Parental Behavior Controls Asynchronous Hatching, But Not Incubation Period, in the Magellanic Penguin: A Commentary on Rebstock and Boersma (2011)

Authors: Laurent Demongin, Maud Poisbleau, and Marcel Eens
Source: The Condor, 115(1) : 1-4
Published By: American Ornithological Society
URL: https://doi.org/10.1525/cond.2012.120026

COMMENTARIES

The Condor 115(1):1–4

PARENTAL BEHAVIOR CONTROLS ASYNCHRONOUS HATCHING, BUT NOT INCUBATION PERIOD, IN THE MAGELLANIC PENGUIN: A COMMENTARY ON REBSTOCK AND BOERSMA (2011)

Laurent Demongin[1], Maud Poisbleau, and Marcel Eens

Department Biology–Ethology, University of Antwerp, Campus Drie Eiken, Universiteitsplein 1, 2610 Antwerp (Wilrijk), Belgium

Abstract. Rebstock and Boersma (2011) recently explored variation in the temperature and incubation period of eggs within clutches of the Magellanic Penguin (*Spheniscus magellanicus*). They defined incubation period as "the time from the laying of an egg to its hatching" and concluded that parental behavior explained why the incubation period of second eggs was shorter than that of first eggs and controlled asynchronous hatching. While we agree that parents influenced asynchronous hatching by delaying the onset of incubation, we argue that their conclusions are based on an unconventional definition of incubation period. They included the period before the delayed onset of incubation in the incubation period, which leads to confusion. We state that the incubation period cannot include the time before the (delayed) onset of incubation when parents are not warming the eggs. As regards this latter and widely accepted definition, Rebstock and Boersma (2011) provided a large dataset showing that incubation consistently lasted for 39 days, whenever the onset of incubation, for both first and second eggs. The divergence in the definition of "incubation period" and the failure to consider the "onset of incubation" for a species in which the first egg is not incubated immediately after laying led to confusion in the interpretation of the results and conclusions from Rebstock and Boersma (2011).

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

El Comportamiento Parental Controla la Asincronía de Eclosión, pero no el Período de Incubación, en *Spheniscus magellanicus*: Un Comentario sobre Rebstock y Boersma (2011)

Resumen. Rebstock y Boersma (2011) exploraron recientemente la variación en la temperatura y el período de incubación de los huevos de las nidadas de *Spheniscus magellanicus*. Ellos definieron el período de incubación como "el tiempo desde la puesta de un huevo hasta su eclosión" y concluyeron que el comportamiento parental explicó por qué el período de incubación de los segundos huevos fue más corto que el de los primeros huevos y controló la asincronía en la eclosión. Mientras que estamos de acuerdo en que los padres influenciaron la asincronía de la eclosión demorando el comienzo de la incubación, argumentamos que sus conclusiones están basadas en una definición no convencional del período de incubación. Ellos incluyeron el periodo anterior a la demora del inicio de la incubación en el periodo de incubación, lo que lleva a confusión. Afirmamos que el periodo de incubación no puede incluir el tiempo antes del (demorado) inicio de la incubación cuando los padres no están calentando los huevos. Considerando esta última y ampliamente aceptada definición, Rebstock y Boersma (2011) brindaron una gran base de datos que muestra que la incubación duró consistentemente 39 días, sea cuando sea el inicio de la incubación, tanto para el primero como para el segundo huevo. La divergencia en la definición del "periodo de incubación" y la falla al considerar el "inicio de la incubación" para una especie en la que el primer huevo no es incubado inmediatamente después de la puesta lleva a confusión en la interpretación de los resultados y las conclusiones de Rebstock y Boersma (2011).

There is a wide literature concerning the duration of incubation, as well as the ability of parent birds to manipulate both the duration of incubation and asynchronous hatching within their clutches (see reviews in Magrath 1990, Stoleson and Beissinger 1995, Stenning 1996). Some studies have focused on intrinsic differences between eggs, while others have stressed the important role of the behavior of the incubating adults. Penguins have often been used as a model to test this

Manuscript received 13 February 2012; accepted 17 July 2012.
[1]E-mail: laurentdemongin@gmail.com

The Condor, Vol. 115, Number 1, pages 1–4. ISSN 0010-5422, electronic ISSN 1938-5422. DOI: 10.1525/cond.2012.120026

question for several reasons (De León et al. 2001, Massaro and Davis 2005, Poisbleau et al. 2011). The main reason could be the reversed asynchronous hatching of the crested penguins (genus *Eudyptes*, St. Clair 1996), a phenomenon unique among birds of which the underlying mechanisms remain unclear. Recently, Rebstock and Boersma (2011) aimed to test the hypothesis that parental behavior (specifically through a delayed onset of incubation) controls the asynchrony of hatching in the Magellanic Penguin (*Spheniscus magellanicus*). The authors concluded that parental behavior between the laying of the first and the second egg determines the incubation period and thus the resulting asynchronous hatching. However, we argue that their conclusions are based on an unconventional definition of incubation period. Rebstock and Boersma (2011) included within the incubation period the period before the delayed onset of incubation, which leads to confusion. We think that a reinterpretation of their results in the light of the conventional definition is necessary.

DEFINITION OF THE INCUBATION PERIOD

The first sentence of the paper starts with a definition of the incubation period, "the time from the laying of an egg to its hatching." This definition, which was not supported by a proper reference, is inconsistent with the usual terminology and with the different studies Rebstock and Boersma (2011) cited and used for comparison. See, for example, Ricklefs and Smeraski (1983), Martin (2002, 2007), or Sockman et al. (2006).

Wang and Beissinger (2011) have recently clarified the terminology concerning incubation. They defined incubation according to Beer (1964) as "the process by which the heat necessary for embryonic development is transferred to an egg after it has been laid." Rebstock and Boersma (2011) have confused (1) the period from the laying of an egg to its hatching and (2) the period from the onset of incubation of an egg and its hatching. These two notions are not the same. The second, called "effective incubation" in this commentary, sticks to Beer's (1964) and Wang and Beissinger's (2011) definitions and measures the incubation period from the time that the parents heat the eggs sufficiently to allow embryos to develop. The first notion includes both the period between laying and the beginning of effective incubation (egg-attendance period) and the period of effective incubation. According to the definition Rebstock and Boersma (2011) used, it is not correct to employ the wording "delayed onset of incubation" as they did. A delay in the start of incubation cannot be counted in the incubation period because, by definition, the delayed incubation period has not yet begun. Yet Rebstock and Boersma (2011) used the time from laying to hatching to calculate incubation periods including the delay before the onset of incubation within this time. This mistake, which could go unnoticed for birds initiating incubation as soon as the first egg of the clutch is laid, is an issue in Rebstock and Boersma's experimental study (2011) on penguins, especially as regards the experimental design.

We acknowledge that Rebstock and Boersma (2011)'s conclusions are only as "wrong" as their definition of incubation period is wrong since they are consistent with this definition. However, we would like to stress that the presentation of this study may cause confusion for readers that do not read the manuscript very carefully, do not note the unusual definition of incubation period used in it, and then interpret the results and its conclusions in the light of the widely accepted definition. We here state what the conclusions would be if the definition was the conventional one.

DETERMINATION OF THE ONSET OF INCUBATION

First of all, it is necessary to determine when the effective incubation of the first and the second eggs began (i.e., the onset of their incubation). Rebstock and Boersma (2011) have presented a large amount of interesting data that provide this information.

According to Weinrich and Baker (1978), a temperature of 26 °C is enough for some development of Adélie Penguin (*Pygoscelis adeliae*) eggs, which have a mean mass of 113–124 g (Williams 1995), similar to that of Magellanic Penguin eggs, 125 g (Rafferty et al. 2005). Rebstock and Boersma (2011, see their Fig. 2) reported that this threshold temperature was attained at day 3 for the first egg, i.e., 2 days after laying. All their data lead to the same conclusion: Magellanic Penguins start to effectively incubate first eggs 2 days after laying, while second eggs are incubated immediately after laying. But consistent with their definition of incubation period, they did not take this result into account when analyzing and interpreting their results. We feel that it is important to reformulate some of those results, considering that the incubation period starts only at the (delayed) onset of incubation.

REFORMULATION OF THE RESULTS

Rebstock and Boersma (2011) performed a study under control and experimental conditions. Provided that effective incubation started 2 days after the first egg was laid, observations of control nests suggested that both first and second eggs are effectively incubated for 39 days on average (Figs. 1a and 1b). Since second eggs were laid on average 4 days after first eggs, Rebstock and Boersma (2011) concluded that the asynchrony of hatching was 2 days. The egg-swap experiment perfectly confirmed this finding.

Delayed incubation—first egg. First eggs were stored in a cooler during the 4 days until the second egg of their clutches was laid. They were not incubated during this 4-day period. Therefore, the incubation of both first and second eggs started at the same time (i.e., when the eggs were replaced in their nest; compare Fig. 1c to Fig. 1b). Incubation of first eggs lasted 39 days (see Fig. 1c). Actually, Rebstock and Boersma (2011) reported that first eggs hatched 1 day after second eggs on

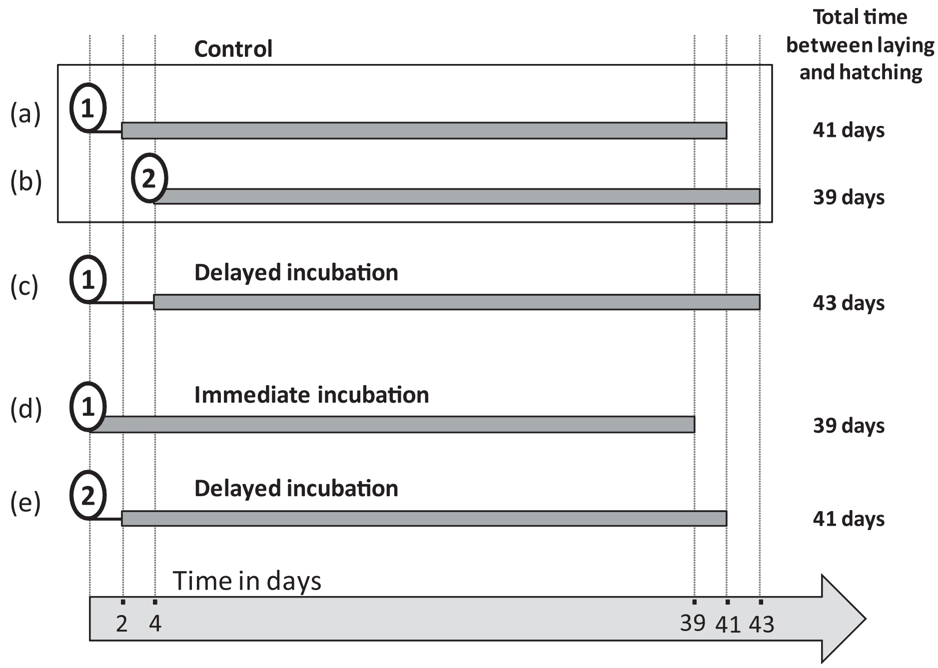

FIGURE 1. Schematic representation of the experimental design of Rebstock and Boersma (2011) and incubation periods expected for first and second eggs of the Magellanic Penguin. Thin lines represent the delay between laying and the onset of incubation. Long rectangles represent the effective incubation period of 39 days. Pattern observed under natural conditions for (a) first eggs and (b) second eggs (control). (c) Pattern when the incubation of first eggs was delayed by their being stored in a cooler for 4 days (delayed incubation). (d) Pattern when the incubation of first eggs was advanced by their treatment as second eggs (immediate incubation). (e) Pattern when the incubation of second eggs was delayed by their treatment as first eggs (delayed incubation). Unmanipulated sibling eggs of the swapped eggs are not shown. Time scale starts from the day first eggs were laid for control eggs (a and b) and at laying for swapped eggs (c, d, and e).

average. They explained that keeping the eggs below 20 °C for several days likely delayed development, and that some development of the second eggs likely occurred before they found them and replaced the first eggs.

Immediate incubation—first egg. Rebstock and Boersma (2011) used first eggs from another nest to replace newly laid second eggs. Effective incubation in the foster nest had already started 2 days prior to the placement of the swapped egg. They were therefore incubated immediately. Their effective incubation period was 39 days (see Fig. 1d).

Delayed incubation—second egg. Second eggs were treated as first eggs for the first 4 days and placed in nests to replace first eggs that had just been laid. They were then returned to their original nests. It was expected and observed that the period from laying to hatching for these delayed second eggs was the same as for first eggs under natural conditions, i.e., 41 days. Nevertheless, the effective incubation period was again 39 days (see Fig. 1e). Actually, these periods were 1 day shorter (40 days from laying to hatching). A possible explanation is that when the second egg was returned to its original nest 4 days after being laid, the incubation temperature (~31 °C) was higher than for first eggs under natural conditions at the same age (28 °C). This temperature difference could have contributed to a slight reduction of the effective incubation period.

REFORMULATION OF THE CONCLUSIONS

To summarize briefly the results from Rebstock and Boersma (2011): the effective incubation period was consistently 39 days, and the variation in the period between laying and hatching came from a delay in the onset of incubation. The finding that the period between laying and hatching, under Rebstock and Boersma's (2011) definition of incubation period was extended by the time that parents were not actually incubating is logical. Finally, the conclusions of Rebstock and Boersma (2011) in the light of the conventional definition of incubation period should, for example, be: (1) Effective incubation starts when first eggs are 2 days old; (2) first and second eggs have the same incubation period of 39 days; (3) it is therefore unlikely that first and second eggs are intrinsically different; (4) under natural conditions, second eggs hatch only 2 days after first eggs despite the 4-day interval between them because effective incubation starts only when first eggs are 2 days old, and not on the day they are laid; and (5) parents can modulate asynchronous hatching (but not the incubation period) by manipulating the onset of incubation.

All available evidence appears to indicate that parental incubation behavior, not an intrinsic difference between the eggs, controls the asynchrony of hatching in the Magellanic Penguin.

We thank David Carslake, Michael A. Patten, and two anonymous reviewers for comments on the manuscript.

LITERATURE CITED

Beer, C. G. 1964. Incubation, p. 396–398. *In* A. L. Thomson [ed.], A new dictionary of birds. Nelson, London.

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.

Magrath, R. D. 1990. Hatching asynchrony in altricial birds. Biological Reviews 65:587–622.

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. 2005. Differences in egg size, shell thickness, pore density, pore diameter and water vapour conductance between first and second eggs of Snares Penguins *Eudyptes robustus* and their influence on hatching asynchrony. Ibis 147:251–258.

Poisbleau, M., L. Demongin, I. J. Strange, M. Eens, and P. Quillfeldt. 2011. Is the reduced incubation time for B-eggs in Rockhopper Penguins *Eudyptes chrysocome* linked to egg density variation? Journal of Ornithology 152:137–142.

Rafferty, N. E., P. D. Boersma, and G. A. Rebstock. 2005. Intraclutch egg-size variation in Magellanic Penguins. Condor 107:921–926.

Rebstock, G. A., and P. D. Boersma. 2011. Parental behavior controls incubation period and asynchrony of hatching in Magellanic Penguins. Condor 113:316–325.

Ricklefs, R. E., and C. A. Smeraski. 1983. Variation in incubation period within a population of the European Starling. Auk 100:926–931.

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. 1996. Multiple mechanisms of reversed hatching asynchrony in Rockhopper Penguins. Journal of Animal Ecology 65:485–494.

Stenning, M. J. 1996. Hatching asynchrony, brood reduction and other rapidly reproducing hypotheses. Trends in Ecology and Evolution 11:243–246.

Stoleson, S. H., and S. R. Beissinger. 1995. Hatching asynchrony and the onset of incubation in birds, revisited: when is the critical period?, p. 191–270. *In* D. M. Power [ed.], Current ornithology, vol. 12. Plenum, New York.

Wang, J. M., and S. R. Beissinger. 2011. Partial incubation in birds: its occurrence, function, and quantification. Auk 128:454–466.

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

Williams, T. D. 1995. The penguins. Oxford University Press, Oxford, England.