EFFECT OF BROOD SIZE ON GROWTH IN THE CHINSTRAP PENGUIN: A FIELD EXPERIMENT

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Abstract.—In order to determine if the patterns of chick growth and mortality observed in two-chick broods of the Chinstrap Penguin (*Pygoscelis antarctica*) are affected by the feeding capacity of parents, we performed an experimental brood reduction at hatching by removing one sibling in some broods and comparing the growth and mortality patterns of these single chicks with those of control broods with two chicks. Chicks in reduced broods had longer flippers than those in control broods at 15, 21 and 47 days of age, and longer bills at 15, 21 and 32 days, but no differences in mass were found. Although more control than reduced broods suffered chick mortality, the productivity of control broods was markedly higher. Brood size has significant effects on final chick size in the Chinstrap penguin. Food limitation operated mainly at the end of the guard stage, although its effects were still significant during the crèche stage. Although the effect of brood size on growth may be more marked in last-hatched chicks, it can also be noted in first-hatched chicks. Growth may act as a fine-tuning mechanism to regulate productivity in this species, allowing parents to raise two chicks, but at the cost of slower growth and smaller final size.

EFECTO DEL TAMAÑO DE NIDADA SOBRE EL CRECIMIENTO EN EL PINGUINO BARBIJO: UN EXPERIMENTO DE CAMPO

Sinopsis.—Para determinar si los patrones de crecimiento y mortalidad de polluelos observados en familias de dos polluelos en el Pingüino Barbijo (*Pygoscelis antarctica*) se ven afectados por la capacidad de conseguir alimento de los padres, realizamos un experimento de reducción de nidada durante la eclosión. Para ello quitamos un polluelo en determinados nidos y comparamos los patrones de crecimiento y mortalidad de estos polluelos solos con los de familias control con dos polluelos. Los polluelos solos mostraron mayores longitudes de aleta a los 15, 21 y 47 días de edad que los control y mayores longitudes de pico a los 15, 21 y 32 días, pero no se detectaron diferencias en el peso a ninguna edad. Aunque más familias control que reducidas sufrieron mortalidad de polluelos, la productividad de las familias control fué claramente superior. El tamaño de nidada afectó significativamente al tamaño final de los pollos. La limitación por el alimento se detectó sobre todo al final de la fase de guarda, aunque su efecto fué también significativo en la fase de guarderia. Aunque el efecto del tamaño de nidada sobre el crecimiento puede ser marcado en los últimos pollos nacidos, también puede apreciarse en los primeros pollos. El crecimiento puede actuar como mecanismo de "ajuste fino" de la productividad en esta especie, permitiendo sacar adelante dos pollos con el costo de un crecimiento más lento y un menor tamaño final.

Food supply can limit growth and chick survival in penguins (Ainley and Schlatter 1972; Boersma 1976, 1991; Bost and Jouventin 1991; Cooper 1977; Moreno et al. 1994; Taylor 1962, Taylor and Roberts 1962; van Heezik and Davis 1990; Williams 1980). The evidence has been descriptive, comparing chick growth and survival between years or areas with

different food availability, or parents caring for one- or two-chick broods
in species that normally raise two chicks. An effect of brood size on chick
growth has been described in the Chinstrap Penguin (*Pygoscelis antarcti-
ca*), single chicks growing faster and reaching a larger final size than those
of two-chick broods, at least in years of low food availability (Moreno et
al. 1994). Growth could serve as a fine-tuning mechanism to adapt the
number of chicks to the feeding capacity of the parents: two chicks, the
maximum brood size in pygoscelid penguins, could be raised only at the
cost of a slower growth or smaller final size (O'Connor 1984). Other
possible mechanisms to adapt brood size to food availability, such as
hatching asynchrony or sibling aggression do not seem to have a signifi-
cant role in the Chinstrap Penguin; eggs usually hatch asynchronously,
but sibling aggression has not been reported and brood reduction or
growth rate variation were not related to hatching asynchrony (Moreno
et al. 1994).

   One-chick broods in penguins may be the result of one-egg clutches,
of clutches reduced through predation, or of early brood reduction.
Thus, the parents of these broods may be of lower quality than those
raising two chicks (Ainley et al. 1983, Williams 1990), confusing the effects
of brood size with those of parental quality. One way to determine to
what degree the growth and mortality of two-chick broods is limited
through the feeding capacity of parents, is through experimental removal
of one chick at hatching. By comparing experimentally reduced broods
with control two-chick broods raised simultaneously, the effect of parental
quality may be diminished, clarifying the importance of brood size for
the determination of patterns of chick growth and mortality. The end of
the guard stage has been proposed as the critical period for parents in
pygoscelid penguins, given the increasing requirements of chicks and the
limited time available for foraging due to guarding duties at the colony
(Culik 1994). The timing of differences in growth between reduced and
control broods may confirm this suggestion.

   In this study we have undertaken experimental brood reductions at
hatching to confirm the observation that single chicks grow better than
those in broods of two (Moreno et al. 1994). No difference in growth or
starvation mortality between reduced and control broods would indicate
that brood size does not influence chick growth and mortality when the
effect of parental quality is reduced. Significant differences would reveal
an effect of brood size, suggesting that two chicks can only be raised by
reducing their growth rate or final size.

METHODS

   We studied one subcolony of the large Chinstrap Penguin rookery of
Vapour Col (20,000 breeding pairs) on Deception Island, South Shetlands
(63°00'S, 60°40'W) during the austral summer of 1993–1994. During the
incubation phase, we randomly selected 56 nests among those containing
two-egg clutches, and marked them with numbered sticks. We visited nests
daily before hatching of the chicks. Two days after hatching, one of the

chicks was removed in half of the nests to create an experimentally re-
duced group. Removed chicks were placed in nearby nests with single
chicks and were not followed. In the control half of the nests, one chick
was removed and placed back soon after to control for possible manip-
ulation effects. Given that hatching date has a strong influence on breed-
ing performance in this species (Moreno et al. 1997, Viñuela et al. 1996),
we assigned each nest with signs of hatching alternately to the control or
experimental groups. Thus, there were no differences in mean hatching
dates between the experimental and control nests ($t_{49} = 0.73$, $P = 0.47$).
In five of the control nests, one of the eggs did not hatch or the chick
died shortly after hatching (less than 2-d old). These nests were discarded
from the sample, in order to include only pairs with complete hatching
success.

Chicks were individually marked with an indelible felt pen. At the age
of 21 d, chicks were banded with standard metallic flipper bands (Lam-
bournes Ltd.). Chicks in both groups were weighed and measured (flip-
per length and culmen) on the day of the manipulation, and subsequent-
ly at the ages of 7, 15, 21, 32, and 47 days. These ages included the period
of maximum growth (15–21 d). Chicks 47-d old have practically finished
growth, except for bill length (Moreno et al. 1994). Only a reduced sam-
ple of chicks were weighed and measured at the ages of 2 and 32 d due
to inclement weather and the need to minimize disturbance in crèches.
There were chick losses due to predation, starvation or nest desertion by
parents, reducing sample sizes through the season (see Table 1). At the
end of the study, we checked carefully the surroundings of the study
colony for dead marked chicks. Skuas (*Catharacta lonnbergi*) consume
chicks of crèche age close to the natal colonies and usually leave skeletons
and flippers untouched (pers. obs.). We have assumed that all chicks of
crèche age that were not found dead fledged successfully. Some 47-d-old
chicks were not found on the day of measurement, but this could be due
to the confusion produced by handling chicks in crèches. As chicks of
the same brood frequently hatch asynchronously in this species, we have
analyzed brood means when both chicks in control families were mea-
sured at the same age. Otherwise, the value for the first-hatched chicks
was used in statistical analyses. Given the clear directional prediction of
improved growth in the reduced broods, one-tailed t-tests have been used
in comparisons. Means are reported ±1 SD.

RESULTS

There were no initial differences in mass, bill length, or flipper length
between chicks in the two groups of broods (Table 1). Chicks in reduced
broods were significantly larger than chicks in control broods at the age
of 15 and 21 d (Table 1). The mean crèching age (end of guard phase)
in the study year was 30 d (Viñuela et al. 1996). Only bill length was
longer for reduced broods at the age of 32 d, but differences were near
significance for flipper length and mass, despite sample size being the
smallest for this age group (Table 1). At 47 d, chicks in reduced broods

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TABLE 1. Mass (g), bill length (mm) and flipper length (mm) of chicks in reduced and control broods of Chinstrap Penguins, South Shetlands, 1993–1994. Means ± 1 SD. Results of unpaired *t*-tests (one-tailed).

Age	Reduced	Control	*t*	*P*
2 days				
Mass (g)	136.5 ± 72.4	118.5 ± 60.9	0.81	0.211
Bill (mm)	14.7 ± 1.2	14.5 ± 1.2	0.38	0.354
Flipper (mm)	38.9 ± 6.4	38.2 ± 5.3	0.37	0.355
n	22	16		
7 days				
Mass (g)	356.2 ± 127.6	327.0 ± 85.4	0.94	0.177
Bill (mm)	17.5 ± 1.3	17.2 ± 0.9	0.70	0.245
Flipper (mm)	55.0 ± 6.9	53.1 ± 4.9	1.12	0.137
n	28	23		
15 days				
Mass (g)	1053 ± 204	1007 ± 163	0.86	0.196
Bill (mm)	22.9 ± 1.4	21.8 ± 1.8	2.62	0.006
Flipper (mm)	102.4 ± 11.1	95.5 ± 10.3	2.28	0.013
n	27	23		
21 days				
Mass (g)	1651 ± 269	1644 ± 249	0.09	0.463
Bill (mm)	27.5 ± 1.7	26.3 ± 1.9	2.35	0.011
Flipper (mm)	145.7 ± 11.6	139.2 ± 11.9	1.95	0.028
n	27	22		
32 days				
Mass (g)	3080 ± 321	2927 ± 256	1.41	0.084
Bill (mm)	35.9 ± 2.3	34.3 ± 1.6	2.11	0.011
Flipper (mm)	190.5 ± 7.3	186.7 ± 5.4	1.60	0.061
n	17	13		
47 days				
Mass (g)	3039 ± 534	2911 ± 550	0.76	0.255
Bill (mm)	42.5 ± 2.1	41.8 ± 2.4	1.00	0.160
Flipper (mm)	195.4 ± 6.6	190.9 ± 6.5	2.20	0.016
n	24	18		

had significantly longer flippers (Table 1). No significant difference in mass was detected at any age (Table 1). The differences in size measurements were proportionally largest at 15 d of age and decreased afterwards, becoming modest shortly before fledging (Table 1).

Considering only first-hatched chicks in control broods, chicks in reduced broods had longer bills at 15 d (22.95 ± 1.42 mm vs. 22.04 ± 1.72 mm; $t = 2.06$, $P = 0.045$), longer flippers at 47 d (195.42 ± 6.55 mm vs. 191.11 ± 6.43 mm; $t = 2.12$, $P = 0.04$), and differences were marginally significant for flipper length at 15 d (102.41 ± 11.55 vs. 97.22 ± 9.65; $t = 1.75$, $P = 0.087$) and bill length at 21 d (27.55 ± 1.75 vs. 26.53 ± 2.21; $t = 1.37$, $P = 0.076$). No other comparison was significant. Thus, chicks of reduced broods were more similar to first chicks of control broods than to brood averages.

Two control broods and one reduced brood suffered a complete loss, and four control broods suffered a partial loss. Complete losses occurred when chicks were between the ages of 7 and 32 d; partial losses occurred when the older chick was between the ages of 2 and 21 d. The number of broods suffering chick losses was significantly different between treatments ($G = 4.84$, $P = 0.028$). The number of chicks lost was not significantly different between treatments ($G = 1.4$, $P > 0.10$). Complete brood losses were due to desertion or predation, while partial losses were due to starvation or partial predation.

DISCUSSION

Reductions in breeding success due to low food availability have been reported in several penguin species for some years and/or localities (Boersma et al. 1990, Bost and Jouventin 1991, van Heezik and Davis 1990, Williams 1980). Differences in growth between single chicks and chicks in broods of two have also been reported in the Galapagos Penguin (*Spheniscus mendiculus*, Boersma 1976), in the Yellow-eyed Penguin (*Megadyptes antipodes*, van Heezik and Davis 1990), in the Magellanic Penguin (*Spheniscus magellanicus*, Boersma 1991), and in the Adelie Penguin (*Pygoscelis adeliae*, Ainley and Schlatter 1972), although Volkman and Trivelpiece (1980) did not find any significant differences in rate of mass gain between single chicks and two-chick broods in the three pygoscelid species. As in the Chinstrap Penguin (Moreno et al. 1994), these differences were observed in some but not all years (Boersma 1991, van Heezik and Davis 1990). However, parents with single chicks may have lost one egg prior to hatching through poor parental care, or be inefficient breeders that usually lay one egg (Ainley et al. 1983). Thus, their subsequent chick losses may be an expression of their low parental quality. By experimentally reducing broods, we can reduce variation in growth due to parental quality.

There is observational evidence that single chicks grow better than chicks in broods of two in the Chinstrap Penguin (Moreno et al. 1994). Single chicks are fed more frequently than chicks in broods of two and receive larger meals (Lishman 1985). However, in a year with a high breeding success in the study colony, the differences in chick growth at 15 d of age between single chicks and those in broods of two had disappeared by the age of 46 d (Moreno et al. 1994). Thus, the importance of food limitation may be apparent only in certain years. We here show experimentally that there is evidence of food limitation at the end of the guard stage, during the period of maximum growth (Moreno et al. 1994), but that its effects become smaller, although still significant, during the crèche phase. At the end of the guard phase, parents are limited in their food provisioning due to their guarding shifts at the colony, while they can forage simultaneously at sea during the crèche phase (Culik 1994, Moreno and Sanz 1996). Single chicks had significantly longer flippers throughout growth, and attained a larger structural size before independence. A small size before fledging may have an important effect on subsequent survival (Moreno et al., unpubl. data). It could be argued that

the impaired growth in two-chick broods could be due to sibling com-
petition and hatching asynchrony, so it could be a non-adaptive conse-
quence of a behavioral mechanism, and not be related to a higher de-
mand of food in larger broods. However, hatching asynchrony does not
seem to have a clear effect on brood reduction or growth in this species
(Moreno et al. 1994), and sibling aggression has never been observed in
this colony. Furthermore, our tests are conservative, because in some con-
trol broods only data for first hatched chicks have been included, due to
hatching asynchrony. If both chicks had been included, differences be-
tween brood averages would have been more marked, as can be deduced
from the closer similarity in growth between first-hatched chicks in con-
trol broods and chicks in reduced broods.

Chick mortality in one year on Deception Island, did not differ between
broods with one and two chicks (Moreno et al. 1994). This led to the
productivity of two-chick broods being twice as large as for one-chick
broods (1.35 vs. 0.73 fledged chicks, Moreno et al. 1994). In the present
experiment, control broods suffered significantly higher chick mortality
per brood, although not per chick. Thus 96% of single chicks fledged,
while only 83% of chicks in broods of two did. Reduced broods raised
0.96 chicks on average, while control broods raised 1.65 chicks. These
values are similar to the 87% chick survival measured in a year with high
food availability (Moreno et al. 1994). This indicates that the study year
was not especially poor with respect to breeding success. In spite of this,
some parents with two chicks had problems in collecting enough food to
avoid starvation in their broods.

Interestingly, differences in growth between control and experimental
chicks were observed for morphometric parameters (bill and flipper
length), but not for mass. Mass may be highly variable in penguin chicks,
because they probably experience irregular feeding rates with large meals,
so differences may be more difficult to detect statistically. Alternatively,
they could exhibit a strategy of resource storage, as an adaptation to an
irregular feeding regime in a harsh environment (O'Connor 1984).
Chicks exposed to lower feeding rates could reduce skeleton growth, but
keep a level of resources (mass) similar to chicks growing faster (Viñuela
and Ferrer, 1997), making it more difficult to detect differences in mass.

Our results support the notion that growth may act as a fine-tuning
mechanism to regulate productivity, allowing parents to raise two chicks,
but at the cost of slower growth and smaller final size (O'Connor 1984).
Although this effect may be more marked in last-hatched chicks, it can
also be noted in first-hatched chicks. This was observed once the effect
of parental quality was reduced, and in an average year with respect to
apparent food availability. Food limitation operates mainly at the end of
the guard phase, but its effects become less important, although still sig-
nificant, during the crèche phase. The effects of reduced growth on pa-
rental reproductive success may be important. The costs for parents of
raising two chicks remain to be explored.

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