Egg temperature and embryonic metabolism of A- and B-eggs of macaroni and rockhopper penguins

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Macaroni and rockhopper penguins lay two eggs but rear only one chick to independence. The eggs are markedly dimorphic in size and, although the smaller A-egg is laid several days before the B-egg, in nests where both eggs are incubated, the B-egg always hatches first. Incubation temperatures and embryonic oxygen consumption were measured to determine whether the observed hatching sequence could be accounted for by differences in egg temperatures or rate of embryonic development. Lowest egg temperatures were recorded from A-eggs incubated in the less favourable anterior position in the brood patch and highest temperatures from A-eggs incubated singly and B-eggs. Differences, however, were not significant. Levels of embryonic oxygen consumption of A-eggs of the same age showed a similar pattern to egg temperatures, but differences were slight. A-eggs incubated singly, and those incubated for several days after laying in a hot-room, still had incubation periods longer than B-eggs, suggesting that egg temperature alone does not account for differences in the hatching sequence. Consequently, it appears that there are inherent differences in embryonic metabolism of A- and B-eggs that result in the B-egg, which represents the greater parental investment, hatching first.

Macaroni- en geelkuifpikkewyne lê twee eiers op 'n keer maar net een kuiken word grootgemaak. Die eiers is opvallend dimorf in grootte en al word die kleiner A-eier verskeie dae voor die B-eier gelê, in neste waar altwee eiers bebroei word, broei die B-eier altyd eerste uit. Broeitemperature en embrioniese suurstofverbruik is gemeet om te bepaal of die waargenome uitbroeivolgorde toegeskryf kan word aan verskillende broeitemperature of embrioniese ontwikkelingstempo's. Die laagste eiertemperature is gemeet by A-eiers wat in die minder gunstige voorste posisie in die broeikol bebroei is en die hoogste temperature is by A-eiers wat alleen bebroei is en by B-eiers gemeet, maar die verskille was nie betekenisvol nie. Embrioniese suurstofverbruik het 'n soortgelyke patroon as eiertemperature getoon, en die verskille was eweneens baie klein. A-eiers wat alleen bebroei is en A-eiers wat vir verskeie dae nadat hulle gelê is in 'n broeikamer bebroei is, het nog broeiperiodes gehad wat langer was as dié van B-eiers. Dit dui aan dat die temperatuur van die eiers alleen nie vir die verskil in die uitbroeivolgorde verantwoordelik is nie. Dit blyk dus asof daar inherente verskille in die embrioniese metabolisme van A- en A-eiers is, wat verseker dat die B-eier, wat die grootste ouerlike bydrae verteenwoordig, altyd eerste uitbroei.

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Crested penguins of the genus *Eudyptes* lay two eggs which are markedly dimorphic in size (Gwynn 1953). This dimorphism is most pronounced in macaroni penguins *E. chrysolophus* and rockhopper penguins *E. chrysocome* in which the first laid A-eggs average 59% and 44% lighter, respectively, than the second laid B-eggs (Williams 1980a). Although both eggs are viable, only one chick is reared. In macaroni penguins brood reduction usually occurs through loss or ejection of the A-egg from the nest before the B-egg is laid (Warham 1963, 1971; Williams 1980b). However, in rockhopper penguins, both A- and B-eggs are incubated in about 30% of nests (Williams 1980b). The laying interval between A- and B-eggs of both species averages 4–5 days, but the B-egg hatches before or on the same day as the A-egg (Williams 1981a). Williams (1980a) suggested two possible reasons for this. Firstly, in nests where both eggs are incubated, incubation of the A-egg does not begin until the B-egg has been laid. Also, because eggs are positioned one behind the other in the elongated brood patch and the birds incubate in a semi-upright position, the anterior egg is more exposed. A-eggs are more frequently placed in the anterior position. Consequently, A-eggs are incubated for the same period as B-eggs but generally experience lower and less steady temperatures during incubation (*cf.* Burger & Williams 1979) which might retard embryonic growth. Secondly, the time required for embryonic development is different for A-and B-eggs.

In this study I investigated egg temperatures and embryonic oxygen consumption of A- and B-eggs of macaroni and rockhopper penguins. In order to test the suggestions of Williams (1980a), egg temperatures and embryonic oxygen consumption were measured on (i) A-eggs incubated normally with B-eggs, (ii) A-eggs incubated alone and (iii) A-eggs which were incubated at temperatures above 30°C from day of laying.

Methods

The study was carried out at sub-Antarctic Marion Island (46°52'S / 37°51'E), between October and December 1985. Selected nests of both macaroni and rockhopper penguins were numbered prior to egg laying and nests were checked daily for eggs, whose laying dates were recorded. Because the A-egg of macaroni penguins is usually lost before the B-egg is laid, A-eggs were substituted for B-eggs in a number of nests at the beginning of incubation. In order to obtain rockhopper penguin nests in which A-eggs were incubated alone, B-eggs were removed from several nests on the day they were laid. Because A-eggs of rockhopper penguins are not normally incubated until the B-egg is laid, A-eggs were

removed from four nests and 'pre-incubated' at 33–35°C in a hot-room. These eggs were then replaced in their nests once the B-eggs were laid.

Measurement of egg temperatures

Egg temperatures of B-eggs of macaroni penguins and A- and B-eggs of rockhopper penguins were measured using previously collected and blown eggs of the respective species filled with water and containing previously calibrated Model T or Model L minimitters (Minimitter Co., Indianapolis). Minimitters were held in place in the centre of the eggs by cut off, perforated, plastic syringe barrels inserted into the eggs through a hole in the blunt end and glued into place in the long axis of the eggs. Water and the minimitter were introduced into each egg through the hole in the blunt end which was then sealed using the rubber plunger from the syringe.

Eggs containing transmitters were substituted for fertile eggs in the field when the latter were removed for measurements of oxygen consumption and were readily accepted and incubated by the birds. Because the macaroni penguin colony was about 2,5 km from the research station, temperatures of the dummy eggs were measured prior to replacement of the fertile eggs, between 3–4 h and 24 h after their initial removal. Temperatures were then recorded at 5-min intervals over a period of 15–30 min. Rockhopper penguins, however, nest under some of the buildings of the research station and on the adjacent point. Consequently, a series of egg temperature measurements was usually made, when convenient, over periods of 12–24 h. The mean egg temperature over each period was subsequently used.

Embryonic oxygen consumption

Measurements of embryonic oxygen consumption were made at approximately 5-day intervals from 6–10 days into incubation. Dummy eggs containing transmitters were substituted for fertile eggs in the nests and fertile eggs taken to the laboratory, a trip of less than 5 min for eggs of rockhopper penguins, but 25 min for those of macaroni penguins, which were wrapped in cotton wool for the trip. In the laboratory, eggs were weighed to the nearest 0,01 g on a Mettler analytical balance and placed in a hot-room at 33–35°C, within the range of egg temperatures previously measured for penguins (Burger & Williams 1979 and references therein).

Embryonic oxygen consumption was measured in closed respiratory systems consisting of plexiglass syringes of 2 800 ml (macaroni penguin eggs) or 1 400 ml (rockhopper eggs) maximum volume. Chamber volume depended on how far back the plunger was drawn and, because this was varied depending on the size of the egg and the age of the embryo, chamber volume was calculated for each measurement. The net volume of air in the chamber was calculated by subtracting the volume of each egg (measured by water displacement) from the calculated chamber volume. Eggs were left for 1–3 h to come into thermal equilibrium with the hot-room air before being placed in a chamber. Chambers were then flushed with air and the open ends sealed off with three-way stopcocks. Eggs were left in the chambers for periods estimated to reduce the oxygen concentration in the chamber by 0,5–2,0%. This required as long as 24 h for young embryos (7–10 days) to 5–10 min for pipped eggs and hatchlings. Final oxygen concentration in the chambers was measured by injecting the chamber air through a tube of soda asbestos and silica gel into a Taylor Servomex OA 570 paramagnetic oxygen analyser. Initial oxygen concentration in the hot-room was measured by pumping hot-room air through the analyser with a hand-held aspirator. Embryonic oxygen consumption ($\dot{V}O_2$) was calculated from Equation 1 of Vleck, Hoyt & Vleck (1979) and corrected to STPD. Eggs were returned to their nests after measurement.

Oxygen consumption was measured throughout incubation or until the embryo died. Measurements from embryos which died were only used from that portion of incubation in which oxygen consumption was similar to that of eggs which hatched. All means are given ± 1 standard deviation.

Results

A-eggs of rockhopper penguins incubated alone had slightly shorter incubation periods (mean = 38,8 ± 1,7 days; range 36–41; n = 6) than did those incubated in two-egg clutches (mean = 39,9 ± 1,3 days; range 38–42; n = 7), although the difference was not significant (t = 1,383; $p > 0,02$). Two A-eggs that were incubated above 30°C from laying hatched in 39 days; the remaining two pre-incubated eggs were found next to their nests once the B-eggs had hatched and were presumably ejected from their nests (Williams 1980b). Overall incubation periods and fresh egg masses of A- and B-eggs of macaroni and rockhopper penguins, recorded during the present study (Table 1), were similar to those previously measured for the species at Marion Island (Williams 1980, 1981a) and at other localities (Warham 1963, 1971; Strange 1982).

Egg temperatures

Egg temperatures of rockhopper penguins measured over 12–24 h fluctuated by as little as 1°C to as much as 7°C,

Table 1 Incubation periods and fresh egg mass of A- and B-eggs of macaroni and rockhopper penguins at Marion Island

		Macaroni penguins		Rockhopper penguins	
		A-eggs	B-eggs	A-eggs	B-eggs
Incubation period (days)	Mean	38,8	34,6	39,1	33,6
	S.D	1,3	1,8	1,3	1,1
	Range	37–41	32–39	38–42	31–35
	N	4	12	14	20
Egg mass (g)	Mean	99,2	163,3	77,5	111,9
	S.D.	7,7	16,0	8,5	12,9
	Range	87,7–109,3	138,7–179,0	63,4–91,4	98,1–131,8
	N	8	9	8	7

Table 2 Egg temperatures of macaroni and rockhopper penguins during natural incubation at Marion Island. Figures are means ± standard deviation, range and sample size

Day of incubation	Egg temperature (°C)											
	Macaroni penguins				Rockhopper penguins							
					A-eggs				B-eggs			
1– 7	27,9			[1]			—				—	
8–14	33,6	± 0,8	(33,0–34,9)	[5]	31,0	± 0,6	(30,4–31,6)	[3]	31,2			[1]
15–21	34,0	± 1,8	(31,1–35,9)	[6]	33,9		(33,7–34,0)	[2]	33,8	± 0,7	(33,0–34,4)	[4]
22–28	35,4	± 1,1	(33,2–36,1)	[6]	32,8		(31,9–33,6)	[2]	33,5	± 0,7	(32,7–34,0)	[3]
29–35	34,1			[1]			—		33,7		(32,8–34,5)	[2]
Overall	34,0	± 2,1	(27,9–36,1)	[19]	32,3	± 1,4	(30,4–34,0)	[7]	33,5	± 1,2	(31,2–34,5)	[10]

presumably as a result of egg turning, changes in adult attentiveness, nest ventilation and the position of the egg in the nest.

There were slight differences in temperatures of dummy eggs placed in different positions within rockhopper penguin nests, with single eggs (33,4 ± 1,0°C; $n = 9$) being incubated at a higher temperature than eggs placed in the posterior position in a two-egg clutch (32,7 ± 1,1°C; $n = 4$) and lowest temperatures being recorded from eggs placed anteriorly in a two-egg clutch (31,9 ± 1,9°C; $n = 3$). Differences, however, were not significant ($p > 0,05$), probably because of the small sample sizes involved, and results were pooled. A single macaroni penguin B-egg recorded prior to 7 days after laying had a temperature of 27,9°C. However, from the second week of incubation until hatching there was no consistent trend in dummy egg temperatures of either macaroni penguins or A- and B-eggs of rockhopper penguins (Table 2). Overall egg temperature of macaroni penguins averaged 34,0 ± 2,1°C and those of rockhopper penguins A-eggs (32,2 ± 1,4°C) averaged slightly, but not significantly, lower than those of B-eggs (33,5 ± 1,2°C; $t = 1,90$; $p > 0,20$) (Table 2).

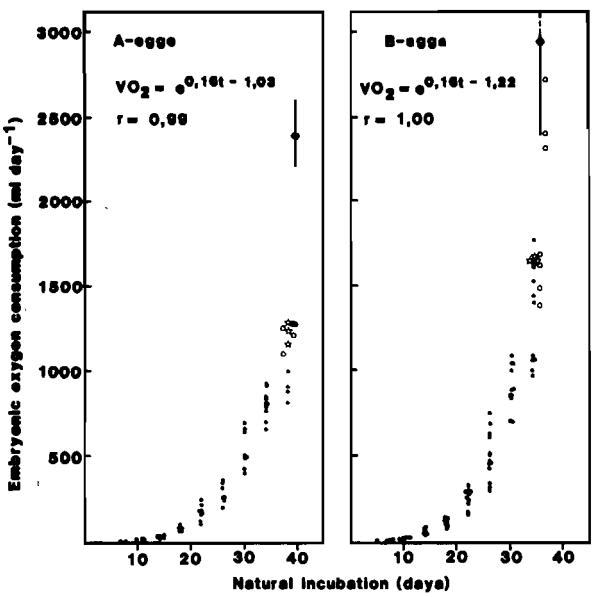

Figure 1 Embryonic oxygen consumption of A- and B-eggs of macaroni penguins in relation to age. Solid circles = unpipped eggs, stars = fractured eggs, open circles = pipped eggs (holed) and diamond = hatchlings ± 1 *S.D.* Data for A-eggs based on 76 measurements on seven eggs and those of B-eggs on 98 measurements on nine eggs. Equations relate to unpipped eggs only.

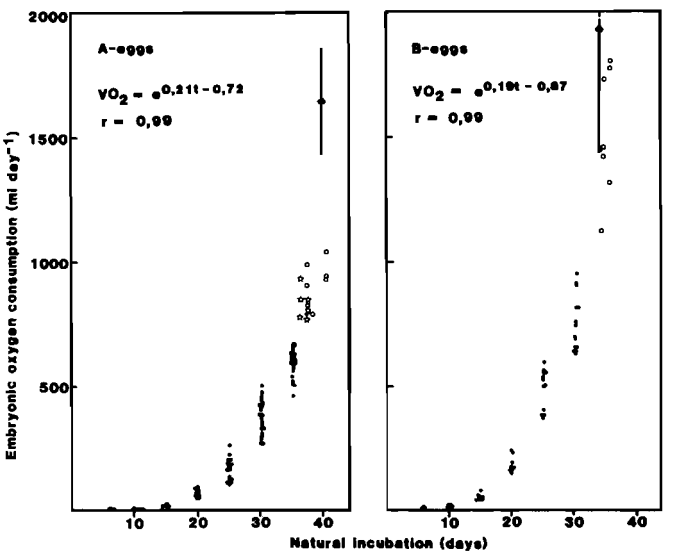

Figure 2 Embryonic oxygen consumption of A- and B-eggs of rockhopper penguins in relation to age. Symbols as for Figure 1. Data for A-eggs based on 149 measurements on 17 eggs and those of B-eggs based on 68 measurements on nine eggs. Equations relate to unpipped eggs only.

Embryonic oxygen consumption

Oxygen consumption ($\dot{V}O_2$) increased throughout incubation in A- and B-eggs of macaroni and rockhopper penguins (Figures 1 & 2). Mean $\dot{V}O_2$ prior to fracture of the egg shell averaged 821 and 1 337 ml day^{-1} for A- and B-eggs of macaroni penguins, respectively (Table 3). In the first 10–25 days of incubation, A-eggs of rockhopper penguins which were pre-incubated for the first 3–4 days in the hot-room had rates of $\dot{V}O_2$ similar to those

Table 3 Mean pre-pipping oxygen consumption ($\dot{V}O_2$) of macaroni and rockhopper penguin embryos at Marion Island

	Pre-pipping $\dot{V}O_2$ ml O_2/day	Day of incubation	No. of eggs
Macaroni penguins			
A-eggs	820,6 ± 90,3	38	7
B-eggs	1337,0 ± 295,0	33	4
Rockhopper penguins			
A-eggs	592,6 ± 55,0	35	12
B-eggs	732,3 ± 78,7	30	7

incubated alone on the nest, both of which were slightly higher than A-eggs incubated in two-egg clutches. However, differences in mean $\dot{V}O_2$ on comparable days of incubation were not significant, nor were differences in the slopes of the semilog transformed data relating $\dot{V}O_2$ to incubation time ($p > 0,05$). Consequently, results for all A-eggs were pooled, overall pre-pipping $\dot{V}O_2$ averaging 593 ml day^{-1} (Table 3). Pre-pipping $\dot{V}O_2$ of rockhopper penguin B-eggs averaged 732 ml day^{-1} (Table 3) but was, however, measured about three days prior to initial fracture of the shell and is thus probably a slight underestimate of actual pre-pipping $\dot{V}O_2$.

Mean embryonic $\dot{V}O_2$ of both macaroni and rockhopper penguin B-eggs was always significantly greater than that of A-eggs measured on the same day of incubation (macaroni penguins $p < 0,02$; rockhopper penguins $p < 0,001$), although there was no difference in the slopes of the semilog transformed data relating embryonic $\dot{V}O_2$ to incubation time (macaroni penguins $t = 1,527$; $p > 0,10$; rockhopper penguins $t = 1,183$; $p > 0,20$).

After initial pipping, $\dot{V}O_2$ increased markedly in all eggs measured and reached a peak in hatchlings at levels 2–3 times pre-pipping levels (Figures 1 & 2). Although hatchlings from B-eggs of both species had higher metabolic rates than hatchlings from A-eggs, differences were not significant (macaroni penguins $t = 2,04$; $p > 0,05$; rockhopper penguins $t = 1,67$; $p > 0,01$). Total oxygen consumption during embryonic development, estimated from graphical integration of the areas under the curves in Figures 1 & 2, was 12,6 and 14,5 ℓ O_2 for A- and B-eggs of macaroni penguins, respectively, and 7,0 and 10,6 ℓ O_2 for those of rockhopper penguins (Table 4), of which 70–74% was consumed prior to pipping.

Table 4 Total embryonic oxygen consumption of macaroni and rockhopper penguins

	Total $\dot{V}O_2$		Pre-pipping $\dot{V}O_2$		Pip-to-hatch $\dot{V}O_2$	
	ml	ml/g egg	ml	% total	ml	% total
Macaroni penguins						
A-eggs	12 558	126,6	9 314	74,2	3 244	25,8
B-eggs	14 540	89,0	10 700	73,6	3 840	26,4
Rockhopper penguins						
A-eggs	6 985	90,1	4 955	70,9	2 030	29,1
B-eggs	10 552	94,2	7 788	73,8	2 764	26,2

Discussion

Egg temperature

Incubation temperatures measured for both A- and B-eggs of macaroni and rockhopper penguins in the present study were within the range measured for several other species of penguins (Table 5). In particular, those of rockhopper penguins were similar to those measured for the same species by Burger & Williams (1979) during the second half of incubation. Although Burger & Williams (1979) reported low egg temperatures in both macaroni and rockhopper penguins during the first half of incubation, egg temperatures of both species in the present study were maintained above 30°C from eight and 10 days after laying, respectively (see Table 2).

Consistent with Burger & Williams (1979), B-eggs of rockhopper penguins were maintained at a higher temperature than were A-eggs, although in the present

Table 5 Egg temperatures of penguins during incubation, measured with transmitters (M) and thermistors or thermocouples (T) on dummy (D), infertile (I) or in the centre (L) or air space (A) of live eggs

Species	Egg temperature (°C) Mean	Range	Method	Reference
Emperor penguin	32,6 ± 0,7		MD	1
	32,7 ± 0,4			
Adélie penguin	33,7	(29,2–36,8)	MD	2
	35,2	(30,0–38,0)	TL	3
	35,9 ± 1,1	(34,7–37,2)	TL	4
Chinstrap penguin	37,4 ± 0,5	(34,8–38,0)	TI	5
	34,5 ± 2,9	(29,0–38,0)		
Gentoo penguin	32,9 ± 4,0	(16,8–37,9)	TA	6
Yellow-eyed penguin	35,2[a]		—	7
Macaroni penguin A-egg[b]	11,7	(1,3–33,0)	TA	6
B-egg	23,4	(17,2–32,5)	TA	
	37,3 ± 0,6	(34,0–37,8)	TI	5
	34,0 ± 2,1	(27,9–36,1)	MD	8
Rockhopper penguin A-egg	32,9	(22,8-37,9)	TA	6
	32,3 ± 1,4	(30,4–34,0)	MD	8
B-egg	25,9 ± 10,1	(8,4–37,9)	TA	6
	33,5 ± 1,2	(31,2–34,5)	MD	8
Jackass penguin	34,9[c]	(14,0–36,0)	–	9
	34,5 ± 1,5	(31,9–36,0)	TA	6

[a]Estimated as the midpoint between the egg-brood patch interface and the egg-nest substrate interface.

[b]Measured on day of laying.

[c]Calculated indirectly from water-vapour pressure difference between the egg and the nest microclimate.

1 Bucher *et al.* (1986); 2 Eklund & Charlton (1959); 3 Derksen (1977); 4 Rahn & Hammel (1982); 5 Haftorn (1986); 6 Burger & Williams (1979); 7 Farner (1958); 8 This study; 9 Yom-Tov *et al.* (1986).

study the differences were not very marked. Burger & Williams (1979) attributed differences in temperature to the position of the eggs in the nest, B-eggs being found more frequently in the posterior position where they are more covered by the brood patch and less exposed to cool ambient temperatures than are A-eggs. Differences in temperatures of eggs placed singly or in different positions in a two-egg clutch in the present study, although slight, support this, temperatures of A-eggs incubated alone and those placed posteriorly in two-egg clutches being close to those of B-eggs.

Egg temperatures of macaroni penguins measured by Haftorn (1986) were made with thermistors placed near the egg surface and are probably more representative of brood patch temperatures than of central egg temperatures measured in the present study (see Farner 1958; Yom-Tov, Wilson & Ar 1986).

Embryonic metabolism

Low egg temperatures in penguins are known to retard embryonic development (Weinrich & Baker 1978) and the slightly higher rates of embryonic oxygen consumption of pre-incubated A-eggs of rockhopper penguins, and those of A-eggs incubated singly, are consistent with the slightly higher incubation temperatures and slightly shorter incubation periods observed in these eggs compared to those incubated in two-egg clutches. However, even A-eggs which were incubated singly or at temperatures similar to those of B-eggs from day of laying had incubation periods longer than B-eggs. Furthermore, the incubation period of macaroni penguin A-eggs was 2–4 days longer than those of B-eggs, even though the A-eggs were substituted for B-eggs on the day of laying and consequently occupied the posterior position in the brood patch throughout incubation (Williams 1981a; this study). Similarly, a comparison of macaroni penguin A-eggs and rockhopper penguin B-eggs, both of which are similar in size (see Table 1), are incubated posteriorly in the brood patch and produce similarly sized hatchlings (Williams 1980a, Table 6), shows that A-eggs of macaroni penguins have rates of oxygen consumption significantly lower than those of rockhopper penguin B-eggs at equivalent stages of incubation between 10 and 30 days ($p < 0{,}005$). From the above observations, it is evident that the different temperatures experienced by A- and B-eggs of, in particular rockhopper penguins, do not, by themselves, account for the differences in incubation periods which result in B-eggs hatching earlier than A-eggs.

Embryonic metabolism of A-eggs could be retarded if oxygen conductance across the eggshell was limiting. Because conductances of oxygen and water across eggshells are proportional to their respective diffusion coefficients, oxygen conductances of eggshells at 38°C ($G_{O_2}^{38}$) can be calculated from their water vapour conductances, measured at 25°C ($G_{H_2O}^{25}$), using the relationship $G_{O_2}^{38} = 1{,}08\ (G_{H_2O}^{25})$ (Hoyt, Board, Rahn & Paganelli 1979). Water vapour conductances of A- and B-eggs of both macaroni and rockhopper penguins have been measured (C.R.Brown unpubl. data) and oxygen conductances calculated from these have values of 19,5 and 27,0 ml d^{-1} $torr^{-1}$ for A- and B-eggs of macaroni penguins, respectively, and 15,9 and 19,2 ml d^{-1} $torr^{-1}$ for those of rockhopper penguins. Higher oxygen conductances of B-eggs are consistent with their larger size and larger functional pore area, but oxygen conductances of rockhopper penguin B-eggs, which had oxygen uptakes significantly greater than macaroni penguin A-eggs of similar size, were the same. Consequently, it must be concluded that oxygen conductance of the shell does not limit embryonic metabolism in A-eggs. This suggests that Williams' second suggestion, that the time required for embryonic development of A- and B-eggs is different, is more likely. Presumably, embryos have to reach a particular level of development and metabolism before hatching can occur. The generally higher levels of metabolism in B-eggs result in this level being attained earlier than in A-eggs. A-eggs have proportionately less albumen than do B-eggs (Williams, Siegfried & Cooper 1982). Since the proportion of albumen has a controlling effect on post-hatching development (*cf.* Nisbet 1978), Williams (1980a) suggested that it might also affect embryonic development.

Williams (1980a) hypothesized that ancestral *Eudyptes* penguins were inshore foragers which laid two eggs of similar size and were capable of rearing two chicks, as do present inshore-foraging species. He speculated that the ability to raise only a single chick resulted from a move to

Table 6 Metabolic rates of penguin embryos during development

Species	Fresh egg mass (g)	Pre-pipping $\dot{V}O_2$ (ml day^{-1})	Total embryonic $\dot{V}O_2$ (ml)	Total embryonic $\dot{V}O_2$ (ml g^{-1} egg)	Hatchling mass (g)	Hatchling $\dot{V}O_2$ (ml day^{-1})	Hatchling $\dot{V}O_2$ (ml.g day^{-1})
Emperor penguin[a]	465,5	1 621	43 997	94,5	—	—	—
Adélie penguin[a]	114,2	830	11 865	99,7	81,0	1 640	20,2
Macaroni A-eggs[b]	99,2	821	12 558	126,6	84,2	2 393	28,4
penguin B-eggs	163,3	1 337	14 540	89,0	106,7	2 946	27,6
Rockhopper A-eggs[b]	77,5	593	6 985	90,1	53,1	1 634	30,8
penguin B-eggs	111,9	732	10 552	94,2	81,0	1 934	23,9

[a] Bucher *et al.* (1986). [b] This study.

offshore-foraging, characteristic of present *Eudyptes* penguins. Under these circumstances, where feeding frequency is reduced, early brood reduction would allow all energy delivered by the adults to be channelled into the single chicks which would survive, rather than wasting it on a second chick which could not be raised. Chicks from large eggs grow larger, survive better and, in penguins, are fed preferentially (Williams 1981b). Consequently, an inherently slower rate of embryonic metabolism, and presumably slower embryonic development, brought about through differences in egg composition, ensures that hatching of eggs in *Eudyptes* penguins is such that the larger B-egg, which represents the greater parental investment, always hatches first. Clearly, however, the relationship between egg composition and embryonic development in these and other species of *Eudyptes* penguins needs to be investigated further.

Embryonic metabolism has previously been measured only for emperor penguins *Aptenodytes forsteri* and Adélie penguins (Bucher, Bartholomew, Trivelpiece & Volkman 1986). Relevant results are compared with those from macaroni and rockhopper penguins in Table 6. Adélie penguin eggs and hatchlings have similar masses to those of B-eggs of rockhopper penguins and pre-pipping $\dot{V}O_2$, total embryonic $\dot{V}O_2$ and hatchling $\dot{V}O_2$ for the two species are also similar (Table 6). Overall, despite the large range of egg sizes (78 g for rockhopper penguin A-eggs to 466 g for emperor penguin eggs), total embryonic $\dot{V}O_2$ per gram fresh egg mass was, with the single exception of macaroni penguin A-eggs, very similar for all species.

On the basis of egg composition and the ability of their chicks to leave the nest and fend for themselves (Nice 1962; Williams *et al.* 1982), penguins have generally been classified as semi-altricial species. However, Bucher *et al.* (1986) compared measured embryonic and hatchling metabolic rates with those predicted for altricial and precocial species and concluded that embryos and hatchlings of emperor and Adélie penguins had metabolic rates more characteristic of semi-precocial and precocial species than with those of semi-altricial species. Although embryonic oxygen consumption of macaroni and rockhopper penguins shows no indication of a plateau in the days immediately preceding pipping, a feature characteristic of precocial species (Vleck *et al.* 1979), pre-pipping, total, and hatchling $\dot{V}O_2$ of both species were, as with emperor and Adélie penguins, more closely predicted by equations for precocial species than by those for altricial species. However, it is notable that post-natal metabolism of macaroni and rockhopper penguins is consistent with that of semi-altricial chicks (Brown 1987).

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