

## PARENTAL BEHAVIOR CONTROLS INCUBATION PERIOD AND ASYNCHRONY OF HATCHING IN MAGELLANIC PENGUINS

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**Abstract.** In many species of birds, periods of incubation of eggs within a clutch depend on the order in which the eggs were laid and determine whether the eggs hatch asynchronously or on the same day. Magellanic Penguins (*Spheniscus magellanicus*) lay two eggs 4 days apart that hatch 2 days apart; first eggs take 41 days to hatch, and second eggs take 39 days. We tested whether temperatures of the two eggs differ and whether delayed onset of incubation caused this pattern. First eggs were cooler than second eggs during their first few days ( $P < 0.001$ ). First eggs averaged  $23.4 \pm 0.3$  °C in the first 24–48 hours after they were laid. Second eggs averaged  $27.9 \pm 0.3$  °C, warm enough for development. Egg temperature did not stabilize ( $33.9$  °C) until eggs were about 18 days old. We swapped first and second eggs of different nests to determine if parental behavior caused the differences in temperatures and incubation periods. First eggs treated as second eggs developed as fast as control second eggs, and second eggs treated as first eggs developed nearly as slowly (40 days) as control first eggs. First eggs that were stored in a cooler until second eggs were laid took 2 days longer to hatch than control first eggs. Parental incubation behavior explained why the incubation period of second eggs was shorter than that of first eggs and controlled asynchrony of hatching, which affects chick growth and survival.

**Key words:** egg temperature, incubation behavior, incubation period, onset of incubation, *Spheniscus magellanicus*.

### El Comportamiento Parental Controla el Período de Incubación y la Asincronía de Eclósión en *Spheniscus magellanicus*

**Resumen.** En muchas especies de aves, el período de incubación de los huevos en una nidada depende del orden en que los huevos fueron puestos y determina si los huevos eclosionan asincrónicamente o en el mismo día. El pingüino *Spheniscus magellanicus* pone dos huevos separados por 4 días, que eclosionan con una diferencia de 2 días; el primer huevo demora 41 días para eclosionar y el segundo 39 días. Evaluamos si la temperatura de los dos huevos era distinta y si el inicio retrasado de la incubación causa ese patrón. Los primeros huevos estuvieron más fríos que los segundos huevos durante los primeros días ( $P < 0.001$ ). Los primeros huevos tuvieron en promedio una temperatura de  $23.4 \pm 0.3$  °C durante las primeras 24–48 horas después de que fueron puestos. Los segundos huevos tuvieron una temperatura promedio de  $27.9 \pm 0.3$  °C, una temperatura suficiente para el desarrollo. La temperatura de los huevos no se estabilizó ( $33.9$  °C) hasta que los huevos tuvieron alrededor de 18 días de puestos. Alternamos primeros y segundos huevos de diferentes nidos para determinar si el comportamiento parental causaba las diferencias en temperatura y en el período de incubación. Los primeros huevos que fueron tratados como segundos se desarrollaron tan rápidamente como los segundos huevos del control, y los segundos huevos tratados como primeros huevos se desarrollaron casi tan lentamente (40 días) como los primeros huevos del control. Los primeros huevos que fueron almacenados en un conservador de frío hasta que fueran puestos los segundos huevos requirieron dos días más para eclosionar que los primeros huevos del control. El comportamiento de incubación parental explica porque el período de incubación es más corto para los segundos huevos y controla la eclosión asincrónica, la cual afecta el crecimiento y la supervivencia de los pichones.

## INTRODUCTION

The incubation period, the time from the laying of an egg to its hatching, varies both among and within species of birds and among and within clutches in a species. Explanations for the variation in incubation period generally fall into two broad categories: parental behavior and intrinsic differences in the eggs.

The behavior of the incubating adults determines egg temperature (Boersma 1982, Stoleson and Beissinger 1995, Sockman et al. 2006, Rowe and Weatherhead 2009). Eggs that are incubated more constantly at higher temperatures hatch sooner than eggs kept cooler or neglected (Boersma and Wheelwright 1979, Haftorn 1988, Martin 2002, Martin et al. 2007). The type or quality of nest that the adults build can affect egg

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temperature and incubation period (Frost et al. 1976, Frere et al. 1992, Lombardo et al. 1995). Some studies, however, have found no relationship between egg temperature and incubation period (Tieleman et al. 2004, Robinson et al. 2008).

Intrinsic differences in the eggs, such as size, eggshell porosity, embryonic metabolic rate, or concentrations of yolk, albumen, or hormones, are reported to control incubation period alone or in concert with incubation temperature, and they may be under maternal control (Brown 1988, St. Clair 1996, Massaro and Davis 2004, Sockman et al. 2006, Boonstra et al. 2010). In addition, some embryos near hatching adjust the time of their hatching in response to acoustic signals from nestmates or changeovers of adults at the nest (Vince 1964, Boersma 1992, Persson and Andersson 1999, Brua 2002).

In many species of birds, an egg's incubation period depends on the order in which it is laid in the clutch. Most birds lay one egg per day until the clutch is complete (Lack 1968). In altricial species, partial incubation often begins before clutch completion (Sockman et al. 2006) and hatching is neither completely synchronous (within one day) nor as prolonged as laying. In precocial species, hatching is usually synchronous in spite of long laying periods where clutch completion takes between 1 and 2 weeks; the last-laid eggs of large clutches have much shorter incubation periods than the first-laid eggs (Lack 1968, Loos and Rohwer 2004, Boonstra et al. 2010). In the extreme case of the crested penguins (*Eudyptes* spp.), the first-laid smaller egg hatches (if at all) after the second-laid (last) egg, a hatch-order reversal (Burger and Williams 1979).

Incubation periods of eggs within a clutch determine how synchronously chicks hatch, which may maximize reproductive output in a variety of ways (Stoleson and Beissinger 1995, Sockman et al. 2006). Synchronous hatching is necessary when the entire brood leaves the nest together soon after the first chick hatches. Synchronous hatching and fledging of altricial chicks may facilitate care by adults (Lack 1968). Alternatively, asynchronous hatching may be advantageous because the difference in size of chicks hatched on different days allows facultative brood reduction (Sockman et al. 2006). Stoleson and Beissinger (1995) listed 17 hypotheses for the evolution of asynchronous hatching; most assume it is adaptive, but a few propose that it is due to physiological constraints.

We tested the hypothesis that parental behavior, specifically delayed onset of incubation, controls the asynchrony of hatching in the Magellanic Penguin (*Spheniscus magellanicus*), a semi-altricial species (Williams and Boersma 1995) with a clutch size of two eggs, biparental incubation, and asynchronous hatching. The second egg has a consistently shorter incubation period than the first; the eggs are laid 4 days apart but hatch 2 days apart on average (Boersma 1992). We suspected that delayed onset of incubation explained the longer incubation period of first eggs because first eggs within 1 or 2 days of laying usually felt cool or cold to the touch, indicating they were not well incubated and embryos were not developing

rapidly, but second eggs were more likely to feel warm, indicating embryonic development (Boersma and Stokes 1995). We tested this hypothesis by measuring egg temperatures in naturally incubated clutches and by swapping first and second eggs between nests and temporarily removing some eggs from nests to manipulate the incubation period.

## METHODS

### STUDY SPECIES

A long-term study of Magellanic Penguins at Punta Tombo, Argentina (44.05° S, 65.22° W) began in 1983 (Boersma et al. 1990, Boersma 2008). Males and females share incubation, alternating long incubation shifts while fasting with long trips to forage at sea. Females usually take the first incubation shift, lasting an average of 15 days after the second egg is laid. Males take the second incubation shift, lasting 17 days on average (Boersma et al. 1990, Yorio and Boersma 1994b).

Magellanic Penguins lay one clutch per year with a maximum of two eggs. Clutch size and replacement clutches influence incubation periods in some species (Runde and Barrett 1981, Hipfner et al. 2001) but not in the Magellanic Penguin, as replacement eggs and clutches of only one egg are rare (Boersma, unpubl. data). Both sexes incubate, and adults do not forage during their incubation shifts. The first chick in a clutch is usually fed before the second chick hatches, resulting in the first chick being larger than the second and the smaller second chick being more susceptible to starvation when food is scarce (Boersma 1992).

### TEMPERATURE

*Initial subjective egg temperature.* We recorded whether eggs felt warm, cool, or cold by touching them to a cheek before we measured them. The face is more sensitive to temperature sensation than the hands (Nakamura et al. 2008). Two to six people classified the temperature of an egg in 10 or more nests at the beginning of each season, 1983 to 2009, and always agreed on the classification of the egg temperature. Although cold and warm eggs are unlikely to be misclassified, we found the variation in classification of cool eggs was unimportant because of the large sample size (1148 two-egg clutches). We measured the egg and categorized the temperature within 24 hr of laying in two-egg clutches where both eggs hatched and we knew the dates of laying and hatching of both eggs within 24 hr. We calculated the intervals of hatching and laying (days) between the two eggs in each nest. We assumed that the temperature we noted when we found the first egg was representative of that egg's temperature before the second egg was laid, and we predicted that warm first eggs would hatch earlier relative to the second eggs (longer interval of hatching) than would cold first eggs because warm first eggs indicate that development has begun and the eggs should have a shorter incubation period.

*Measured egg temperature.* We measured egg temperature in 13 nests in 2004 with DS1921G Thermochron iButton temperature loggers (Maxim Integrated Products, Inc., Sunnyvale, CA) programmed to record temperature every hour. Each logger contained a digital thermometer, a clock/calendar, and a history log encased in a stainless-steel cylinder 5.89 mm high by 17.35 mm diameter; it recorded temperature to the nearest 0.5 °C with an accuracy of  $\pm 1.0$  °C. We taped the loggers to the blunt ends of first and second eggs, where the loggers were in contact with the outer eggshell over the air cell. The temperature loggers were external to the eggs. When the adult was not incubating, direct contact with the warm egg affected the recorder temperature more than the air temperature did (Maxim support, pers. comm.). We checked four nests daily and nine other nests every 6 days. We recorded temperature until a few days before hatching, removing the loggers before eggs hatched to prevent losing the loggers. Loggers fell off seven eggs and were reattached. If we found a logger off the egg, we excluded all temperatures from the time the temperature dropped suddenly until we reattached the logger.

We removed first eggs within 24 hr of laying from 58 nests in 2008 and placed them in an insulated cooler for storage until the second egg was laid (see egg-swap experiment, delayed incubation—first egg treatment). We replaced the first eggs with hollow plastic Easter eggs, similar in size to the Magellanic Penguin's eggs ( $7.67 \pm 0.02$  cm by  $5.59 \pm 0.01$  cm,  $n = 20$ ). Each plastic egg was filled with sand and had an iButton temperature logger in the center programmed to record temperature every 15 min. The eggs were taped closed with duct tape and painted white. We removed the plastic eggs and replaced the real first eggs in the nests within 24 hr of the second egg being laid. In one nest, we never found a second egg, and we excluded this nest from analyses. All eggs were immediately accepted, and no egg in any experiment was abandoned. Magellanic Penguins accept and incubate objects of odd shapes and colors (pers. obs.; E. Wagner et al., unpubl. data).

We measured egg temperature in 1983 with a WESCOR Digital TC thermometer/thermocouple. We compared these egg temperatures with those taken with iButton data loggers. During incubation we inserted the thermocouple wires into the middle of one egg in each nest and sealed them with wax ( $n = 9$  eggs). These eggs were not viable. The other ends of the wires were left on the ground beside the nests, and attached to the digital thermometer one to four times a day to measure temperatures. We started taking temperatures at each nest between 27 October and 1 November, at least 17 days past 10 October, the median date of laying (Boersma et al. 1990), and recorded temperature for 3 to 10 days (2–23 measurements per egg).

*Air temperature and egg temperature.* We recorded ambient air temperature in 2008 every hour with an iButton data logger approximately 1 m above the ground in the shade of a large molle bush (*Schinus molle*). Magellanic Penguins

nest in burrows that they dig or in scrapes under bushes, including molle bushes (Stokes and Boersma 1991). We subsampled the fourth temperature logged for each plastic egg to match the frequency at which we logged air temperature. We then calculated the plastic eggs' mean temperature across all nests for each hour of each calendar day.

*Penguin temperatures.* We measured the brood-patch and body temperatures of adult penguins with the thermocouple in 1983 to determine how much heat a penguin could apply to an egg. To measure brood-patch temperature, we held the thermocouple tips against the brood patch ( $n = 20$ ). To measure core temperature, we inserted the thermocouple wires 4 to 18 cm down the esophagus ( $n = 18$ ). In both cases, we allowed the temperature to stabilize for at least 15 sec before recording it. All body and brood-patch temperatures were taken on 4 November 1983, between 14:00 and 15:30, except one measurement was made at 19:15 and the time of one was not recorded.

#### EGG-SWAP EXPERIMENT

In October to December 2008 we did an experiment to determine the effects of parental behavior on incubation periods and intervals of hatching. We moved eggs among nests so parents treated first eggs as second eggs and second eggs as first eggs, functionally reversing the egg order. Each egg was manipulated for approximately 4 days after it was laid. After the experiment was completed, we returned the eggs to their parents and nests of origin. We checked nests daily once a pair occupied the nest, continuing until both eggs were laid. We again checked each nest daily from before expected hatch dates until both chicks hatched, to measure the incubation periods and intervals of hatching. The experiment had three treatments and a control. All eggs were removed, marked, and measured within 24 hr of being laid and assigned to one of three treatment groups or to the control group.

*Delayed incubation—first egg.* We removed the first egg and stored it in an insulated cooler in an unheated storage building, replacing it with a plastic egg containing an iButton temperature logger. When the second egg was laid, we removed the plastic egg and returned the first egg from storage to the nest. In this treatment, first eggs, because they were in storage, were not incubated until after the second eggs were laid. We predicted the incubation period of first eggs would be 2 days longer than average and the two eggs in a clutch would hatch on the same day. The mean storage temperature in the cooler was 13.1 °C (range 4–19.5 °C). There were 58 nests with two eggs in this treatment. Both eggs hatched in 45 nests.

*Immediate incubation—first egg and delayed incubation—second egg.* We reciprocally swapped the first egg from one nest with the second egg from another nest, where each swapped egg was laid within the previous 24 hr. The swapped first egg was treated as a second egg in its foster nest (immediate incubation—first egg) and the swapped second egg was

TABLE 1. Laying and hatching intervals and incubation periods of Magellanic Penguin eggs at Punta Tombo, Argentina, by treatment (see Methods). Values are modes (ranges in parentheses). Sample sizes in laying-interval column indicate number of nests assigned to each treatment. All nests had two eggs. Sample sizes in hatching-interval column indicate number of nests in each treatment in which both eggs hatched. Predation caused most of the decreases in sample size between laying and hatching. Median assignment date is the date in October that nests were assigned to a treatment (ranges in parentheses).

Treatment	Laying interval (days)	Hatching interval (days)	Incubation period: first egg (days)	Incubation period: second egg (days)	Median assignment date (Oct)
Control	4 (2–5) <i>n</i> = 27	2 (1–5) <i>n</i> = 18	41 (39–42) <i>n</i> = 19	39 (38–41) <i>n</i> = 18	14 (7–23)
Delayed incubation—first egg	4 (1–5) <i>n</i> = 58	–1 (–3–1) <sup>a</sup> <i>n</i> = 45	43 (40–45) <sup>a</sup> <i>n</i> = 47	No treatment	13 (6–17)
Delayed incubation—second egg	4 (2–5) <i>n</i> = 56	3 (0–6) <i>n</i> = 40	No treatment	40 (38–42) <sup>a</sup> <i>n</i> = 42	10 (5–21)
Immediate incubation—first egg	4 (2–5) <i>n</i> = 56	3 (2–5) <i>n</i> = 35	39 (38–42) <sup>a</sup> <i>n</i> = 40	No treatment	14 (7–24)

<sup>a</sup>Treatments significantly different at 0.05 by  $\chi^2$ .

treated as a first egg in its foster nest (delayed incubation—second egg). We returned both eggs to their nest of origin when the second egg was laid in the immediate incubation—first egg treatment nest. For first eggs treated as second eggs we predicted the incubation period would be 2 days shorter than average for first eggs and the two eggs in a clutch would hatch 4 days apart. For second eggs treated as first eggs we predicted the incubation period would be 2 days longer than average for second eggs and the two eggs in a clutch would hatch 4 days apart. There were 56 nests with two eggs for each treatment. Both eggs hatched in 35 immediate incubation—first egg nests and in 40 delayed incubation—second egg nests.

*Control.* Within 24 hr of being laid, both eggs were removed, measured, marked, and immediately returned to their nest. There were 27 control nests with two eggs. Both eggs hatched in 18 nests.

We assigned nests to treatments haphazardly because nests in two of the treatments had to be matched by dates of laying and there was no way to predict when an egg would be laid in any nest (Table 1). The median assignment date of delayed incubation—second egg nests was earlier than that of the other treatments because we matched dates of laying of first eggs in immediate incubation—first egg treatment nests with those of second eggs in delayed incubation—second egg treatment nests. However, the ranges of assignment dates for all treatments overlapped.

#### STATISTICAL ANALYSES

*Initial subjective egg temperature.* We used  $\chi^2$  to test whether the interval of hatching was independent of whether the first egg felt warm, cool, or cold when we found it (*n* = 1148 clutches). The interval of laying ranged from 0 to 6 days but was 3 or 4 days in 91% of clutches. Intervals of hatching ranged from –4 days (the second egg hatched 4 days before the first) to +6 days (the second egg hatched 6 days after the first). We

binned the intervals into four categories for the  $\chi^2$  test: –4 to 0 days, 1 to 2 days, 3 to 4 days, and 5 to 6 days, with 95% of the observations falling into the middle two categories (1 to 4 days). We created an index of hatching interval corrected for laying interval by dividing hatching interval by laying interval (times 100). We also used  $\chi^2$  to test for independence of this index from how the first egg felt (warm, cool, or cold).

*Measured egg temperature.* We calculated the mean temperature of each real egg for the first 4 days after it was laid (the average period between laying of the first and second eggs) and for the remainder of the incubation period (*n* = 13 clutches). We tested for differences between these temperatures in first and second eggs with *t*-tests. We calculated the daily (24-hr) mean temperature of each egg throughout incubation and used mixed-effects regression to test the relationship between mean daily egg temperature and the egg's age (days since each egg was laid) and the order in which it was laid, with nest as a random factor.

*Air temperature and egg temperature.* We compared the hourly mean temperatures of 57 plastic eggs (359 hourly averages from 6 to 21 October 2008) with the air temperatures for daytime (sunrise to sunset) and night (sunset to sunrise) with linear regression.

*Penguin temperatures.* We tested for differences in brood-patch (*n* = 16 males, 4 females) and body temperatures (*n* = 14 males, 4 females) between males and females with  $\chi^2$ . We also tested for differences between brood-patch and body temperatures with  $\chi^2$ .

*Egg-swap experiment.* We tested for differences among treatments in intervals of laying and hatching and incubation periods of the first and second eggs with  $\chi^2$  tests on the distributions of the numbers of days (see Table 1 for sample sizes). The null hypothesis was that the distribution of numbers of days was independent of the treatment. We could not use ANOVA because the data were not continuous; nonparametric ANOVA

was not appropriate because of the small ranges of numbers and large numbers of ties.

All tests were done in Stata 9.2 (StataCorp, College Station, TX). All *t*-tests were two-tailed. Results are presented as means  $\pm$  SE or modes and ranges. We rejected null hypotheses when  $P < 0.05$ .

## RESULTS

### TEMPERATURE

*Initial subjective egg temperature.* Incubation periods of first eggs ( $40.5 \pm 0.04$  days) were longer than those of second eggs ( $38.8 \pm 0.03$  days; paired  $t_{1147} = 47.0$ ,  $P < 0.001$ ,  $n = 1148$  clutches). Clutches in which the first egg felt warm when found hatched over a longer interval and those in which the first egg felt cold hatched over a shorter interval than those in which the first egg felt cool (Fig. 1;  $\chi^2_6 = 23.2$ ,  $P < 0.001$ ). For the hatching intervals corrected for laying intervals, results were similar in that clutches with cold first eggs hatched over shorter intervals than did those with warm first eggs ( $\chi^2_6 = 25.3$ ,  $P < 0.001$ ).

*Measured egg temperature.* Daily mean egg temperature was a logarithmic function of egg age and varied among nests (Fig. 2). On average, first eggs started at a lower temperature ( $23.4 \pm 0.3$  °C vs.  $27.9 \pm 0.3$  °C) and warmed at a faster rate [ $3.2 \pm 0.1$  °C per  $\ln(\text{egg age})$  vs.  $1.8 \pm 0.1$  °C per  $\ln(\text{egg age})$ ] than did second eggs. Both log of egg age ( $Z = 41.3$ ,  $P < 0.001$ )

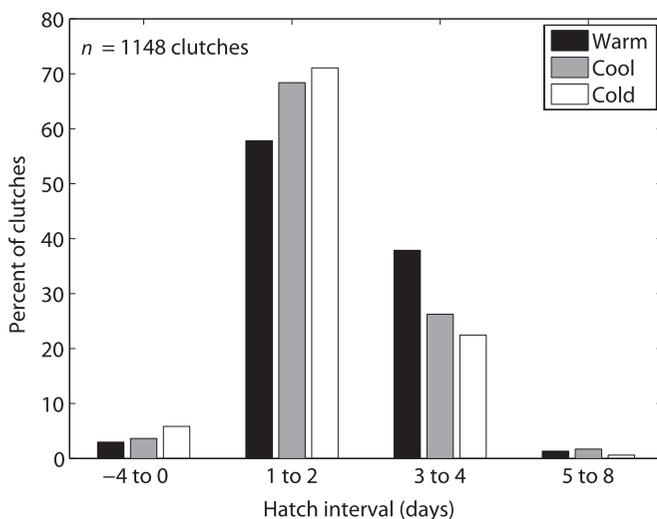


FIGURE 1. Clutches of Magellanic Penguins at Punta Tombo, Argentina, from 1983 to 2009; clutches in which the first egg felt warm (black bars,  $n = 301$ ) when found (within 24 hr of being laid) were more likely to hatch over a longer interval than clutches in which the first egg felt cold (white bars,  $n = 325$ ) when found. In clutches in which the first egg felt cool (gray bars,  $n = 522$ ) the interval was intermediate. Hatch interval is the number of days between the hatching of the first egg and the hatching of the second egg ( $-4 =$  second egg hatched 4 days before the first egg). Eggs were replaced in the nest after we measured them and recorded the temperature of the egg surface as warm, cool, or cold.

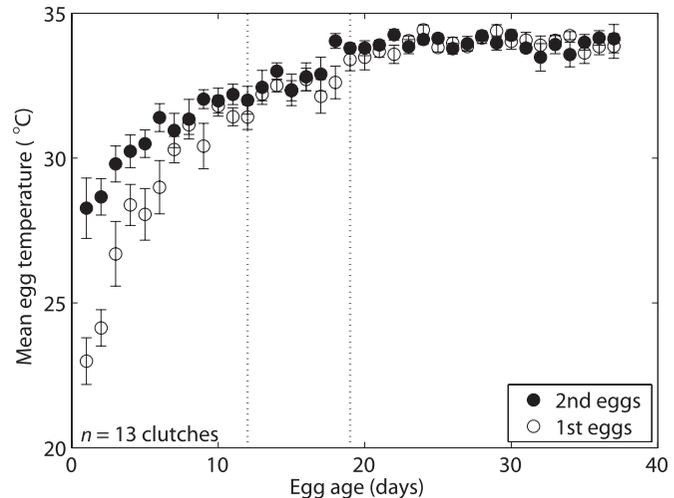


FIGURE 2. Daily mean egg temperature as a function of egg age (days since egg was found; nests were checked every day or every other day) for Magellanic Penguins at Punta Tombo, Argentina, in 2004 ( $n = 13$  two-egg clutches). On average, second eggs (filled circles) were laid 4 days later than first eggs (unfilled circles) but the eggs are aligned by egg age rather than calendar day. Error bars represent standard errors. For first eggs, daily mean egg temperature =  $23.4 + 3.2 \times \ln(\text{egg age})$ ,  $R^2 = 0.95$ . For second eggs, daily mean egg temperature =  $27.9 + 1.8 \times \ln(\text{egg age})$ ,  $R^2 = 0.94$ . The vertical dotted line on the left is age 12 days, when temperatures of first and second eggs no longer differed significantly in the regression. The line on the right is age 19 days, when mean temperature stopped rising at  $33.9$  °C.

and order in which the egg was laid ( $Z = 7.3$ ,  $P < 0.001$ ) affected egg temperature significantly (Wald  $\chi^2_2 = 1756.2$ ,  $P < 0.001$ ). After eggs were 11 days old, laying order no longer affected egg temperature significantly in the regression ( $Z = 1.8$ ,  $P = 0.07$ ). After eggs were 18 days old, neither age ( $Z = 1.7$ ,  $P = 0.09$ ) nor laying order ( $Z = 0.6$ ,  $P = 0.57$ ) affected egg temperature (Wald  $\chi^2_2 = 3.2$ ,  $P = 0.21$ ), and daily mean egg temperature was constant at  $33.9$  °C.

We checked four nests with temperature loggers on eggs daily throughout incubation. In three of these nests, the eggs' daily mean temperatures reached their maximum on the day the male returned from foraging and relieved the female. In the fourth nest that was checked daily, daily mean egg temperatures reached the maximum 3 days after the male returned. First eggs were 16 to 22 days old and second eggs 12 to 18 days old when the males returned.

The mean temperature of real eggs during the first four days of incubation was lower for first eggs ( $26.2 \pm 0.7$  °C,  $n = 13$ ) than for second eggs ( $29.4 \pm 0.5$  °C,  $n = 13$ ;  $t_{24} = -3.5$ ,  $P = 0.002$ ), consistent with the finding of Boersma and Stokes (1995) that second eggs are more likely than first eggs to feel warm within a day of being laid.

In nests in which we placed plastic eggs, before the second egg was laid (approximately the first 4 days of incubation), the plastic egg's temperature averaged  $25.0$  °C (range

4–34.5 °C,  $n = 57$  plastic eggs). Most (68%) plastic-egg temperatures were less than 28 °C, the mean daily starting temperature for real second eggs ( $n = 13$  eggs). Fewer than 1% of plastic-egg temperatures were above 34 °C, the mean temperature of steady incubation of real eggs.

Mean maximum incubation temperatures were within 1.4 °C of each other, whether measured on real or plastic eggs, internally or externally, or with thermocouples or iButton loggers. The mean asymptotic incubation temperature in real eggs was 33.9 °C. In plastic eggs, in the nest in which we never found a second egg, the plastic egg was kept at a mean of 34.0 °C for four days, 12 days after being placed in the nest. Plastic eggs placed in two other nests in 2008, as part of another experiment, were incubated at means of 33–34 °C. The mean temperature in the centers of real eggs measured with thermocouples was  $34.4 \pm 0.2$  °C (range 16.4–38.3 °C). Real first eggs measured with external loggers averaged 23.4 °C on their first day and 26.2 °C over their first 4 days, whereas plastic eggs averaged 25 °C during their first 4 days.

*Air temperature and egg temperature.* There was no general warming of air temperatures between the laying of first and second eggs in each nest. Minimum air temperatures on the days that first eggs were found ( $6.5 \pm 1.0$  °C) were similar to minimum air temperatures on the days that second eggs were found ( $6.6 \pm 0.6$  °C;  $t_{24} = -0.06$ ,  $P = 0.95$ ) in 2004. Maximum air temperatures on the days that first eggs were found ( $17.9 \pm 1.0$  °C) were also similar to maximum air temperatures on the days that second eggs were found ( $16.2 \pm 1.4$  °C;  $t_{24} = 0.97$ ,  $P = 0.34$ ).

Very few plastic-egg temperatures were as low as the concurrent air temperature. Hourly means of plastic-egg temperature were positively correlated with air temperature (Fig. 3,  $F_{1,357} = 342.9$ ,  $P < 0.001$ ,  $R^2 = 0.49$ ). The relationship was not as strong at night ( $F_{1,157} = 40.9$ ,  $P < 0.001$ ,  $R^2 = 0.20$ ) but was stronger during the day ( $F_{1,198} = 262.8$ ,  $P < 0.001$ ,  $R^2 = 0.57$ ), indicating that penguins incubated more at night than during the day. Plastic-egg temperatures were higher during the day ( $25.6 \pm 0.2$  °C) than at night ( $23.4 \pm 0.2$  °C,  $n = 57$  nests, 359 hourly averages;  $t_{357} = -8.4$ ,  $P < 0.001$ ), but time of day was not significant when added to the regression of plastic-egg temperature on air temperature ( $t = 0.2$ ,  $P = 0.81$ ). Air temperatures were also higher during the day ( $13.5 \pm 0.3$  °C) than at night ( $8.3 \pm 0.3$  °C,  $t_{357} = -13.1$ ,  $P < 0.001$ ). The relationship between mean plastic-egg temperature and air temperature appeared to be equally strong during the day and at night when the air temperature was above about 7 °C (Fig. 3), but air temperature was seldom lower than 7 °C during the day.

*Penguin temperatures.* Mean brood-patch temperature was  $37.0 \pm 0.2$  °C, similar for males ( $n = 16$ ) and females ( $n = 4$ ;  $t_{18} = 1.1$ ,  $P = 0.29$ ). Body temperature averaged  $38.2 \pm 0.2$  °C and was also similar for males ( $n = 14$ ) and females ( $n = 4$ ;  $t_{16} = 1.5$ ,  $P = 0.15$ ). Body temperature was significantly higher than brood-patch temperature ( $t_{16} = -4.7$ ,  $P < 0.001$ ).

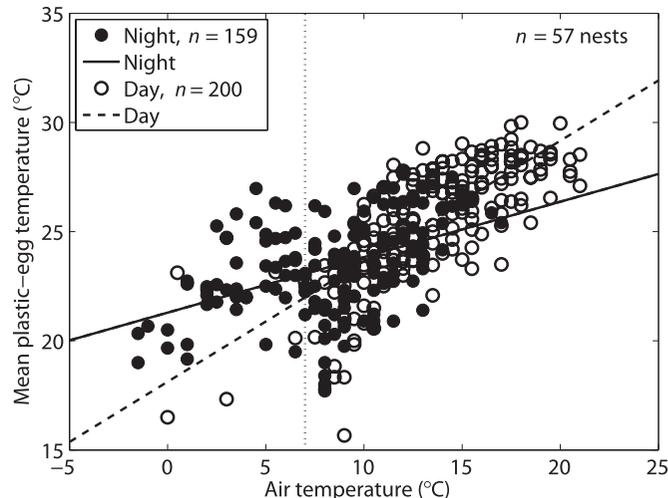


FIGURE 3. Hourly mean temperature of plastic eggs incubated by Magellanic Penguins at Punta Tombo, Argentina, in 2008, as a function of air temperature, from within 24 hr of the first egg being laid to when the second egg for that nest was found (within 24 hr of being laid);  $n = 57$  nests. For nighttime (sunset to sunrise) egg temperature =  $21.3 + 0.25 \times$  air temperature,  $R^2 = 0.20$ ,  $n = 159$  hourly averages (filled circles, solid regression line). For daytime (sunrise to sunset) egg temperature =  $18.1 + 0.55 \times$  air temperature,  $R^2 = 0.57$ ,  $n = 200$  (unfilled circles, dashed regression line). The vertical dotted line represents air temperature of 7 °C, below which Magellanic Penguins incubated first eggs more tightly.

#### EGG-SWAP EXPERIMENT

As predicted, the experimental manipulations changed incubation periods (Table 1, Fig. 4). The incubation period was lengthened in first and second eggs in the delayed-incubation treatments and shortened in first eggs in the immediate incubation—first egg treatment. In the delayed incubation—first egg treatment, in which the first egg was removed from its nest and not incubated until the second egg was laid, the incubation period of first eggs increased by 2 days over that of control eggs, and 30 out of 45 first eggs hatched 1 to 3 days after the second egg in their nests (the reverse of the usual hatch order). In the remaining 15 nests, both eggs hatched on the same day ( $n = 13$ ) or the first egg hatched 1 day before the second egg ( $n = 2$ ). The modal interval was  $-1$  days, significantly shorter than the control interval of 2 days. In the delayed incubation—second egg treatment, in which second eggs were treated as first eggs for the first 4 days, the incubation period of second eggs increased by 1 day over that of control eggs. In the immediate incubation—first egg treatment, in which first eggs were treated as second eggs for the first 4 days, the incubation period of first eggs decreased by 2 days below that of control eggs. In both these treatments, the hatching interval increased to 3 days, compared to 2 days in the controls, although this difference was not statistically significant.

Our treatments did not decrease the hatching success of eggs (92% in normal clutches, Boersma and Rebstock 2009b).

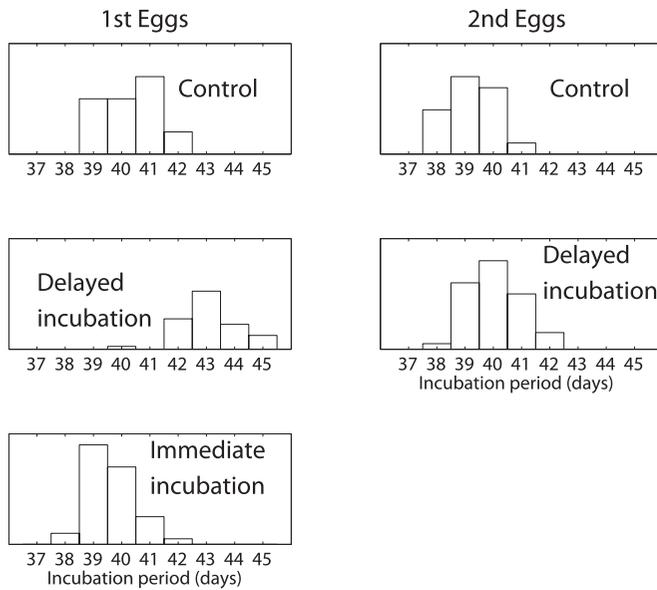


FIGURE 4. In a cross-fostering experiment with Magellanic Penguins at Punta Tombo, Argentina in 2008, delaying the start of incubation increased the incubation period (middle panels) and accelerating the start of incubation decreased it (bottom panel). Histograms of incubation periods in first eggs (left panels) and second eggs (right panels). Top panels, control eggs; middle left panel, first eggs placed in storage until the second egg was laid (delayed incubation—first egg); middle right panel, second eggs treated as first eggs for about 4 days in foster nests (delayed incubation—second egg); bottom panel, first eggs treated as second eggs for about 4 days in foster nests (immediate incubation—first egg).

In the three treatment groups, 253 of 259 eggs (98%) not lost to predation hatched (about 15% of eggs were lost to predators). Neither did treatment affect the initial mass of first chicks ( $89.1 \pm 0.7$  g;  $F_{4,334} = 1.3$ ,  $P = 0.27$ ) or second chicks ( $89.3 \pm 0.8$  g;  $F_{4,267} = 0.4$ ,  $P = 0.84$ ; chicks were weighed within 1 day of hatching). We used chicks in nests outside the study area ( $n = 202$  first chicks, 149 second chicks) as a fifth category in the ANOVA.

## DISCUSSION

Our data support the hypothesis that in the Magellanic Penguin parental behavior (delayed onset of incubation) causes first eggs to take 2 days longer to hatch than second eggs, reducing the asynchrony of hatching from 4 to 2 days. Magellanic Penguins raised more chicks when the interval between hatching was 1–3 days than when it was 0 or 4 days (Boersma 1992). First eggs were cooler than second eggs in the first few days after they were laid because they were often poorly incubated or were guarded but not incubated. There was no increase in air temperature during laying that could explain the temperature difference between eggs. By swapping first and second eggs between nests we showed that parental incubation behavior, not an intrinsic difference between the eggs, controls

the asynchrony of hatching. When first eggs were treated as second eggs for the first few days, they developed as rapidly as second eggs, and when second eggs were treated as first eggs for the first few days, they developed nearly as slowly as first eggs. Most second eggs were already at temperatures conducive to development when we found and swapped them, likely accounting for their incubation period being slightly shorter than that of control first eggs.

Boersma and Rebstock (2009a) found no support for the hypothesis that differences in eggshell porosity are responsible for the differences in incubation periods. First and second eggs from the same clutch are similar in weight (Boersma and Stokes 1995) and volume (Boersma and Rebstock 2010), so size differences cannot account for the differences in incubation period. Magellanic Penguin embryos near hatching can adjust their hatching time somewhat to match their parents' changeovers at the nest (Boersma 1992), but our manipulations started and ended within a few days of each egg's being laid, indicating that delayed incubation is likely the strongest determinant of incubation period.

We expected steady incubation to begin after clutch completion, but egg temperatures did not reach their maxima until about 2 weeks later. Why should Magellanic Penguins prolong incubation? The mates take turns incubating and fast during their long shift of 2–3 weeks. The attending bird need only stop incubating for short periods to excrete, defend the nest, change positions, or rotate the eggs (Derksen 1977, Haftorn 1986). However, our data show large temporary drops in temperature throughout incubation, and we have observed penguins lying outside their nests with unattended eggs inside. Risk of nest predation should select for shorter incubation periods (Ricklefs 1993, Stoleson and Beissinger 1995), but this risk is less for many seabirds that breed on islands or other areas not accessible to mammalian predators (Lack 1968). Over 7 years at Punta Tombo, between 4% and 18% of eggs were lost to predation (Yorio and Boersma 1994a), consistent with the 15% lost during this study and far less than for many passerines for which nest predation can exceed 50% (Martin 1995). Embryos that are not kept at the optimal temperature are likely to die or suffer developmental abnormalities (Webb 1987), but this is not true for many seabirds that neglect eggs for varying periods (Wheelwright and Boersma 1979, Boersma et al. 1980, Boersma 1982). Magellanic Penguins may still incur energetic costs during prolonged incubation (Reid et al. 2002), as each penguin fasts for 2 to 3 weeks while it incubates and its mate forages (Boersma et al. 1990). Periodic cooling of eggs may affect embryonic metabolism, producing smaller embryos that use more of their energy reserves before hatching (Boersma 1982, Olson et al. 2006).

The slow increase in egg temperature may be an artifact of our method of measuring temperature, or it may be due to the generation of heat by older embryos. Embryos tend to stay on the side of the egg close to the adult's brood patch (Drent

1975), and we measured temperature externally at the blunt end of the egg, so we may not have measured the temperature experienced by the embryo until it was large enough to fill most of the egg. Large embryos begin generating heat during incubation and help keep egg and nest temperatures steady (Drent 1975). Fertile eggs of the King Penguin (*Aptenodytes patagonicus*) are warmer than infertile eggs after about 20 days of incubation (Handrich 1989). However, Poussart et al. (2000) found a gradual increase in the temperature of artificial eggs incubated by Greater Snow Geese (*Chen caerulescens atlantica*); embryonic heat generation cannot explain the increase in that case.

Alternatively, the gradual increase in egg temperature may be due to constraints on the adults, such as delayed brood-patch development, the inability of fasting birds to heat the eggs, or the need to take long foraging trips to recover physiological condition. Delayed development of the adults' brood patch is common in penguins that lay two eggs (Burger and Williams 1979, St. Clair 1992, de León et al. 2001, Massaro et al. 2006). Burger and Williams (1979) suggested that female Rockhopper Penguins (*Eudyptes chrysocome*) may not be able to keep eggs at the optimal temperature early in incubation because of their long (33–45 days) fast. The Magellanic Penguin also forages offshore and has long incubation shifts (Boersma et al. 1990). Females fast up to a month during courtship, egg laying, and the male's long foraging trip before being relieved at the nest. In three of the four nests we studied, the eggs reached a steady temperature at the same time as the male relieved the female.

The long incubation period of many seabirds allows them to recover body condition. Many Magellanic Penguin chicks die because the foraging parents fail to return until several days after they have hatched (Boersma and Stokes 1995). Reid (1965) suggested that the longer incubation period of the Adélie Penguin (*Pygoscelis adeliae*) prevents newly hatched chicks from starving if foraging adults do not return "on schedule." Selection may favor longer incubation periods so adults can recover body condition before young hatch.

Three different methods yielded similar mean egg temperatures during steady incubation (33–34.4 °C), but mean temperatures measured by thermocouples were slightly higher than those measured by iButton temperature loggers. The thermocouples were more accurate than the temperature loggers so may reflect the true mean more closely. We may have missed temperature extremes, both low and high, in the automatic measurements, because of the intervals at which we recorded (15 min and 1 hr). In small passerines, recording at an interval as short as 3–5 min results in a significantly higher minimum temperature than does recording every 1 min because true minima during absences of the female are missed (Haftorn 1988). However, because penguin eggs are larger they take longer to cool or warm than passerine eggs. Sand-filled plastic eggs and data loggers on the outsides of eggshells

may have cooled and/or warmed faster than embryos, but the mean asymptotic egg temperatures were similar regardless of method.

In neither the delayed incubation—second egg treatment or the immediate incubation—first egg treatment did we find a change in the asynchrony of hatching as large as expected because steady incubation does not start immediately after clutch completion and some development of the first egg normally occurs before the second egg is laid. Before the second eggs were laid, nearly 1/3 of temperatures in the plastic (first) eggs were above 28 °C, warm enough for some development of Adélie Penguin eggs (Weinrich and Baker 1978). Only in the delayed incubation—first egg treatment, in which eggs were removed completely from parental control, did we see the expected change in asynchrony of hatching. In this treatment, the change was a little greater than we predicted. Keeping the eggs below 20 °C for several days likely delayed development, and some development of the second eggs likely occurred before we found them and replaced the first eggs. It is interesting that these low temperatures did not affect embryo survival, showing penguins are tolerant of low temperature at the start of incubation.

Magellanic Penguins incubated first eggs when the air temperature dropped below about 7 °C, regardless of whether it was day or night, but air temperature was generally that low only at night. Females of some passerine species begin nest attentiveness or incubation at night before the clutch is complete, but steady daytime incubation does not start until after clutch completion (Haftorn 1988, Wang and Weathers 2009). Even after clutch completion, female passerines in species with uniparental care incubate more steadily at night than during the day, resulting in more variable egg temperatures during the day (Martin et al. 2007).

Parental attentiveness and incubation behavior control egg temperature and explain differences in incubation period among species (Martin 2002, Martin et al. 2007), within species (Ricklefs and Smeraski 1983, Martin 2002), and within clutches (Sockman et al. 2006). In many birds, even precocial species (Loos and Rohwer 2004, Boonstra et al. 2010), development begins before clutch completion, influencing intervals of hatching (Sockman et al. 2006). We show that for the Magellanic Penguin, parental behavior between the laying of the first and second egg reduces the interval between the eggs' hatching from 4 to 2 days. Parental behavior and not egg characteristics is the major determinant of incubation period and the resulting asynchronous hatching in the Magellanic Penguin and many other birds.

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#### LITERATURE CITED

- BOERSMA, P. D., AND N. T. WHEELWRIGHT. 1979. Egg neglect in the Procellariiformes: reproductive adaptations in the Fork-tailed Storm-Petrel. *Condor* 81:157–165.
- BOERSMA, P. D., N. T. WHEELWRIGHT, M. K. NERINI, AND E. S. WHEELWRIGHT. 1980. The breeding biology of the Fork-tailed Storm-Petrel (*Oceanodroma furcata*). *Auk* 97:268–282.
- BOERSMA, P. D. 1982. Why some birds take so long to hatch. *American Naturalist* 120:733–750.
- BOERSMA, P. D., D. L. STOKES, AND P. M. YORIO. 1990. Reproductive variability and historical change of Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina, p. 15–43. *In* L. Davis and J. Darby [EDS.], *Penguin biology*. Academic Press, San Diego.
- BOERSMA, P. D. 1992. Asynchronous hatching and food allocation in the Magellanic Penguin *Spheniscus magellanicus*. *Acta XX Congressus Internationalis Ornithologici* 20:961–973.
- BOERSMA, P. D., AND D. L. STOKES. 1995. Mortality patterns, hatching asynchrony, and size asymmetry in Magellanic Penguin *Spheniscus magellanicus* chicks, p. 3–25. *In* P. Dann, I. Norman and P. Reilly [EDS.], *The penguins: ecology and management*. Surrey Beatty, Chipping Norton, Australia.
- BOERSMA, P. D. 2008. Penguins as marine sentinels. *BioScience* 58:597–607.
- BOERSMA, P. D., AND G. A. REBSTOCK. 2009a. Magellanic Penguin eggshell pores: does number matter? *Ibis* 151:535–540.
- BOERSMA, P. D., AND G. A. REBSTOCK. 2009b. Intraclutch egg-size dimorphism in Magellanic Penguins: adaptation, constraint, or noise? *Auk* 126:335–340.
- BOERSMA, P. D., AND G. A. REBSTOCK. 2010. Calculating egg volume when shape differs: when are equations appropriate? *Journal of Field Ornithology* 81:442–448.
- BOONSTRA, T. A., M. E. CLARK, AND W. L. REED. 2010. Position in the sequence of laying, embryonic metabolic rate, and consequences for hatching synchrony and offspring survival in Canada Geese. *Condor* 112:304–313.
- BROWN, C. R. 1988. Egg temperature and embryonic metabolism of A- and B-eggs of Macaroni and Rockhopper Penguins. *Suid-Afrikaanse Tydskrif vir Dierkunde* 23:166–172.
- BRUA, R. B. 2002. Parent–embryo interactions, p. 88–99. *In* D. C. Deeming [ED.], *Avian incubation: behaviour, environment, and evolution*. Oxford University Press, Oxford, England.
- BURGER, A. E., AND A. J. WILLIAMS. 1979. Egg temperatures of the Rockhopper Penguin and some other penguins. *Auk* 96:100–105.
- DE LEÓN, A., G. SOAVE, V. FERRETTI, AND J. MORENO. 2001. Factors that affect hatching asynchrony in the Chinstrap Penguin (*Pygoscelis antarctica*). *Polar Biology* 24:338–342.
- DERKSEN, D. V. 1977. A quantitative analysis of the incubation behavior of the Adélie Penguin. *Auk* 94:552–566.
- DRENT, R. 1975. Incubation, p. 333–420. *In* D. S. Farner, J. R. King and K. C. Parkes [EDS.], *Avian biology*, vol. 5. Academic Press, New York.
- FRERE, E., P. GANDINI, AND P. D. BOERSMA. 1992. Effects of nest type and location on reproductive success of the Magellanic Penguin *Spheniscus magellanicus*. *Marine Ornithology* 20:1–6.
- FROST, P. G. H., W. R. SIEGFRIED, AND A. E. BURGER. 1976. Behavioural adaptations of the Jackass Penguin, *Spheniscus demersus* to a hot, arid environment. *Journal of Zoology* 179:165–187.
- HAFTORN, S. 1986. A quantitative analysis of the behaviour of the Chinstrap Penguin *Pygoscelis antarctica* and Macaroni Penguin *Eudyptes chrysolophus* on Bouvetøya during the late incubation and early nestling periods. *Polar Research* 4:33–45.
- HAFTORN, S. 1988. Incubating female passerines do not let the egg temperature fall below the “physiological zero temperature” during their absences from the nest. *Ornis Scandinavica* 19:97–110.
- HANDRICH, Y. 1989. Incubation water loss in King Penguin egg. I. Change in egg and brood pouch parameters. *Physiological Zoology* 62:96–118.
- HIPFNER, J. M., A. J. GASTON, D. L. MARTIN, AND I. L. JONES. 2001. Seasonal declines in incubation periods of Brünnich’s Guillemots *Uria lomvia*: testing proximate causes. *Ibis* 143:92–98.
- LACK, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.
- LOMBARDO, M. P., R. M. BOSMAN, C. A. FARO, S. G. HOUTTEMAN, AND T. S. KLUSZA. 1995. Effect of feathers as nest insulation on incubation behavior and reproductive performance of Tree Swallows (*Tachycineta bicolor*). *Auk* 112:973–981.
- LOOS, E. R., AND F. C. ROHWER. 2004. Laying-stage nest attendance and onset of incubation in prairie nesting ducks. *Auk* 121:587–599.
- MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101–127.
- MARTIN, T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. *Proceedings of the Royal Society of London B* 269:309–316.
- MARTIN, T. E., S. K. AUER, R. D. BASSAR, A. M. NIKLISON, AND P. LLOYD. 2007. Geographic variation in avian incubation periods and parental influences on embryonic temperature. *Evolution* 61:2558–2569.
- MASSARO, M., AND L. S. DAVIS. 2004. The influence of laying date and maternal age on eggshell thickness and pore density in Yellow-eyed Penguins. *Condor* 106:496–505.
- MASSARO, M., L. S. DAVIS, AND R. S. DAVIDSON. 2006. Plasticity of brood patch development and its influence on incubation periods in the Yellow-eyed Penguin *Megadyptes antipodes*: an experimental approach. *Journal of Avian Biology* 37:497–506.
- NAKAMURA, M., T. YODA, L. I. CRAWSHAW, S. YASUHARA, Y. SAITO, M. KASUGA, K. NAGASHIMA, AND K. KANOSUE. 2008. Regional differences in temperature sensation and thermal comfort in humans. *Journal of Applied Physiology* 105:1897–1906.
- OLSON, C. R., C. M. VLECK, AND D. VLECK. 2006. Periodic cooling of bird eggs reduces embryonic growth efficiency. *Physiological and Biochemical Zoology* 79:927–936.
- PERSSON, I., AND G. ANDERSSON. 1999. Intraclutch hatch synchronization in pheasants and Mallard ducks. *Ethology* 105:1087–1096.
- POUSSART, C., J. LAROCHELLE, AND G. GAUTHIER. 2000. The thermal regime of eggs during laying and incubation in Greater Snow Geese. *Condor* 102:292–300.

- REID, B. 1965. The Adélie Penguin (*Pygoscelis adeliae*) egg. *New Zealand Journal of Science* 8:503–514.
- REID, J. M., P. MONAGHAN, AND R. G. NAGER. 2002. Incubation and the costs of reproduction, p. 315–325. *In* D. C. Deeming [ED.], *Avian incubation: behaviour, environment, and evolution*. Oxford University Press, Oxford, England.
- RICKLEFS, R. E., AND C. A. SMERASKI. 1983. Variation in incubation period within a population of the European Starling. *Auk* 100:926–931.
- RICKLEFS, R. E. 1993. Sibling competition, hatching asynchrony, incubation period, and lifespan in altricial birds, p. 199–276. *In* D. M. Power [ED.], *Current Ornithology*, vol 11. Plenum, New York.
- ROBINSON, W. D., J. D. STYRSKY, B. J. PAYNE, R. G. HARPER, AND C. F. THOMPSON. 2008. Why are incubation periods longer in the tropics? A common-garden experiment with House Wrens reveals it is all in the egg. *American Naturalist* 171:532–535.
- ROWE, K. M., AND P. J. WEATHERHEAD. 2009. A third incubation tactic: delayed incubation by American Robins (*Turdus migratorius*). *Auk* 126:141–146.
- RUNDE, O. J., AND R. T. BARRETT. 1981. Variations in egg size and incubation period of the Kittiwake *Rissa tridactyla* in Norway. *Ornis Scandinavica* 12:80–86.
- SOCKMAN, K. W., P. J. SHARP, AND H. SCHWABL. 2006. Orchestration of avian reproductive effort: an integration of the ultimate and proximate bases for flexibility in clutch size, incubation behaviour, and yolk androgen deposition. *Biological Reviews* 81:629–666.
- ST. CLAIR, C. C. 1992. Incubation behaviour, brood patch formation and obligate brood reduction in Fiordland Crested Penguins. *Behavioral Ecology and Sociobiology* 31:409–416.
- ST. CLAIR, C. C. 1996. Multiple mechanisms of reversed hatching asynchrony in Rockhopper Penguins. *Journal of Animal Ecology* 65:485–494.
- STOKES, D. L., AND P. D. BOERSMA. 1991. Effects of substrate on the distribution of Magellanic Penguin (*Spheniscus magellanicus*) burrows. *Auk* 108:923–933.
- STOLESON, S. H., AND S. R. BEISSINGER. 1995. Hatching asynchrony and the onset of incubation in birds, revisited. When is the critical period? *Current Ornithology* 12:191–270.
- TIELEMAN, B. I., J. B. WILLIAMS, AND R. E. RICKLEFS. 2004. Nest attentiveness and egg temperature do not explain the variation in incubation periods in tropical birds. *Functional Ecology* 18:571–577.
- VINCE, M. A. 1964. Social facilitation of hatching in the Bobwhite Quail. *Animal Behaviour* 12:531–534.
- WANG, J. M., AND W. W. WEATHERS. 2009. Egg laying, egg temperature, attentiveness, and incubation in the Western Bluebird. *Wilson Journal of Ornithology* 121:512–520.
- WEBB, D. R. 1987. Thermal tolerance of avian embryos: a review. *Condor* 89:874–898.
- WEINRICH, J. A., AND J. R. BAKER. 1978. Adélie Penguin (*Pygoscelis adeliae*) embryonic development at different temperatures. *Auk* 95:569–576.
- WHEELWRIGHT, N. T., AND P. D. BOERSMA. 1979. Egg chilling and the thermal environment of the Fork-tailed Storm-Petrel (*Oceanodroma furcata*) nest. *Physiological Zoology* 52:231–239.
- WILLIAMS, T. D., AND P. D. BOERSMA. 1995. Magellanic Penguin, p. 249–258. *In* T. D. Williams [ED.], *The penguins*. Oxford University Press, Oxford.
- YORIO, P., AND P. D. BOERSMA. 1994a. Consequences of nest desertion and inattendance for Magellanic Penguin hatching success. *Auk* 111:215–218.
- YORIO, P., AND P. D. BOERSMA. 1994b. Causes of nest desertion during incubation in the Magellanic Penguin (*Spheniscus magellanicus*). *Condor* 96:1076–1083.