

S38-2 Developmental phenotypic plasticity in embryos during incubation

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Abstract Bird embryos depend on the attendance of parents to provide the optimal temperature for development. When parents cannot incubate optimally, the embryos need to adjust rates of growth and modes of development to compensate. I review data on the plasticity of embryo growth in birds, and relate this to mode of incubation, climate, nest insulation, and the continuum between precocial and altricial species. I also review the effects on hatchling survival of ensuing suboptimal growth trajectories. In several precocial species that require hatching synchrony, growth rate and mode of growth in embryos can be accelerated or retarded depending on the position of the embryo in the laying sequence. Communication between embryos in eggs late in incubation conveys information on the degree of maturity and time to hatching of each. This makes it possible for embryos in eggs produced after the start of incubation to accelerate growth in order to hatch at the same time as their siblings. I evaluate the circumstances under which such acceleration (or retardation) will occur, and how this affects the mode of growth and hatchling performance and survival.

Key words Embryo development, Incubation, Accelerated hatching, Embryo communication

1 Conditions for embryonic development in the wild

Developing avian embryos depend on their parents for food and nutrients in the egg, supplied by the female during egg formation, and the right temperature and humidity in the egg, provided by parental incubation. This review centers on the role and effects of parental incubation.

Through more-or-less continuous contact with the eggs, parents provide a benign environment for developing embryos. As a rule, species that are precocial or biparental in incubation are more attentive than altricial species and those in which only one sex incubates (Deeming, 2002). Recently, evidence for significant parental costs in incubation has come to light (Monaghan and Nager, 1997; Thomson et al., 1998; Visser and Lessells, 2001), suggesting that optimal incubation performance is not always possible. What happens then? In such cases, embryos need to adjust their rate of growth or mode of development to try to cope with the thermal environment. Such developmental plasticity has its limits as well as its costs for both embryos and hatchlings forced to follow growth trajectories other than the norm.

To evaluate embryo performance under suboptimal conditions, knowledge is needed of the optimal thermal environment for embryonic development. The development of chicken embryos, which have served as a model for all avian species, stops below 26°C, the so-called physiological zero temperature. Even between 26 and 36°C, the rate of development and growth is reduced; and long exposure to these temperatures may cause developmental abnormali-

ties and death. The thermal range between 36 and 40 °C is considered optimal for optimal development of most avian embryos. Embryos are generally very sensitive to temperatures above 40 °C with a rapid increase in risk of mortality (Lundy, 1969; Conway and Martin, 2000). Thus, whereas developmental plasticity seems to be very low at high temperatures, embryos at suboptimal temperatures seem able to cope with a range of thermal environments.

What then are the incubation temperatures found in nature? Data from four avian orders (Fig. 1) show that avian embryos are commonly incubated at temperatures below the optimal thermal range for growth and development (Webb, 1987). Clutches of more precocial orders are incubated at a little higher mean temperature, consistent with the higher levels of attentiveness in precocial species (Fig.

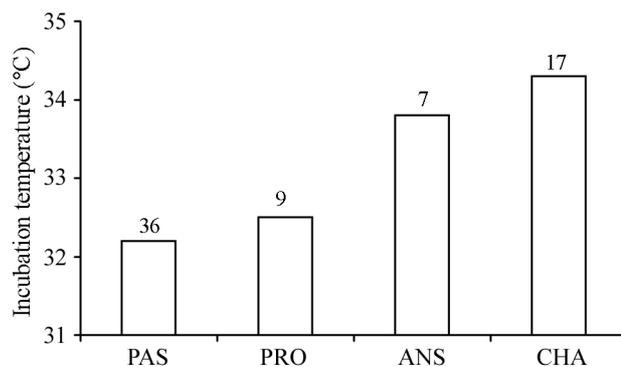


Fig. 1 Mean incubation temperature for clutches of four avian orders

PAS = Passeriformes, PRO = Procellariiformes, ANS = Anseriformes, CHA = Charadriiformes. Number of species screened stated above each bar. Compiled after Webb (1987).

1). Thus, the avian embryo does not have to cope with suboptimal incubation temperatures now and then, but most of the time. Such deviations from optimal incubation efficiency may therefore call for well-developed response plasticity in embryos.

2 Developmental limits in response to suboptimal incubation

Ambient temperature is an obvious factor affecting incubation efficiency. Here the northerly expansion of the breeding range of the pied flycatcher (*Ficedula hypoleuca*) into harsh and variable environments provides an illustrative example. This migratory species started to breed in northern Finland in 1957 (Järvinen, 1989), and has continued to do so. Mean ambient temperature during incubation was found to influence hatching success significantly each year. A reduction in mean temperature of 5 °C resulted in a 50 % fall in hatching success (Järvinen, 1983). Low ambient temperatures resulted in reduced incubation efficiency which increased the length of the incubation period (Järvinen, 1990). Concordant with this, most embryo deaths happened during the final days of incubation (Ylimaunu and Järvinen, 1987). The total metabolic rate of embryos increases as incubation temperature decreases (Booth, 1987) and the duration of incubation increases (Vleck and Vleck, 1996). This may then deplete energy-rich nutrients in the yolk before the embryos can hatch. Thus, increase in the duration of incubation can quickly fall outside the response range of embryos.

Looking for limits to developmental plasticity, I used field experiments to both increase or decrease incubation efficiency. The experiments included manipulative enlargement and reduction of clutch sizes, supplemental feeding, and the removal of courtship-feeding males. To measure the extent to which the experiments affected incubation efficiency, I used reported lengths of incubation period from the literature. Results showed that quite small increases in incubation time reduce hatching success (Fig. 2), indicating that some embryos are sensitive to increases in the length of the incubation period to a point where they are not plastic enough to survive. Increased hatching success in the treatments with shortened incubation period shows that normal incubation efficiency in the species investigated is suboptimal for the growth and development of embryos (Fig. 2).

3 Developmental costs in response to suboptimal incubation

Concerning post-hatching costs to those embryos that succeed in changing development and growth trajectories, data interpretation precipitates several issues. Clutch size and other manipulations must be restricted to the incubation period, otherwise fitness-related effects that arise later in hatched young cannot be separated from those resulting from the manipulation. Even then, poor nestling

condition can be explained either by deviations from optimal embryonic development or by reduced parental ability to provision the nestlings (Monaghan and Nager, 1997; Reid et al., 2000a). What is needed are records of hatchling condition, which is a direct consequence of embryonic development. Few studies meet these criteria.

Two out of four studies, in which a decrease in hatching success had been manipulated by clutch size enlargement, reported significantly reduced mass among young hatched from enlarged clutches (Sanz, 1997; T. Lislevand, pers. com., for the lapwing, *Vanellus vanellus*). The third study reported reduced growth rates in young hatched from enlarged clutches (Heaney and Monaghan, 1996), whereas the fourth found no such effects in enlarged clutches of the starling, *Sturnus vulgaris* (Reid et al., 2000b). In all these studies, however, a reduction in fledgling mass was found in clutches with low hatching success.

Another study on starlings is also relevant because measures of mass are available just after hatching (Reid et al., 2002). In this study, single-parent incubation was compared with biparental incubation. Hatching success and hatchling mass were significantly lower in clutches incubated by one parent (Reid et al., 2002). Thus, direct effects on hatchlings reported in some of the studies can be interpreted as the consequence of reduced incubation efficiency. The more general finding of reduced fledgling mass in these studies has been interpreted as the consequence of reduced rates of provisioning by females due to increased incubation costs. That some of the explanation lies in carry-over effects from suboptimal embryonic development, however, cannot be eliminated.

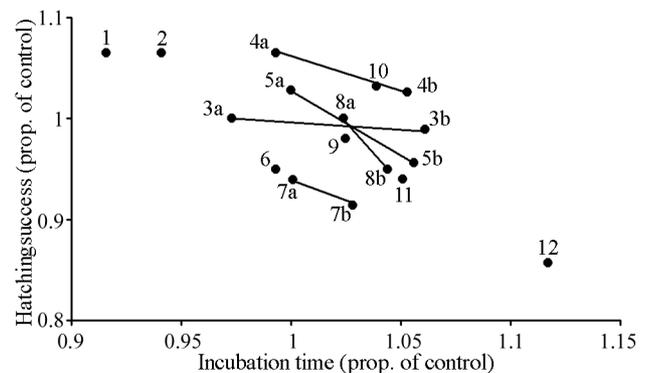


Fig. 2 The relation between length of incubation period and hatching success in experimental studies designed to test incubation efficiency

Both incubation period and hatching success are expressed as the ratio of experimental to control clutches. Values larger than 1 denote an increase in the length of incubation and hatching success, respectively, due to the experiment. Points connected with a line denote studies where data is presented for both reduced (a) and enlarged (b) clutches. Data from: Moreno (1989) = 1, Nilsson and Smith (1988) = 2, Moreno and Carlson (1989) = 3, Møller (1993) = 4, Siikamäki (1995) = 5, Heaney and Monaghan (1996) = 6, Sanz (1997) = 7, Moreno et al. (1991) = 8, Cichón (2000) = 9, Smith (1989) = 10, Baltz and Thompson (1988) = 11, Lyon and Montgomerie (1985) = 12.

4 Developmental costs in response to accelerated and delayed hatching

Another approach for assessing the costs of suboptimal embryonic development is through an evaluation of the post-hatching effects of accelerations or delays towards the end of embryonic development in precocial species. Females of many precocial species continue to lay eggs after the start of incubation, thus generating developmental asynchrony within the clutch (Wilson and Verbeek, 1995; Persson and Andersson, 1999). This is paradoxical because synchronization of hatching is vital for rapid and coordinately chick departure from the nest, to limit exposure to predation (Clark and Wilson, 1981; Spencer et al., 2001). It is also important for individual embryos to hatch simultaneously in the frequent case of females that abandon the nest soon after hatching, even if unhatched eggs remain (Björvall, 1968). To overcome this problem, embryos click to communicate their stage of development to one another through the egg towards the end of incubation (Vince, 1969; Brua, 2002). From such sounds, individual embryos can correct their hatching date coordinant with the perceived development of other embryos in the clutch. This correction may be accomplished either by shortening or prolonging incubation (Vince, 1964, 1968; Persson and Andersson, 1999).

In an experiment, artificial clutches of pheasants (*Phasianus colchicus*) and mallards (*Anas platyrhynchos*) were incubated in an incubator to produce embryos that had to either accelerate or delay hatching to synchronize their hatching with the bulk of their siblings (Nilsson and Persson, in prep.). This resulted in pheasant embryos having to accelerate by two days in a shortened incubation period, and mallard embryos having to hold back for up to 2.5 days longer than the normal incubation period. Both of these experimental groups had higher mortality rates after hatching, indicating that deviations from the normal incubation period had detrimental effects noticeable soon after hatching. Reducing the length of incubation, in this case, seemed to be more serious than prolonging it, as accelerated embryos suffered from reduced growth rate and impaired balance as well.

These costs, due to deviations from the normal incubation period, may help in evaluating possible constraint mechanisms in the development of precocial chicks, at least. Precocial chicks already possess functional sensory, neuromuscular and thermoregulatory systems at hatching (Starck, 1998), as they may be exposed to stressful environmental conditions requiring them to walk considerable distances soon after hatching. It is suggested that the maturation of these systems takes place late in embryonic development (Ricklefs and Starck, 1998), during the plateau phase. As this is the time when chicks appear able to communicate with each other (Vince, 1969), acceleration and delay of hatching must also take place during that phase (Cannon et al., 1986). Thus, chicks that have shortened this phase of

organ maturation may have to pay the cost of less developed or impaired body systems: hatching earlier than normal should make it harder for precocial hatchlings to find and handle food items, which has consequences for survival.

5 Conclusions

Embryo growth and development within species thus appears to be regulated rather strictly. Small deviations from normal incubation efficiency increase the risk of embryo mortality. Reduced incubation efficiency, resulting in longer incubation periods, seems to increase metabolic rates in embryos, and thereby cause starvation in late stages. In precocial species, this may lead to a delayed cost due to decreased residual yolk reserves, which are important for the survival of newly hatched chicks. In both precocial and altricial species, embryos are assumed to follow similar growth trajectories until late in embryogenesis when the two types need different lengths of time to pass through developmental stages (Ricklefs and Starck, 1998). This gives rise to variation in functional maturity of tissues, which seems to be more plastic than growth *per se*. How plasticity in the functional maturity of important tissues, for example the brain and nervous system, is related to fitness, early or late in life, is still largely unknown, especially in wild populations.

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