Influence of hatching order and brood size on growth in jackass penguins

Yolanda M. van Heezik * and P.J. Seddon
Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Private Bag, Rondebosch, 7700 Republic of South Africa

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Jackass penguins *Spheniscus demersus* hatch two different-sized eggs asynchronously: the second-hatched chick, being, on average, 59% of the weight of the first-hatched chick on hatching. We examined the effect of hatching order on growth rates of mass, culmen length and culmen depth by comparing: (i) growth rates of first- and second-hatched chicks, and (ii) chicks from experimentally synchronized broods to chicks from normal asynchronous broods. Only growth rates in mass showed significant variation. Within a brood, B chicks grew more slowly than A chicks. The effect of synchronizing a brood was to lower the growth rate of both chicks to that of a B chick, suggesting that equal-sized siblings feed less efficiently. Chicks hatching from larger A eggs, that had been synchronized for age and size with chicks from B eggs, did not grow faster, indicating that chicks hatching from A and B eggs do not have intrinsically different growth rates. Single-chick nests result usually from egg infertility. Singletons showed only a non-significant trend towards faster growth in mass than offspring in two-chick broods, even though food availability in one-chick nests should be better than in two-chick nests. Overall, hatching order had more impact on growth rates of mass than did brood size or egg dimensions.

Brilpikkewyne *Spheniscus demersus* broei twee eiers van verskillende groottes asinchronies uit: met die uitbroei het die tweede uitgebroeide kuiken gemiddeld 59% van die massa van die eerste kuiken. Ons het die effek van broei-orde op die groeitempo van massa, snawellengte en -diepte ondersoek deur die volgende te vergelyk: (i) groeitempo's van die eerste en tweede kuikens, en (ii) kuikens van eksperimenteel gesinchroniseerde broeisels met kuikens van normale asinchroniese broeisels. Slegs groeitempo's in massa het betekenisvolle variasie getoon. Binne 'n broeisel het die B kuikens stadiger as die A kuikens gegroei. Die effek van die sinchronisasie van 'n broeisel was die verlaging van die groeitempo van beide kuikens tot dié van die B kuiken, wat suggereer dat ewegroot lede van dieselfde broeisel minder doeltreffend voed. Kuikens wat uit A eiers uitbroei wat t.o.v. ouderdom en grootte met die kuikens van B eiers gesinchroniseer is, het nie vinniger gegroei nie, wat aandui dat kuikens vanuit A en B eiers nie op sigself verskillende groeitempo's het nie. Enkel-kuiken-neste is gewoonlik die gevolg van eier-onvrugbaarheid. Enkelinge het slegs 'n nie-betekenisvolle neiging tot vinniger groei in massa getoon as die kroos in twee-kuiken-broeisels, selfs al behoort die beskikbaarheid van voedsel beter te wees in een-kuiken- as in twee-kuiken-neste. In die geheel het die broei-orde meer invloed op die groeitempo's gehad as die broeiselgrootte of eierafmetings.

* To whom correspondence should be addressed at: National Wildlife Research Centre, P.O. Box 1086, Taif, Saudi Arabia

Seabird growth rates have been shown to vary primarily in response to variations in environmental food supply, which may adversely affect rates of provisioning to chicks, food quantity, or food quality (Boersma 1976; Gaston, Chapdelaine & Noble 1983; Wehle 1983; Pettit, Byrd, Whittow & Seki 1984; Hulsman & Smith 1988). At the level of the brood, the availability of food to each chick may be determined independently of environmental prey availability, being rather a function of hatching order whereby first-hatched chicks obtain more food through preferential allocation by parents (Henderson 1975; Stamps, Clark, Arrowood & Kus 1989), and/or sibling competition for food (Blaker 1969; Léger & McNeil 1987). If this is the case, the competitive advantage of the older sibling has been hypothesized as resulting in the reduction of the growth rate of the weaker sibling (Parker, Mock & Lamey 1989). When chicks hatch on the same day, as in yellow-eyed penguins *Megadyptes antipodes*, no significant differences in growth rates of weight or morphometric parameters are found between siblings (van Heezik & Davis 1990). Differences in brood size may also influence how much food each chick is fed, and may result in different growth rates when availability of food is limiting (Taylor & Roberts 1962; Ainley & Schlatter 1972; Boersma 1976; van Heezik & Davis 1990).

Jackass penguins *Spheniscus demersus* usually lay two eggs of different sizes (first-laid is, on average, 4,6 g ± 3,3 g heavier, $N = 40$) and hatch eggs asynchronously (Williams & Cooper 1984). As a result, at hatching, second-hatched (B) chicks are, on average, 59% ($SD = 13,5$, $N = 38$ this study) of the weight of first-hatched (A) chicks. Previous work on the growth of jackass penguins has been mainly descriptive (Cooper 1977; Randall 1983; Williams & Cooper 1984).

This study is part of a larger study: chick starvation and the adaptive advantage of asynchronous hatching are discussed in Seddon & van Heezik (in press), and the timing and probability of all causes of chick mortality is examined in Seddon & van Heezik (1991). In this paper we examine growth rates of surviving chicks in order to (i) determine whether hatching order influences growth rates by comparing growth rates of A and B chicks, and of asynchronous and experimentally synchronized chicks; (ii) examine whether chicks hatching from A and B eggs have intrinsically different growth rates, and (iii) compare growth rates of chicks from one- and two-chick broods.

Methods

We collected data between June and October 1989, at Dassen Island (33°25'S; 18°06'E), situated off the west coast of South Africa. The main hatching period occurred throughout June and July, at which time we established three study groups:

(i) Two-chick broods which had a mean sibling mass difference at the hatching of the second chick of 55,6g; *SD* = 32,7 g, and a mean hatch interval of 2,32 days; *SD* = 1,02 days (n = 24);

(ii) One-chick broods, which resulted from one fertile plus one infertile egg being laid;

(iii) To control for hatching order, we created an experimental same-sized synchronous group in which we transferred chicks between nests at hatching to produce broods of equal-sized synchronously hatched young. The mean sibling mass difference at hatching was 2,1 g; *SD* = 1,3 g, and the mean hatch interval was 0,52 days; *SD* = 0,88 days (N = 23).

We individually identified chicks by a felt pen marking on the down at hatching until two weeks of age, when we attached velcro tags to flippers. These were replaced by metal flipper rings when chicks were about six weeks old. We weighed chicks using 'Pesola' balances to an accuracy of at least 1% of capacity, and measured culmen length and culmen depth to the nearest 0,1 mm using Vernier calipers. All chicks were measured on their respective days of hatching. Thereafter we measured all chicks on the same day at five-day intervals, until fledging (at between 60–120 days). Consequently most chicks were weighed more than once in the first five days after hatching.

The chick phase is divided into two parts: (i) the guard phase between 1 and 30–40 days after hatching, when chicks are accompanied constantly by one or other parent, and (ii) the post-guard phase when both parents may forage at sea during the day. Chicks are fed by direct regurgitation.

Growth data analysis

We used the non-linear least-squares method of curve fitting to fit the growth data to logistic, Gompertz and Richards curves (BMDP Dixon 1988). We plotted mean residuals for five-day age classes to determine which equation best fitted the data. Logistic and Richards models fitted considerably better than the Gompertz model, and mean residuals of the logistic model were slightly closer to zero than those of the Richards. This, and the prevalence of highly correlated parameters for between 80–100% of all fitted Richards curves, led us to choose the logistic model as best describing the data, since correlated parameters meant that the Richards curve was in effect behaving as a three parameter curve (Zach 1988). We compared growth rates between groups using analysis of variance.

Results

Mean chick weights calculated for five-day intervals, for A and B chicks from all control broods are plotted (Figure 1). We found no overall significant differences in growth rates and asymptotes of body mass, culmen length or culmen depth between A and B chicks (Tables 1 & 2). However, we did find significant within-brood differences in growth for

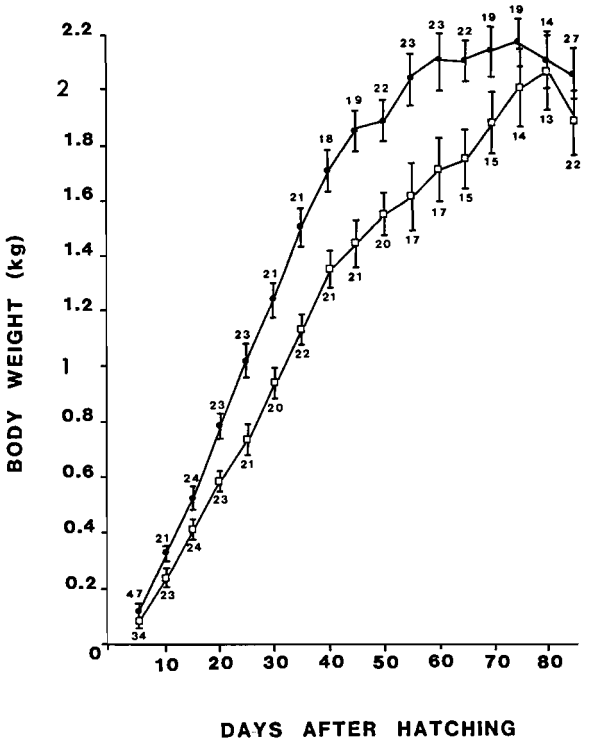

Figure 1 Growth of first- (closed circles) and second-hatched (open squares) jackass penguin chicks, plotted as means for each five-day interval. Standard errors are plotted with n values.

mass, with A chicks showing faster growth than their B siblings (Sign Test; one-tailed, 10 out of 13, $p < 0,05$), but not for culmen length or depth (Sign Test; one-tailed, 5/10, n.s., 7/8, n.s., respectively).

Growth constants and asymptotes of singletons did not differ from control A or B chicks for body mass, culmen length or culmen depth (Tables 1 & 2), but growth rates of mass were significantly higher than those of synchronized/same-sized chicks. Means of body mass calculated for five-day intervals are plotted for singletons, control (A & B chicks combined) and synchronous same-sized chicks (Figure 2). Although not significant, the trend is that one-chick broods showed fastest growth, followed by control A chicks, followed by control B chicks, with synchronized/same-size chicks showing slowest growth (Table 1). Mean growth rate of synchronous chicks was closest to that of control B chicks. We found no differences in growth rates or

Table 1 Mean ($\bar{x}$ ± *SD*) growth rate constants of groups of jackass penguins

	Chick	Control	n	Synch/same[1]	n	one chick	n
Mass	A	0,104±0,017	18	0,087±0,027	44	0,113±0,024	15
	B	0,098±0,027	13				
Culmen length	A	0,050±0,005	18	0,049±0,007	43	0,052±0,004	15
	B	0,048±0,006	13				
Culmen depth	A	0,039±0,010	18	0,037±0,007	41	0,039±0,007	15
	B	0,034±0,007	13				

[1] Data for this experimental group are pooled for comparison with chicks in the other groups.

Table 2 Analyses of variance on growth rate constants and asymptotes of fitted logarithmic curves of jackass penguins, comparing control/first-hatched, control/second-hatched, synchronized/same-sized and one-chick broods

	Body mass	Culmen length	Culmen depth
(1) Growth rate			
F	6,17	1,97	1,13
d.f.	3/87	3/85	3/83
p	$p < 0{,}001$	n.s.	n.s.
Tukey test	One-chk > S/S $p < 0{,}01$	n.s.	n.s.
(2) Asymptote			
F	1,06	0,52	1,04
d.f.	3/87	3/85	3/83
p	n.s.	n.s.	n.s.
Tukey test	n.s.	n.s.	n.s.

asymptotic values of culmen length or depth (Table 2).

Because A eggs are significantly larger than B eggs (Williams & Cooper 1984), chicks from A eggs may be better provisioned and have intrinsically faster growth rates than chicks from B eggs. To test for this possibility, we compared growth rates of chicks hatched from A and B eggs, which had been paired to form same-size synchronous broods. By matching chicks for size and hatching order, we assumed that any differences in growth rates observed would not be due to the size advantage of one sibling over the other. Of the 28 synchronous broods that survived, 14 were A:A combinations, two were B:B, eight were A:B and four were other (combined with a single chick or an unidentified chick collected from outside the study area). We compared growth rates of chicks from A and B eggs from the eight A:B matched pairs (Table 3), and found no significant difference in growth rates (Mann-Whitney *U* test, two-tailed; $n = 8/8$, $p = 0{,}104$), though there was a tendency for mean A chick growth to be faster than that of B chicks.

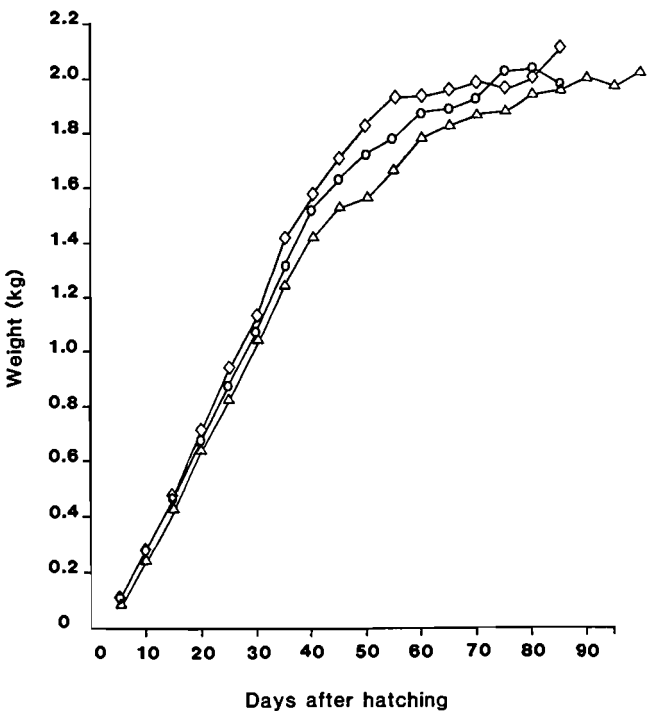

Figure 2 Growth in body mass of jackass penguins, calculated as means over five-day intervals, of singletons (diamonds), control chicks (A & B chicks combined), (circles) and synchronized/same-size chicks (triangles).

Discussion

Hatching order in jackass penguins influenced growth rates so that within a brood, B-chick growth was reduced relative to that of A chicks. However, as a group, A chicks did not have faster growth rates than B chicks, suggesting that parents vary in their foraging abilities, or in the way they allocate food within the brood. Randall (1983) also found considerable variation between individuals in the same years, and ascribed most of the observed differences in growth rates to parental ability to feed chicks. The effect of creating broods with no difference in hatching order was to depress the growth rate of the brood overall similar to that of a B chick in an asynchronous nest, indicating that feeding is less efficient overall in broods with two chicks of equal size. This suggests that an adaptive advantage of asynchronous hatching is that it allows for rapid growth in at least one sibling. Further advantages of asynchronous hatching in this species are shorter fledging periods and higher weights achieved during fledging (Seddon & van Heezik in press).

In penguins that show some degree of asynchrony of hatching, the incidence of differential growth rates within a brood appears to depend on food availability: weight differences between little penguin *Eudyptula minor* broods were more marked at some localities than others and this was attributed to differences in food supply (Gales 1987); A chicks of Galapagos penguins *Spheniscus mendiculus* generally grew faster than B chicks, although not at all localities (Boersma 1976). Similarly, Taylor (1962) found Adélie penguin *Pygoscelis adeliae* A chicks grew faster than B chicks at Cape Royds, Ross Island, but, Volkman & Trivelpiece (1980) found no within-brood differences in Adélie, gentoo

Table 3 Growth rate constants of mass of jackass penguin chicks paired at hatching, but matched for size and age

Nest	A-egg chick K	B-egg chick K
43W	0,1028	0,1184
55W	0,1138	0,0647
103P	0,1312	0,0909
107P	0,0713	0,0892
110P	0,1650	0,0676
112P	0,0755	0,0833
117P	0,0935	0,0519
120P	0,0706	0,0709
Mean	0,103	0,080
SD	0,0330	0,0210

P. papua or chinstrap *P. amtarctica* penguin growth rates at King George Island. They attributed this to an abundance of food. However, growth of yellow-eyed penguin chicks in one- and two-chick broods only differed when food supply was sufficiently limiting as to cause unusually high chick starvation (van Heezik & Davis 1990).

Evidence suggests that during the year of this study food supply was poor (Seddon & van Heezik in press). In these circumstances we might expect growth rates of A and B chicks, and one- and two-chick broods to differ more. However, although small within-brood differences were evident, only a non-significant trend towards faster growth in one-chick broods was found. Randall (1983) reported faster growth of one-chick broods, but made no statistical comparisons. This lack of difference may result from varying parental care. Younger parents are more likely to lay infertile eggs (Richdale 1957; Ainley, Leresche & Sladen 1983), thus ending up with a brood of one. It is well established that young inexperienced seabirds show lower breeding success (Richdale 1957; Coulson 1966; Ainley *et al.* 1983; Weimerskirch 1990; Williams 1990), and may feed less effectively, resulting in differing growth rates of offspring (Lequette & Weimerskirch 1990; Weimerskirch 1990). In Adélie penguins poor parental care may result not only in the loss of a chick, but also in poor growth of survivors (Taylor & Roberts 1962).

Alternative factors that may influence relative growth rates of one- and two-chick broods are parental response to brood size and/or begging rates. Parents may adjust the amount of food brought back according to brood size (Henderson 1975; Léger & McNeil 1987), or may feed in response to chick begging rates (Henderson 1975; Bengtsson & Rydén 1983; Stamps *et al.* 1989). If this was the case, in one-chick broods begging rates are likely to be lower, resulting in the parents bringing back less food.

Within-brood and between-brood differences in growth rates of body mass were not reflected in growth rates of culmen length and depth, although there was a non-significant trend towards slower growth of morphometric parameters in synchronous groups. Williams & Cooper (1984) found growth of foot and flipper in jackass penguins were also similar, irrespective of brood size and position in brood. Body mass tends to vary more than morphometric parameters, such as culmen length and depth, in most growth studies (Schreiber 1976; Wingham 1984; van Heezik & Davis 1990). In yellow-eyed penguins, chick growth rates of morphometric parameters slowed only when feeding conditions were so bad as to result in chick mortality (van Heezik & Davis 1990).

Chicks from A and B eggs did not show significantly intrinsically different growth rates; it is not possible to determine whether the non-significant trend towards faster A-chick growth was real or a product of inter-brood variability. The evidence suggests that differences in growth rates observed in chicks in asynchronous broods must be a product of hatching order only. The maintenance throughout the fledging period of asymmetries in size established at hatching indicates that food availability at the level of the brood must be determined by factors other than environmental abundance, such as parental allocation of food and/or competitive feeding mechanisms between siblings. These factors appear to have a greater potential to influence growth rates than does brood size.

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