Parental Behavior Controls Incubation Period and Asynchrony of Hatching in Magellanic Penguins: Reply to Demongin, Poisbleau and Eens (2013)

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Source: The Condor, 115(1) : 5-7

Published By: American Ornithological Society

URL: https://doi.org/10.1525/cond.2012.120114

The Condor 115(1):5–7

PARENTAL BEHAVIOR CONTROLS INCUBATION PERIOD AND ASYNCHRONY OF HATCHING IN MAGELLANIC PENGUINS: REPLY TO DEMONGIN, POISBLEAU AND EENS (2013)

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Abstract. We defined incubation period as the time from the laying of an egg to its hatching (Rebstock and Boersma 2011) because this full period is ecologically important and matters to both parents' and offspring's fitness. Birds have many patterns of incubation onset and various degrees of egg neglect following onset of incubation. Onset of incubation is difficult to measure in the field and even if known, ignoring the period before onset of incubation misses many of the selective forces acting on incubation patterns and periods.

Key words: *incubation period, onset of incubation, incubation costs, parental behavior.*

El Comportamiento Parental Controla el Periodo de Incubación y la Asincronía de Eclosión en *Spheniscus magellanicus*: Respuesta a Demongin, Poisbleau y Eens (2013)

Resumen. Definimos el periodo de incubación como el tiempo desde la puesta de un huevo hasta su eclosión (Rebstock y Boersma 2011) porque este periodo completo es ecológicamente relevante e importa para la adecuación biológica tanto de padres como de hijos. Las aves tienen muchos patrones de inicio de la incubación y varios grados de negligencia del huevo luego del inicio de la incubación. El inicio de la incubación es difícil de medir en el campo e incluso si se conoce, ignorar el periodo antes del inicio de la incubación pierde muchas de las fuerzas selectivas que actúan en los patrones y los periodos de incubación.

Demongin and colleagues (2013) disagreed with our definition of incubation period (Rebstock and Boersma 2011) as "the time from the laying of an egg to its hatching" (see also Welty 1962), preferring the more common definition of "the period from the onset of incubation of an egg to its hatching." Both definitions describe periods that can be highly variable within a species (Boersma and Wheelwright 1979, Frere et al. 1992, Hipfner et al. 2001) and may vary between eggs in a clutch (Greenlaw and Miller 1983, Boonstra et al. 2010, Rebstock and Boersma 2011). The time from when the egg was laid to when it hatches is ecologically important and matters to both parents' and offspring's fitness because of risks of predation at the nest (Stoleson and Beissinger 2001) and other costs (Ricklefs 1993). Birds have many patterns of incubation onset (Wang and Beissinger 2011) and various degrees of egg neglect following onset of incubation (e.g., Boersma and Wheelwright 1979, Boersma 1982, Nuechterlein and Buitron 2002, Marín 2008). The onset of incubation is harder to determine than when each egg is laid, and the minimum temperature at which development begins is often unknown. We argue how the eggs are treated is important. As our study showed, parental incubation behavior, not an intrinsic difference between the eggs, controlled the incubation period and the asynchrony of hatching of eggs of the Magellanic Penguin (*Spheniscus magellanicus*).

Defining the incubation period as the time between the laying and hatching of the last egg in a clutch misses the ecological and physiological importance of the variation in the time the eggs spend in the nest. How long eggs remain in the nest, regardless of whether they are incubated, affects parents and eggs. Incubation is energetically costly and reduces foraging time (Dobbs and Martin 1998, Cooper et al. 2005, Carey 2011, Galván and Sanz 2011). Female Magellanic Penguins stay on (or next to) the nest fasting from egg laying until relieved by the mate, which can be up to 3 weeks (Boersma et al. 1990). Eggs are at risk of predation every day they are in the nest (Bosque and Bosque 1995, Walls et al. 2011). A long period before the onset of incubation increases the eggs' risk of predation. In many species the parents are also at risk of predation while incubating (Martin 2002; Cervencl et al. 2011). A prolonged egg period increases the breeding season, a disadvantage to species with long breeding seasons and short windows of appropriate weather and food availability (Hodum 2002, Creuwels et al. 2008). Eggs may lose viability prior to the beginning of effective incubation, especially if ambient temperatures are high (Beissinger et al. 2005). Longer incubation

Manuscript received 9 July 2012; accepted 17 July 2012.
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The Condor, Vol. 115, Number 1, pages 5–7. ISSN 0010-5422, electronic ISSN 1938-5422. © 2013 by The Cooper Ornithological Society. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintInfo.asp. DOI: 10.1525/cond.2012.120114

periods associated with reduced egg temperatures may result in smaller chicks and disfavor their growth and survival (Boersma and Wheelwright 1979, Olson et al. 2006, Ardia et al. 2010).

Patterns of incubation onset vary widely by species. Eggs are warmed to full incubation temperature before clutch completion in some species (Stoleson and Beissinger 2001, Ruiz-de-Castañeda et al. 2012). For example, the female may incubate the eggs at night before clutch completion, but may not incubate steadily during the day until the clutch is complete (Haftorn 1988, Wang and Weathers 2009). In other species, such as the Yellow-eyed Penguin (*Megadyptes antipodes*) and Black-legged Kittiwake (*Rissa tridactyla*), partial incubation may persist long after clutch completion (Wang and Beissinger 2011). We showed that the daily mean temperature of Magellanic Penguin eggs increases steadily for about the first 18 days after laying, at least 2 weeks after clutch completion. A gradual increase in egg temperature is common among penguins (Burger and Williams 1979, St. Clair 1992, de León et al. 2001, Massaro et al. 2006).

Egg neglect or intermittent incubation is common in tubenose seabirds (Procellariiformes), and exposure to low temperatures after the egg has reached effective incubation temperatures does not prevent hatching but lengthens the incubation period (Boersma 1982, Carey 2011). In the Fork-tailed Storm-Petrel (*Oceanodroma furcata*) eggs must be warm for 37 days but, because of egg neglect, may take up to 68 days to hatch (Boersma and Wheelwright 1979). Egg neglect is also found in other groups of birds, such as hummingbirds (Webb 1987), alcids (Sealy 1984), and swifts (Marín 2008). Throughout incubation of Magellanic Penguin eggs, large temporary temperature drops are common, as our paper showed.

Onset of incubation is nearly impossible to determine in the field for four reasons. (1) Embryonic growth and development is difficult to measure in the field. (2) The temperature required for development is usually unknown. There is not a single "physiological zero" temperature at which no development occurs for all species or even all ages of embryos within a species (Webb 1987, Decuypere and Michels 1992). Embryogenesis starts at fertilization, and the developmental stage of the embryo at egg laying varies (Decuypere and Michels 1992). The assumption is often made that 24–27 °C is the minimum temperature required for development (Beissinger et al. 2005), and lower temperatures are seldom tested. In eggs of the Adélie Penguin (*Pygoscelis adeliae*), Weinrich and Baker (1978) found that some development occurred at 26° C, the lowest temperature they tested. (3) During active incubation, an egg's temperature decreases from top (brood patch) to bottom (nest), making it difficult to determine the temperature experienced by the embryo (Boersma 1982). (4) Patterns of incubation onset vary by species (Wang and Beissinger 2011).

Our point is that parental behavior controlled the dates and asynchrony of hatching of Magellanic Penguin eggs, as it does in many species (Martin et al. 2007). First eggs spent more time in the nest than second eggs, which matters. Parental behavior, not intrinsic differences between the eggs, causes this discrepancy. The appropriate definition depends on the question being asked. Arguing over definitions detracts from the point and obscures the ecological importance and fitness consequences of the time the egg spends in the nest.

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