $P = 0.77$; M = males; Fig. 1).

Thus, hatching date and hatching order were the most important factors to explain variation in mortality. Differences in mortality of males and females were not significant whether they were first, second or third hatched chicks. However, as the season advanced, second and third-hatched females suffered a

greater increase in mortality than males in similar positions in the hatching sequence.

Age at death of males and females

The age at which chicks died did not differ with the sex of the chick ($F_{1,133} = 0.57, P = 0.45$), or their position in the hatching sequence ($F_{2,133} = 0.23, P = 0.79$; Table 2). Likewise, male and female died at similar ages whether they were first, second or third hatched chicks ($F_{2,133} = 1.59, P = 0.21$; Table 2).

Discussion

Our data partially support the predictions from the hypothesis that differential mortality by sex results from different male and female vulnerability to food shortages. Overall mortality of last-hatched females was 27% greater than mortality of last-hatched males, although the difference was not significant. The year of our study was an unusually favorable reproductive season. For instance, the number of fledglings produced in 1989 (169) was considerably greater than the average number of fledglings produced annually during 1982-1993 in the same nesting area ($\bar{X} = 68 \pm 59.6$ fledglings per year, range 0 - 169; Garcia-Cerecedo, A. & Saavedra-Sordo, T., unpublished data). Further analysis comparing male and female mortality in good and bad years is

desirable; we would expect the sexual difference in mortality among last-hatched chicks to be greater during poor years.

In agreement with the second prediction, females suffered a greater increase in mortality than males through the season when they were in the last positions of the hatching sequence. High mortality of last-hatched individuals in late broods indicates that under presumed extreme conditions, blue-footed booby females do indeed suffer greater mortality than males.

For the chicks that died during our study, one of the most common and conspicuous causes of mortality was brood reduction, probably associated with food shortage (Drummond *et al.* 1986). Approximately 30% of the dead bodies bore lesions, indicating sibling aggression, and some were found away from their nests and bore severe lesions, undoubtedly caused by adults. Chicks expelled by their brood mates frequently become targets of aggression by adult neighbors.

In species where females are the larger sex, greater male mortality as a result of a size-based advantage of females in sibling competition has been suggested (Bortolotti 1986; Edwards *et al.* 1988; Anderson *et al.* 1993). In blue-footed booby nestlings this is not the case; siblings establish a dominant-subordinate relationship at an early stage, when the size advantage of the first-hatched chick is overwhelming, and this relationship is usually stable even if differential growth of males and females results in inversion of the size difference (Drummond *et al.* 1991; Drummond & Osorno 1992). Consequently,

last-hatched chicks suffer greater mortality than their older siblings. Also, there is not evidence that a chicks' survival is affected by the sex of the sibling (Drummond *et al.* 1991). In our sample of two-chick broods, 27% of 59 males with older brother and 27% of 48 males with older sister died, and 20% of 55 females with older brother, and 25% of 28 females with older sister died. However, our results show that females may be more vulnerable to food-related stress than males of the same status within the brood.

Differential mortality by sex could have implications for the population sex ratio. When the costs of rearing males and females are similar, parents should invest equally in offspring of each sex (Fisher 1930). Consistently greater mortality of one sex may reduce the cost of producing that sex, and a sex ratio biased at hatching towards the cheaper sex is expected (Maynard Smith 1980). Blue-footed boobies produce a male biased-sex ratio at hatching (56%) and at fledging (56%; Torres & Drummond unpublished). Male-biased sex ratios at fledging varied among four years from 52% to 72%, in correlation with mean sea surface temperature: the proportion of males was greater in years when water was warmer and food was presumably scarce (Torres & Drummond, unpublished). Thus, the male-biased sex ratio found in the blue-footed booby is not the result of sex-biased mortality of chicks, though greater female mortality during poor years may increase the bias toward males.

Adaptive explanations for differential mortality of males when they are the larger sex are related to sexual selection. It is suggested that sexual selection favoring large adult size in males has increased their growth rate to a point at which costs to juvenile survival during periods of food shortage balance the benefits of large size in adulthood (Clutton-Brock et al. 1985). In species where females are the larger sex, size dimorphism has also been attributed to sexual selection. Jehl & Murray (1986) suggested that small size enables males to perform superior aerial courtship displays. However, other explanations of size dimorphism based exclusively on natural selection have also been offered. For example, larger females may be favored because of a partitioning of dietary niche or division of roles in parental care (Newton 1979; Olsen & Cockburn 1991).

In the blue footed-booby, males provide two to five times less food to broods after chicks reach 12 d of age than do females, and there is little evidence that males have a superior role in any other component of parental care (Guerra & Drummond 1995). This may imply that sexual selection has driven males to a smaller size, although it remains possible that some ecological difference between the sexes explains their size dimorphism. Whatever the explanation of dimorphism, it appears that nestlings of the larger sex are more vulnerable to food shortage. Taken together with the observations of male-biased mortality in mammal and bird species with large males, this strongly suggests that large size itself is the critical variable.



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References

- Anderson, D.J., Budde, C., Apanius, V., Martinez Gomez, E., Bird, D.M. & Weathers, W.W. (1993) Prey size influences female competitive dominance in nestling American kestrels (*Falco sparverius*). *Ecology*, **74**, 367-376.
- Breitwisch, R. (1989) Mortality patterns, sex ratios, and parental investment in monogamous birds. *Current Ornithology* vol. 6 (ed. D.M. Power), pp. 1-50. Plenum Press, New York.
- Bortolotti, G.R. (1986) Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *American Naturalist*, **127**, 495-507.
- Castillo, A. & Chavez-Peón, A. (1983) *Ecología reproductiva e influencia del comportamiento en el control del número de crías en el bobo de patas azules Sula nebouxii en la Isla Isabel, Nayarit*. Bch thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México.
- Crawley, M.J. (1993) *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.
- Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1985) Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature*, **313**, 131-133.
- Clutton-Brock, T.H. (1986) Sex ratio variation in birds. *Ibis*, **120**, 317-329.
- Clutton-Brock, T.H. (1991) *The evolution of parental care*. Princeton University Press, Princeton, New Jersey.
- Cronmiller, J.R. & Thompson, C.F. (1981) Sex-ratio adjustment in malnourished red-winged blackbird broods. *Journal of Field Ornithology*, **52**, 65-67.
- Dhondt, A.A. (1970) The sex ratio of nestling Great Tits. *Bird Study*, **17**, 282-286.
- Dijkstra, C., Daan, S. & Buker, J.B. (1990) Adaptive seasonal variation in the sex ratio of kestrel broods. *Functional Ecology*, **4**, 143-147.
- Drummond, H., Gonzalez, E. & Osorno, J.L. (1986) Parent-offspring cooperation in the blue-footed booby (*Sula nebouxii*): social roles in infanticidal brood reduction. *Behavioral Ecology and Sociobiology*, **19**, 365-372.

- Drummond, H. & García Chavelas, C. (1989) Food shortage influences sibling aggression in the blue-footed booby. *Animal Behaviour*, **37**, 806-819.
- Drummond, H., Osorno, J.L., Torres, R., García Chavelas, C. & Merchant Larios, H. (1991) Sexual size dimorphism and sibling competition: implications for avian sex ratios. *American Naturalist*, **138**, 623-641.
- Drummond, H. & Osorno, J.L. (1992) Training siblings to be submissive losers: dominance between booby nestlings. *Animal Behaviour*, **44**, 881-893.
- Edwards, T.C., Collopy, M.W., Steenhof, K. & Kochert, M.N. (1988) Sex ratios of fledging golden eagles. *Auk*, **105**, 793-796.
- Fisher, R. A. (1930) *The genetical theory of natural selection*. Clarendon Press, Oxford.
- Griffiths, R. (1992) Sex-biased mortality in the Lesser Black-backed gull *Larus fuscus* during the nesting stage. *Ibis*, **134**, 237-244.
- Guerra, C. & Drummond, H. (1995) Reversed sexual size dimorphism and parental care: Minimal division of labour in the blue-footed booby. *Behaviour*, **132**, 7-8.
- Howe, H.F. (1977) Sex ratio adjustment in the common grackle. *Science*, **198**, 744-745.
- Jehl, J.R. Jr. & Murray, B.G. Jr. (1986) The evolution of normal and reversed sexual size dimorphism in shore birds and other birds. *Current Ornithology* vol. 3 (ed. R.F. Johnston), pp. 1-86. Plenum Press, New York.
- Maynard Smith, J. (1980) A new theory of sexual investment. *Behavioral Ecology and Sociobiology* **7**:247-251.
- McClure, P.A. (1981) Sex-biased litter reduction in food-restricted wood rats (*Neotoma floridana*). *Science*, **211**, 1058-1060.
- Myers, J.H. (1978) Sex ratio adjustment under food stress: maximization of quality or numbers of offspring? *American Naturalist*, **112**, 381-388.
- Nelson, J.B. (1978) *The Sulidae: gannets and boobies*. Oxford University Press, London.
- Newton, I. (1979) *Population ecology of raptors*. T. and A. D. Poyser, Berkhamsted.

- Newton, I. & Marquiss, M. (1979) Sex ratio among nestlings of the European sparrowhawk. *American Naturalist*, **113**, 309-315.
- Olsen, P.D. & Cockburn, A. (1991) Female-biased sex allocation in peregrine falcons and other raptors. *Behavioral Ecology and Sociobiology*, **28**, 417-423.
- Roskaf, E. & Slagsvold, T. (1985) Differential mortality of male and female offspring in experimentally manipulated broods of the rook. *Journal of Animal Ecology*, **54**, 261-266.
- Ryder, P.L. & Ryder, J. (1981) Reproductive performance of ring-billed gulls in relation to nest location. *Condor*, **83**, 57-60.
- Slagsvold, T., Roskaf, E. & Engen, S. (1986) Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care: Fisher's theory applied to birds. *Ornis Scandinavica*, **17**, 117-125.
- Teather, K. & Weatherhead, P.J. (1989) Sex-specific mortality in nestling great-tailed grackles. *Ecology*, **70**, 1485-1493.
- Trivers, R.L. (1972) Parental investment and sexual selection. *Sexual selection in the descent of man*. (ed. B. Campbell), pp. 136-179. Aldine, Chicago.
- Trivers, R.L. (1985) *Social evolution*. Benjamin/Cummings, Menlo Park, California.
- Weatherhead, P.J. & Teather, K. (1991) Are skewed sex ratios in sexually dimorphic birds adaptive? *American Naturalist*, **138**, 1159-1172.
- Wiebe, K.L. & Bortolotti, G.R. (1992) Facultative sex ratio manipulation in American kestrels. *Behavioral Ecology and Sociobiology*, **30**, 379-386.

Table 1. Analysis of mortality of 712 chicks. The Goodness-of-fit for each of the variables were fitted in a logistic regression model.

VARIABLES	χ^2	df	P
Hatching order	19.75	2	0.0001
Sex of offspring	0.04	1	0.84
Hatching date	43.68	1	0.0001
Sex and hatching order interaction	4.32	2	0.11
Sex, hatching order and hatching date interaction	12.05	5	0.03

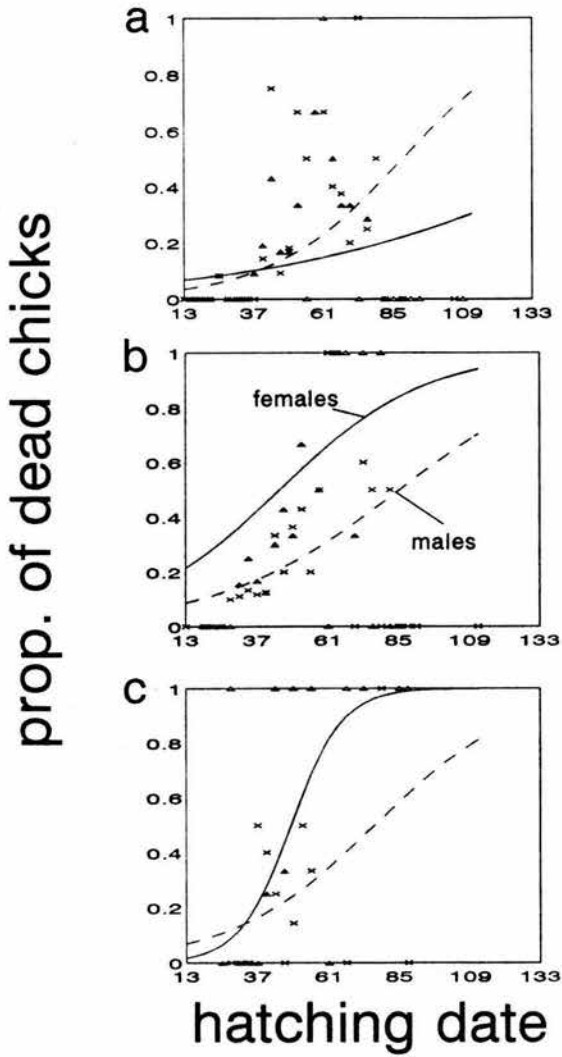
Table 2. Age (d) at death of male and female chicks according to their hatching order.

	Hatching order					
	First		Second		Third	
	Males	Females	Males	Females	Males	Females
Mean age	23.16	26.71	22.78	28.95	28.44	18.75
<i>SD</i>	17.06	19.94	18.34	17.09	28.24	12.67
Range	5 – 94	2 – 95	1 – 55	2 – 69	1 – 98	3 – 42
Total chicks	31	21	38	24	9	16

Figure legend

Fig. 1. Male (X) and female (Δ) mortality of (a) first-hatched, (b) second-hatched, and (c) third-hatched chicks. Day 1 = January 1st. Logistic regressions are shown by dashed lines for males and solid lines for females ($r^2 = 0.16$, $P < 0.0001$). The number of male and female chicks, respectively (Mean \pm SD) included in each observed point in the figure were: 6.89 \pm 7.32 and 5.64 \pm 6.24 in first-hatched chicks, 6.31 \pm 6.94 and 4.30 \pm 4.10 in second-hatched chicks, and 2.84 \pm 1.60 and 2.40 \pm 1.35 in third-hatched chicks.

Fig. 1





DISCUSION GENERAL

El bobo de patas azules produce una proporción de sexos sesgada hacia machos, y este sesgo está presente desde la eclosión. Existen pocos reportes de sesgos a la eclosión, y en general se sugiere que en las aves las proporciones sexuales a la eclosión estan fijas a 1:1 (Charnov 1982, Clutton-Brock 1986). Lo anterior, sin embargo, podría ser sólo reflejo de las dificultades metodológicas que representa la determinación del sexo de crías recién nacidas en especies que se encuentran en su ambiente natural.

No se encontraron diferencias en la mortalidad global de machos y hembras durante la temporada en que se registró diariamente la sobrevivencia de las crías. Sin embargo, (1) el aumento en la mortalidad de hembras al avanzar la temporada reproductiva fue mayor que el de machos en crías que eclosionan en última posición, y (2) la proporción de machos emplumados aumentó durante años de aparente baja disponibilidad de alimento. Esto sugiere que aunque la proporción de sexos está sesgada desde la eclosión, una mayor mortalidad de hembras durante la crianza en años de escasez de alimento contribuye a aumentar el sesgo hacia los machos al final del periodo de cuidado parental.

Aún cuando se han sugerido algunos posibles mecanismos, se desconoce la forma en la cual las aves podrían controlar el sexo de sus hijos (Krackow 1995). En el bobo de patas azules, es



posible que el sesgo hacia machos a la eclosión sea resultado de mayor mortalidad de embriones hembra durante la incubación; en este estudio las crías hembras bajo condiciones de escasez de alimento sufrieron mayor mortalidad, por otro lado, existe evidencia de mayor mortalidad de embriones hembra en otras aves (Landauer 1967 en Myers 1978). Por el momento, no tenemos datos para evaluar el ó los mecanismos por los cuales en esta especie eclosionan más machos que hembras. Sin embargo, con la ayuda de la técnica molecular de determinación sexual recientemente desarrollada para el bobo de patas azules (Del Rio 1996), se podrán hacer estudios para evaluar si hay mortalidad diferencial de machos y hembras durante la incubación y si esto ocurre sólo bajo condiciones de estrés. Esta información sobre los mecanismos nos ayudaría a entender el valor adaptativo de los sesgos en las proporciones sexuales en esta especie.

Mortalidad de machos y hembras

De acuerdo a la teoría de Fisher sobre las proporciones sexuales, la mortalidad durante el periodo de cuidado parental afecta los costos relativos de producir crías macho y hembra (Trivers 1985, Clutton-Brock 1991). Si uno de los sexos tiene una probabilidad mayor de morir, la inversión parental en ese sexo se termina antes, por lo cual, para igualar la inversión en machos y hembras a nivel de la población se predice una proporción de sexos a la fecundación sesgada hacia el sexo que muere con mayor frecuencia (Trivers 1985). En el bobo de patas azules es posible que el

costo per capita de producir hembras sea mayor que el de producir machos, debido a que las crías hembra sufren mayor mortalidad. Para evaluar si la inversión en ambos sexos a nivel de la población es similar, sería necesario determinar la proporción sexual a la fecundación. Una estimación de la proporción de sexos a la fecundación sería posible con la técnica molecular de determinación del sexo (Del Rio 1996).

Existen otras hipótesis, fuera del contexto de la teoría de las proporciones de sexos, que podrían explicar la mortalidad diferencial de machos y hembras. Mittwoch (1971 y 1993) sugirió que en aves y mamíferos la mayor mortalidad de individuos del sexo heterogamético durante el desarrollo embrionario podría ser resultado de presiones de selección a nivel de diferenciación sexual. Esta hipótesis sugiere que en los individuos del sexo heterogamético la gónada en estado rudimentario necesita alcanzar un tamaño crítico en cierto estado de desarrollo para poder diferenciarse en testículo en el caso de mamíferos, y en ovario en el caso de las aves (Mittwoch 1971). Es decir que para poder llegar a este umbral de desarrollo se han favorecido tasas de crecimiento más altas en los individuos del sexo heterogamético, y tasas de crecimiento altas están asociadas a una mayor probabilidad de muerte (Mittwoch 1993).

En especies que presentan dimorfismo sexual en tamaño existe evidencia de mayor mortalidad entre las crías del sexo más grande, y la mortalidad parece aumentar con el grado de dimorfismo de la especie (Clutton-Brock 1991). Se ha sugerido

que la selección sexual ha favorecido el aumento en las tasas de crecimiento hasta un punto en que los costos, por aumento en la mortalidad durante la etapa de crecimiento, son superados por los beneficios por ser grande durante la etapa de adulto (Clutton-Brock et al. 1985).

Ajustes de las proporciones sexuales

No encontramos evidencia de que la proporción de sexos en el bobo de patas azules varíe con la fecha de eclosión, el orden de eclosión en la nidada, o la experiencia reproductiva de los padres. Sin embargo, 1989 fue un año en que las condiciones para la reproducción fueron muy buenas. Por ejemplo, el número de crías emplumadas en 1989 fue 148% mayor que el número promedio de crías emplumadas en la misma área durante 1982-1993 (García-Cerecedo y Saavedra-Sordo, en prep.). Es posible que durante un año en que el alimento fue abundante el costo de producir hijas en comparación con hijos fuera similar, y las diferencias en la capacidad de los padres con diferentes experiencias reproductivas simplemente no se hayan expresado.

Dimorfismo sexual e inversión parental en alimento

La proporción de sexos sesgada hacia machos observada en este trabajo apoya la hipótesis de Fisher, si suponemos que las hembras son más costosas que los machos. No obstante, nuestros experimentos y los registros de alimentaciones parentales indican que en el bobo de patas azules las hijas no reciben una mayor

inversión alimenticia que los hijos. Los resultados del experimento de alimentación de crías sugieren que hay diferencias metabólicas y de desarrollo que permiten a las hembras mantener tasas de crecimiento más altas que las de los machos. Asimismo, machos y hembras recibieron una inversión alimenticia similar, en términos de frecuencia, hacia el final del periodo de cuidado parental.

Se ha sugerido que el dimorfismo sexual en tamaño está relacionado con diferencias en los patrones de crecimiento y desarrollo, que reflejan a su vez estrategias de asignación de recursos diferentes entre machos y hembras (Richter 1983, Stamps 1990). En especies donde la competencia entre hermanos es intensa, los individuos del sexo más pequeño podrían compensar las desventajas en tamaño a través de un desarrollo psicomotriz más acelerado que el de los individuos del sexo más grande. En las crías del bobo de patas azules, la relación de dominancia-subordinación se establece inicialmente con base en las diferencias relativas en edad y tamaño entre las crías, y posteriormente por la experiencia social, que determina la dirección de la dominancia (Drummond y Osorno 1992). Sería interesante investigar si en esta especie existen diferencias en el desarrollo psicomotriz de machos y hembras, y si estas diferencias están relacionadas con la capacidad de los machos para mantener su estatus de dominancia en nidadas mixtas.

Por otro lado, es interesante que sólo en aquellas especies con dimorfismo sexual en tamaño en las que los machos son el sexo

más grande se ha reportado mayor inversión parental en el sexo de mayor tamaño (e.g. *Corvus frugilegus*, Slagsvold et al. 1986; *Quiscalus mexicanus* y *Angelaius phoeniceus*, Teather 1987 y 1992). Esta aparente paradoja podría estar relacionada con el modo e intensidad de la competencia entre hermanos (Newton 1978, Stamps 1990, Anderson et al. 1993). La dominancia por agresión en especies que practican fratricidio facultativo afecta la probabilidad de sobrevivencia de las crías, y la dirección de esta dominancia depende inicialmente del tamaño y madurez relativos de las crías en la nidada (Werschkul y Jackson 1979, Mock 1984, Drummond y Osorno 1992). En particular, esperaríamos que sólo en especies que presentan dimorfismo sexual en tamaño y fratricidio facultativo los individuos del sexo más pequeño presentaran un desarrollo psicomotriz más acelerado, que les permita contrarrestar las desventajas, potencialmente letales, por las diferencias en tamaño entre las crías de una misma nidada (Drummond et al. 1991).

El sesgo hacia los machos en la proporción de sexos del bobo de patas azules, podría en principio, ser una respuesta adaptativa a las diferencias en los costos de producir machos o hembras. Nuestros datos indican que es poco probable que las hijas, por tener un mayor tamaño, sean más costosas que los hijos en cuanto a inversión en alimentación. Sin embargo, difícilmente un sólo factor puede explicar el valor adaptativo de las proporciones sexuales en una población (Frank 1990). En el bobo

de patas azules sería necesario evaluar si producir hijas en comparación con hijos representa costos diferentes en términos de reducción en sobrevivencia o éxito reproductivo futuro, y si el pago genético por producir hijas es mayor que el pago genético por producir hijos.

Por otro lado en especies en donde machos y hembras difieren en la dispersión natal la competencia entre individuos emparentados podría estar favoreciendo sesgos en las proporciones sexuales de la progenie (Hamilton 1967, Clark 1978). En el bobo de patas azules, machos y hembras no difieren en la dispersión natal (Osorio-Beristain y Drummond 1993), y una proporción similar de machos y hembras regresan para reproducirse en la colonia por primera vez (datos no publicados). Sería interesante explorar si en efecto ocurren interacciones de competencia por territorios y apareamientos entre individuos emparentados. Estos factores que están relacionados con los pagos genéticos vía hijas e hijos podrían generar predicciones diferentes en cuanto a las proporciones sexuales. Por ejemplo, aún cuando los promedios de dispersión de machos y hembras no difieren, la probabilidad de interacciones de competencia entre individuos emparentados podría ser diferente para machos y hembras.

Por lo tanto, el sesgo hacia machos en la proporción de sexos de la progenie del bobo de patas azules es consistente con el modelo de Fisher, bajo el supuesto de que las hijas representan mayores costos que los hijos. Nuestros datos no apoyan la explicación de que las diferencias en costo sean

resultado de una mayor inversión en alimento en hijas que en hijos, asociada a las diferencias en tamaños entre machos y hembras. Sin embargo, es posible que la mayor mortalidad de hijas aumente el costo per capita de las hembras en comparación con el de los machos. Otros factores, como las interacciones competitivas entre individuos emparentados y los costos diferenciales en la sobrevivencia y el éxito reproductivo futuros de los padres nos daría más elementos para explicar el valor adaptativo del sesgo hacia machos en la proporción sexual del bobo de patas azules ☒



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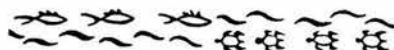
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LITERATURA CITADA

- Anderson, D. J., Budde, C., Apanius, V., Martinez Gomez, J. E., Bird, D. and Weathers, W. 1993. Prey size influences female competitive dominance in nestling american kestrels (*Falco sparverius*). *Ecology* 74:367-376.
- Ankney, C. D. 1982. Sex ratio varies with egg sequence in lesser snow geese. *Auk* 99:662-666.
- Antolin, M. F. 1993. Genetics of biased sex ratios in subdivided populations: models, assumptions, and evidence. Pp. 239-281, Eds. Futuyma, D. y J. Antonovics, Oxford Surveys in Evolutionary Biology, Oxford.
- Blank, J. L., and V. Nolan. 1983. Offspring sex ratio in red winged blackbirds is dependent on maternal age. *Proceedings of the National Academy of Science USA* 80:6141-6145.
- Bortolotti, G. R. 1986. Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *American Naturalist* 127:495-507.
- Castillo, A., and A. Chavez-Peón. 1983. Ecología reproductiva e influencia del comportamiento en el control del número de crías en el Bobo de patas azules *Sula nebouxii* en la Isla Isabel, Nayarit. Tesis de Licenciatura, Facultad de Ciencias, UNAM.
- Charnov, E. 1982. *The theory of sex allocation*. Princeton University Press, Princeton, N.J.
- Clark, A. 1978. Sex ratio and local resource competition in a prosimian primate. *Science* 201:163-165.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313:131-133.
- Clutton-Brock, T. H. 1986. Sex ratio variation in birds. *Ibis* 120:317-329.
- Clutton-Brock, T. H. 1991. *The evolution of parental care*. Princeton University Press, Princeton, New Jersey.
- Darwin, C. 1859. *On the origin of species by means of natural selection*. John Murray, London.

- Del Rio, T. 1996. Análisis genético en el DNA del ave *Sula nebouxii* utilizando la técnica de AP-PCR como marcador molecular. Tesis de Licenciatura, Instituto de Investigaciones Biomédicas, UNAM.
- Dijkstra C., S. Daan, and J. B. Buker. 1990. Adaptive seasonal variation in the sex ratio of kestrel broods. *Functional Ecology* 4:143-147.
- Drummond, H., E. Gonzalez, and J. L. Osorno. 1986. Parent-offspring cooperation in the blue-footed booby (*Sula nebouxii*): social roles in infanticidal brood reduction. *Behavioral Ecology and Sociobiology* 19:365-372.
- Drummond, H., and C. García Chavelas. 1989. Food shortage influences sibling aggression in the blue-footed booby. *Animal Behaviour* 37:806-819.
- Drummond, H., J. L. Osorno, R. Torres, C. García-Chavelas, and H. Merchant Larios. 1991. Sexual size dimorphism and sibling competition: implications for avian sex ratios. *American Naturalist* 138:623-641.
- Drummond, H., and J. L. Osorno. 1992. Training siblings to be submissive losers: dominance between booby nestlings. *Animal Behavior* 44:881-893.
- Edmunds, S. R., and C. D. Ankney. 1987. Sex ratios of hatchlings morning doves. *Canadian Journal of Zoology* 65:871-874.
- Frank, S. 1990. Sex allocation theory for birds and mammals. *Annual Review of Ecology and Systematics* 21:13-55.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford.
- García-Cerecedo, M. A. and M. T. Saavedra-Sordo. Variación interanual en el esfuerzo y éxito reproductivo del bobo de patas azules (*Sula nebouxii*) y sus implicaciones en la reducción facultativa de la nidada. Tesis de Licenciatura, Facultad de Ciencias, Universidad Nacional Autónoma de México. En prep.
- Gowaty, P. A. 1991. Facultative manipulation of sex ratios in birds, rare or rarely observed? Pages 141-171 in R. F Johnson, editor. *Current Ornithology* Volume 8. Plenum, New York, New York, USA.
- Gowaty, P. A. 1993. Differential dispersal, local resource competition and sex ratio variation in birds. *American Naturalist* 141:263-280.

- Hodder, J y M. R. Graybill. 1985. Reproduction and survival of seabirds in Oregon during the 1982-1983 El Niño. *Condor* 87: 535-541.
- Howe, H. F. 1976. Egg size, hatching asynchrony, sex, and brood reduction in the common grackle. *Ecology* 57:1195-1207.
- Howe, H. F. 1977. Sex ratio adjustment in the common grackle. *Science* 198:744-745.
- Karlin, S y S. Lessard. 1986. Theoretical studies on sex ratio evolution. Princeton University Press, Princeton, N.J.
- Krackow, S. 1995. Potential mechanisms for sex ratio adjustments in mammals and birds. *Biological Review of the Cambridge Philosophical Society* 70:225-241.
- Maynard Smith, J. 1980. A new theory of sexual investment. *Behavioral Ecology and Sociobiology* 7:247-251.
- Meathrel, C. E., and J. P. Ryder. 1987. Sex ratios of ring-billed gulls in relation to egg size, egg sequence and female body condition. *Colonial Waterbirds* 10:72-77.
- Mittwoch, U. 1971. Sex determination in birds and mammals. *Nature* 231:432-434.
- Mittwoch, U. 1993. Blastocysts prepare for the race to be male. *Human Reproduction* 8:1550-1555.
- Mock, D. W. 1984. Infanticide, siblicide, and avian nestling mortality. Pages 3-30 in G. Hausfater and S. B. Hrdy, eds. *Infanticide: Comparative and evolutionary perspectives*. Aldine, New York.
- Myers, J. H. 1978. Sex ratio adjustment under food stress: maximization of quality or numbers of offspring? *American Naturalist* 112:381-388.
- Nelson, J. B. 1978. *The Sulidae: Gannets and boobies*. Oxford University Press, London.
- Newton, I. 1978. Feeding and development of Sparrowhawk nestlings. *Journal of Zoology London* 184:465-487.
- Osorio-Beristain, M., and H. Drummond. 1993. Natal dispersal and deferred breeding in the blue-footed booby. *Auk* 110:234-239.
- Richter, W. 1983. Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics. *American Naturalist* 121:158-171.

- Ryder, J. 1983. Sex ratio and egg sequence in ring-billed gulls. *Auk* 1:726-729.
- Slagsvold, T., E. Roskaft, and S. Engen. 1986. Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care: Fisher's theory applied to birds. *Ornis Scandinavica* 17:117-125.
- Schreiber R y E Schreiber. 1984. Central Pacific seabirds and the El Niño Southern Oscillation: 1982 to 1983 perspectives. *Science* 225:713-715.
- Stamps, J. A. 1990. When should avian parents differentially provision sons and daughters? *American Naturalist* 135:671-685.
- Teather, K. L. 1987. Intersexual differences in food consumption by hand-reared great-tailed grackle (*Quiscalus mexicanus*) nestlings. *Auk* 104:635-639.
- Teather, K. 1992. An experimental study of competition for food between male and female nestlings of the red-winged blackbird. *Behavioral Ecology and Sociobiology* 31:81-87.
- Trivers, R. L. 1972. Parental investment and sexual selection. *Sexual selection in the descent of man.* (ed. B. Campbell), pp. 136-179. Aldine, Chicago.
- Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90-92.
- Trivers, R. L. 1985. *Social evolution.* Benjamin/Cummings, Menlo Park, California.
- Weatherhead, P. J. 1985. Sex ratios of red-winged blackbirds by egg size and laying sequence. *The Auk* 102:298-304.
- Weatherhead, P. J., and K. Teather. 1991. Are skewed fledglings sex ratios in sexually dimorphic birds adaptive? *American Naturalist* 138:1159-1172.
- Werschkul, D. F., and J. A. Jackson. 1979. Sibling competition and avian growth rates. *Ibis* 121:97-102.
- Williams, G. C. 1979. The question of adaptive sex ratio in outcrossed vertebrates. *Proceedings of the Royal Society of London* 205:567-580.