EGG TEMPERATURES OF THE ROCKHOPPER PENGUIN AND SOME OTHER PENGUINS

A. E. BURGER AND A. J. WILLIAMS
FitzPatrick Institute, University of Cape Town, Rondebosch 7700, South Africa

ABSTRACT.—Temperatures in penguin eggs were measured by telemetry during undisturbed incubation. During the second half of the incubation period egg temperatures average 29.9–34.4°C in Rockhopper Penguins (*Eudyptes chrysocome*), 35.9–36.2°C in Gentoo Penguins (*Pygoscelis papua*), and 31.9–36.0°C in Jackass Penguins (*Spheniscus demersus*). These temperatures are not markedly lower than those in other birds' eggs. Gentoo and Jackass penguin eggs attain mean temperatures above 30°C within 7 days of incubation but Rockhopper Penguin eggs attain similar high mean temperatures only after 16 days of incubation. Eggs of the Rockhopper Penguin are dimorphic and temperatures in the smaller, first-laid eggs are lower and more variable than in the larger, second-laid eggs. This is attributed to egg size *per se* and to differential positioning of the eggs in relation to the brood patch. *Received 4 April 1978, accepted 28 September 1978.*

PENGUINS spend much of their lives in seawater, a medium with a thermal conductance some 25 times greater than air. Consequently they possess a well insulated integument and other adaptations for reducing loss of body heat to the environment (Stonehouse 1967, Kooyman et al. 1976). Penguins also have lower resting body temperatures than most birds (McNab 1966). This suggests that penguins might have difficulty in maintaining the relatively high temperatures normally associated with successful incubation of avian eggs (Drent 1975). The literature reviewed by Drent (1973, 1975), however, contains very little information on the temperatures of penguin eggs during undisturbed incubation.

During a study of the avifauna of Marion Island in the sub-Antarctic (Williams et al. 1975), we recorded egg temperatures during undisturbed incubation of Gentoo Penguins (*Pygoscelis papua*), Macaroni Penguins (*Eudyptes chrysolophus*) and Rockhopper Penguins (*E. chrysocome*). In addition, we recorded egg temperatures in the Jackass Penguin (*Spheniscus demersus*), a species inhabiting cool seas and breeding on arid, hot islands along the coast of southern Africa (Frost et al. 1976). Special attention was given to the Rockhopper Penguin as part of a study aimed at an understanding of the adaptive significance of the species' markedly dimorphic eggs (Gwynn 1953, Warham 1963).

METHODS

We studied penguins during the austral summers 1974/75–1977/78 at Marion Island (46°54'S, 37°45'E), southern Indian Ocean and at Dassen Island (33°25'S, 18°06'E) and Marcus Island (33°03'S, 17°56'E), South Africa. Internal temperatures of the eggs of free-living penguins were measured using procedures described by Drent (1970). A thermistor probe was inserted into the air-space of each egg and sealed into position with epoxy-resin putty. The inner cell membrane was not punctured. The probed egg could be moved freely in the nest. When the temperatures were to be monitored over several days, a wide-spectrum antibiotic was used to sterilize the probe and the area of the egg surrounding it.

Temperatures were recorded at 5-min intervals using a Prelim 170 telethermometer operated from within a blind. The observer was able to enter the blind without being seen by the incubating birds. The thermistor probes were accurate to ±0.2°C when checked regularly against a mercury thermometer. Data from eggs in which embryos did not develop normally, or which were found to have probes that had shifted, were discarded.

Egg temperatures of four species of penguins were monitored for 24-h periods. In addition, eggs of Rockhopper Penguins were monitored twice daily during hour-long spells, each morning from about 0900 (local time) and each night after dark, from about 2100. These Rockhopper Penguin eggs were probed

TABLE 1. Penguin egg temperatures measured by telemetry for 24-h periods or longer.

Species	Egg	Approx. day of incubation	Egg temperature (°C) Mean	Range	Source
Rockhopper Penguin	Second	5–8	20.8	10.5–36.9	This study
	Second	13–14	14.2	8.4–26.7	This study
	Second	15–18	34.4	29.6–37.9	This study
	Second	28–32	34.2	23.0–37.7	This study
	First	28–32	32.9	22.8–37.9	This study
Macaroni Penguin	First	0[a]	11.7	1.3–33.0	This study
	Second	0–7	23.4	17.2–32.5	This study
Gentoo Penguin	N.D.[b]	0–7	32.0	29.8–33.9	This study
	N.D.	0–7	27.6	16.8–31.8	This study
	N.D.	23–27	35.9	32.3–37.7	This study
	N.D.	23–27	36.2	33.0–37.7	This study
Adélie Penguin	N.D.	N.D.	33.7	29.1–36.8	Ecklund and Charlton 1959
	N.D.	27–28	35.2	30–38	Derksen 1977
Jackass Penguin	First	0[a]	28.9	24.8–33.6	This study
	N.D.	2–5	34.9	31.7–36.9	Frost et al. 1976 and pers. comm.
	N.D.	2–5	34.0	30.2–36.4	Frost et al. 1976 and pers. comm.
	N.D.	13–15	31.9	26.8–36.7	This study
	N.D.	13–15	34.3	29.8–37.6	This study
	N.D.	32–33	36.0	30.0–38.4	This study
	N.D.	34–35	35.8	28.4–38.7	This study

[a] Second egg not yet laid.
[b] Not determined.

and sealed when laid, and remained so until just prior to hatching. Ten eggs were fitted with thermistor probes but embryo development proceeded normally in only four eggs: two first-laid (A) eggs and one second-laid (B) egg in complete clutches, and one B egg in a nest from which the first egg had disappeared at the time the second was laid. Additional data were obtained for a B egg in a complete clutch incubated normally for the first 18 days.

The incubation period is dated from the completion of the clutch. Average incubation periods are: 33–34 days for Rockhopper Penguins (Gwynn 1953, Warham 1963), 35–36 days for Macaroni Penguins (Gwynn 1953, Downes et al. 1959), 35–36 days for Gentoo Penguins (Gwynn 1953), and about 39 days for Jackass Penguins (McLachlan and Liversidge 1978).

The positions of eggs beneath the brood patches of Rockhopper Penguins were recorded at 3 stages of the incubation period by carefully lifting incubating birds off their clutches. This was done at a colony that was otherwise undisturbed by man.

RESULTS

Mean temperatures of incubated eggs of five species of penguins are presented in Table 1. Eggs of Gentoo and Jackass Penguins had mean temperatures of 27.6–32.0°C and 28.9–34.9°C respectively within the first 7 days of incubation. Those of Rockhopper and Macaroni Penguins failed to reach such high temperatures during the first week. Rockhopper Penguin egg temperatures rose markedly above ambient air temperatures only after the second egg had been laid (Fig. 1), and achieved fairly constant temperatures above 30°C only after 16 days of continuous incubation.

Incubation shifts of Rockhopper Penguins (N = 8–12 pairs) at Marion Island are similar to those at Macquarie Island (Warham 1963). Both parents remain at the nest for the first 5 days of the incubation period, with the female usually incubating. The male then leaves for the sea to feed for about 15 days and the female incubates. The male then incubates for about 10 days while the female feeds at sea. The female returns a few days before the chicks hatch.

Among most species of penguins that lay two eggs there is little difference in size

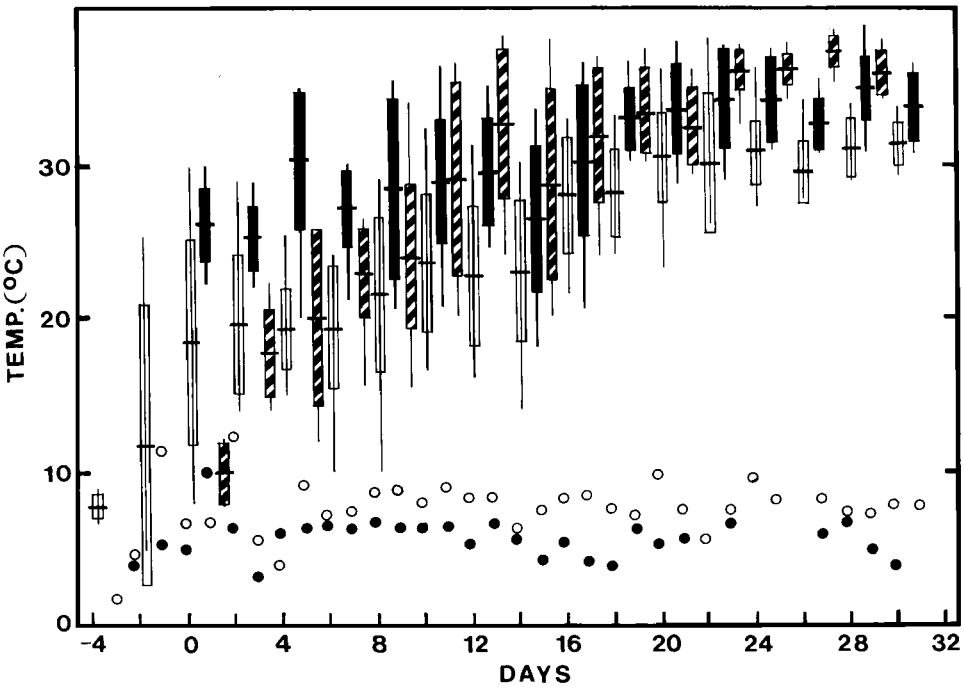

Fig. 1. Internal temperatures of Rockhopper Penguin eggs, including first laid (A) eggs (open boxes) and second laid (B) eggs (black boxes) in complete clutches and a B egg incubated singly (hatched boxes). The mean temperature (horizontal bar), ± one SD (vertical box) and range (vertical line) are given for 2-day intervals. Open and solid circles show the mean shaded air temperature at 20 cm above ground level for daytime and night respectively.

between eggs in a clutch. In the genus *Eudyptes,* however, the first laid (A) egg is significantly smaller than the second laid (B) egg in each clutch (Gwynn 1953, Warham 1963). On average, 4 days elapsed between the laying of the A and B eggs in Rockhopper Penguin clutches at Marion Island (N = 59 clutches). The mean period between laying and hatching of A eggs was 39 days and of B eggs, 34 days. This difference represents an increase of 1 day over the laying interval so that the A egg normally hatches after the B egg at nests where both eggs hatch.

The B eggs in Rockhopper Penguin clutches were maintained at higher and steadier temperatures than the A eggs throughout the incubation period (Fig. 1). The B egg incubated alone initially had a lower temperature than those in completed clutches but this situation was reversed after the tenth day of incubation. After 16 days the mean temperature recorded daily for all A eggs was 29.9°C (range 21.5–38.0°C) and for all B eggs 34.3°C (range 20.4–38.2°C). These results are similar to the means over 24-h periods (Table 1).

Rockhopper Penguin eggs are usually held one in front of the other, or, rarely, laterally placed beneath the elongate brood patch (Table 2). The rear egg contacts the broadest part of the brood patch against which it is pushed by the weight of the bird. The anterior egg makes less contact with the brood patch and, though safe and well covered when the bird is in a prone position, it is often partially exposed when the parent is in a hunched (semi-upright) position (see Warham 1975, Fig. 10.2).

TABLE 2. Positions of Rockhopper Penguin eggs beneath the brood patch in nests containing two eggs.

Week in incubation	Percentage of nests			Number of nests
	First egg anteriorly	Second egg anteriorly	Both eggs laterally	
2	58	37	5	84
3	66	34	0	77
4–5	66	32	2	59

The positioning of Rockhopper Penguin eggs under the brood patch was not random (Table 2). The smaller A egg was usually in the anterior position while the B egg was in the favorable rear position (χ^2 test, $P < 0.05$ for week 2 and $P < 0.01$ for weeks 3–5).

DISCUSSION

Egg temperatures during incubation.—To date, the only published data on temperatures in penguin eggs measured by telemetry, during undisturbed incubation, are those given for the Adélie Penguin (*Pygoscelis adeliae*) (Ecklund and Charlton 1959, Derksen 1977) and the Jackass Penguin (Frost et al. 1976), which are summarized in Table 1. Combining these data with ours, it appears that in four species of penguin the internal egg temperatures during the latter half of the incubation period fall within, or just below, the range of egg temperatures (34–39°C) of 25 species of birds listed by Drent (1973, 1975). This result was not anticipated, since penguins have reduced thermal conductance through the integuments (Kooyman et al. 1976) and their body temperatures at rest are, with those of procellariiform seabirds, some 2°C below the average for species in other avian orders (McNab 1966).

Most birds appear to attain high egg temperatures within a few days of completing laying. Mean egg temperatures of over 30°C were attained during the first 30% of the incubation period in the Herring Gull (*Larus argentatus*) (Drent 1970), the Mallard (*Anas platyrhynchos*) (Caldwell and Cornwell 1975), the Ruddy Duck (*Oxyura jamaicensis*) (Siegfried et al. 1976), the South Polar Skua (*Catharacta maccormicki*) (Spellerberg 1969), the House Wren (*Troglodytes aedon*) (Kendeigh 1963), and in the Gentoo and Jackass Penguins (this study). The delayed maintenance of consistently high egg temperatures in Rockhopper Penguins appears unusual.

An increase in egg temperature during the course of incubation can generally be attributed to increased parental attentiveness, increased heating ability of the brood patch (through increased vascularization and blood flow) or increased heat output by the embryo (Drent 1975). Since parental attentiveness by Rockhopper Penguins approaches 100% once the clutch is complete (Warham 1963), parental inattentiveness seems unlikely to be the cause of the delayed maintenance of high egg temperatures.

In most birds studied to date, the brood patch reaches a definitive temperature by the time the last egg is laid or within a few days therafter (Drent 1975). An exception is the Yellow-eyed Penguin (*Megadyptes antipodes*), in which the brood patch only reached a definitive temperature of 38°C after 36% of the incubation period had passed (15 out of 42 days), with increased vascularization of the brood patch throughout this period (Farner 1958).

Rockhopper Penguin females, which do most of the incubating during the first half of the incubation period, might have a similarly retarded vascularization of the brood patch, although we have no evidence for this to date. The females, having completed ovogenesis and while enduring a fast of 33–45 days (Warham 1963) might not have the energy reserves to afford maximum heat flow to the clutch. The males, however, on their return from the sea to resume incubation duties have replenished energy reserves and can possibly expend more energy in incubation than the females.

Neither Gentoo nor Jackass Penguins endure long fasts during incubation; both species have normal incubation shifts of 1 day (Van Zinderen Bakker 1971, Cooper in press). They can possibly afford greater heat output to the clutch during the first half of incubation than the Rockhopper Penguins. Yellow-eyed Penguins fast for moderately short periods of 1–5 days during incubation (Richdale 1951).

Parental preference within the clutch among Rockhopper Penguins.—The smaller first-laid (A) eggs of Rockhopper Penguins were maintained at lower, more variable temperatures throughout the incubation period than the second-laid (B) eggs. These differences can largely be attributed to size differences *per se* and to parental behavior during incubation.

Small eggs have lower thermal capacities and greater surface area to mass ratios than larger eggs. Under similar conditions small eggs require less heat to be maintained at the same temperature but they would heat and cool faster than larger eggs. This may account for the greater variation and range in temperature of A eggs relative to B eggs of Rockhopper Penguins, but cannot explain the differences between their mean temperatures.

The A and B eggs do not experience similar conditions during incubation. The A eggs occupy the anterior position beneath the brood patch more frequently. Here the brood patch is narrower and the eggs are more exposed to cold air when the parents shift on the nest or adopt the hunched incubation posture. Artificial eggs incubated by Adélie Penguins cooled faster during parental movements when they occupied the anterior position under the brood patch (Derksen 1977).

The relatively less favorable thermal environment experienced by A eggs of Rockhopper Penguins appears to retard embryo growth: although they are laid 4 days before the B eggs and are incubated steadily from at least the same time, A eggs hatch a day or more later than the B eggs. Weinrich and Baker (1978) showed that Adélie Penguin embryonic development was retarded at low temperatures. The A eggs of Rockhopper Penguins might be kept at temperatures low enough to retard embryo growth for appreciable amounts of time, whereas the B eggs seldom were.

Rockhopper Penguins appear to favor the larger B eggs during incubation. Warham (1963) observed that when the parents reposition the eggs following nest relief, the larger B egg was usually tucked under the brood patch first, followed by the A egg. Large eggs generally provide greater stimuli for incubation behavior than small eggs (Tinbergen 1951). Apparently it is advantageous for Rockhopper Penguins to incubate the B egg more diligently than the A egg, since the larger B egg represents a greater investment of energy. Rockhopper Penguins, in common with all eudyptid penguins, have never been known to rear two chicks simultaneously (Warham 1975). In this situation, the B egg, which produces a relatively more robust chick (Gwynn 1953, Warham 1963), is a more valuable investment than the A egg.

ACKNOWLEDGMENTS

We thank Aldo Berruti, Valerie Burger and Ian Sinclair for assistance in the collection and analysis of the data. Dr. D. V. Derksen, P. G. H. Frost, and Professor W. R. Siegfried made valuable comments

on an earlier manuscript. The study was sponsored financially and logistically by the Antarctic Division of the South African Department of Transport. Additional assistance was provided by the South African Scientific Committee for Antarctic Research, the University of Cape Town and the National Geographic Society.

Literature Cited

CALDWELL, P. J., & G. W. CORNWELL. 1975. Incubation behaviour and temperatures of the Mallard Duck. Auk 92: 706–731.

COOPER, J. In press. Breeding biology of the Jackass Penguin, with special reference to its conservation. Ostrich Suppl.

DERKSEN, D. V. 1977. A quantitative analysis of the incubation behavior of the Adélie Penguin. Auk 94: 552–566.

DOWNES, M. C., A. H. M. EALEY, A. M. GWYNN, & P. S. YOUNG. 1959. The birds of Heard Island. Austr. Nat. Antarct. Res. Exped. Rep., Ser. B, 1: 1–135.

DRENT, R. H. 1970. Functional aspects of incubation in the Herring Gull. Behaviour Suppl. 17.

———. 1973. The natural history of incubation. Pp. 262–322 *in* Breeding biology of birds (D. S. Farner, Ed.). Washington, National Academy of Sciences.

———. 1975. Incubation. Pp. 333–420 *in* Avian Biology, vol. 5 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

ECKLUND, C. R., & F. E. CHARLTON. 1959. Measuring the temperature of incubating penguin eggs. Amer. Sci. 42: 80–86.

FARNER, D. S. 1958. Incubation and body temperatures in the Yellow-eyed Penguin. Auk 75: 249–262.

FROST, P. G. H., W. R. SIEGFRIED, & A. E. BURGER. 1976. Behavioural adaptations of the Jackass Penguin *Spheniscus demersus* to a hot, arid environment. J. Zool., Lond. 179: 165–187.

GWYNN, A. M. 1953. The egg-laying and incubation periods of Rockhopper, Macaroni and Gentoo Penguins. Austr. Nat. Antarct. Res. Exped. Rep., Ser. B, 1: 1–19.

KENDEIGH, S. C. 1963. Thermodynamics of incubation in the House Wren *Troglodytes aedon*. Proc. 13th Intern. Ornithol. Congr.: 884–904.

KOOYMAN, G. L., R. L. GENTRY, W. P. BERGMAN, & H. T. HAMMEL. 1976. Heat loss in penguins during immersion and compression. Comp. Biochem. Physiol. 54: 75–80.

MCLACHLAN, G. R. & R. LIVERSIDGE. 1978. Roberts birds of South Africa. Cape Town, John Voelker Bird Book Fund.

MCNAB, B. K. 1966. An analysis of the body temperatures of birds. Condor 68: 47–55.

RICHDALE, L. E. 1951. Sexual behavior in penguins. Lawrence, Kansas, Univ. Kansas Press.

SIEGFRIED, W. R., A. E. BURGER, & P. J. CALDWELL. 1976. Incubation behavior of Ruddy and Maccoa Ducks. Condor 78: 512–517.

SPELLERBERG, I. F. 1969. Incubation temperatures and thermo-regulation in the McCormick Skua. Condor 71: 59–67.

STONEHOUSE, B. 1967. The general biology and thermal balance of penguins. Adv. Ecol. Res. 4: 131–196.

TINBERGEN, N. 1951. The study of instinct. London, Oxford Univ. Press.

VAN ZINDEREN BAKKER, E. M., JR. 1971. A behavior analysis of the Gentoo Penguin (*Pygoscelis papua* Forster). Pp. 251–272 *in* Marion and Prince Edward islands, report on the biological and geological expedition, 1965–1966. (E. M. van Zinderen Bakker, Sr., J. M. Winterbottom & R. A. Dyer, Eds.) Cape Town, A. A. Balkema.

WARHAM, J. 1963. The Rockhopper Penguin *Eudyptes chrysocome*, at Macquarie Island. Auk 80: 229–256.

———. 1975. The crested penguins. Pp. 189–269 *in* The biology of penguins (B. Stonehouse, Ed.). London, Macmillan.

WEINRICH, J. A., & J. R. BAKER. 1978. Adélie Penguin (*Pygoscelis adeliae*) embryonic development at different temperatures. Auk 95: 569–576.

WILLIAMS, A. J., A. E. BURGER, A. BERRUTI, & W. R. SIEGFRIED. 1975. Ornithological research on Marion Island, 1974–75. S. Afr. J. Antarct. Res. 5: 48–50.