Animal Behaviour 134 (2017) 35–43

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Incubation onset maintains survival of most embryos and growth and survival of late-hatched young

Robert A. Aldredge [a], [b], [*]

[a] *Biology Department, University of North Carolina-Chapel Hill, U.S.A.*
[b] *Avon Park Air Force Range, Avon, FL, U.S.A.*

ARTICLE INFO

Article history:
Received 29 November 2016
Initial acceptance 3 March 2017
Final acceptance 26 July 2017

MS. number: A16-01041R

Keywords:
altricial
brood reduction
hatching failure
incubation onset
reproduction

Hatching asynchrony occurs primarily as a consequence of the timing of embryonic development. Despite over 50 years of study, it is unclear why, ultimately, most birds initiate embryonic development (incubation) before all eggs are laid. One hypothesis focuses on prehatching (embryo) survival and predicts that early incubation maximizes embryo survival by reducing exposure of unincubated eggs (egg viability hypothesis). Another set of hypotheses focuses on posthatching growth and survival and predicts that females time incubation to maximize the number or quality of hatched offspring that fledge (adaptive hatching pattern hypotheses). I experimentally manipulated when females could begin incubation to test how timing of embryonic development influences prehatching survival and posthatching growth and survival in the house sparrow, *Passer domesticus*. Despite high embryo survival in both naturally asynchronous and experimentally synchronized nests, early incubation appeared to maximize embryo survival in all but the earliest-laid eggs, suggesting that house sparrows begin incubation too late to maximize survival of all embryos. Early incubation had little effect on overall (i.e. mean) patterns of posthatching growth and survival. However, early incubation increased the initial variation in offspring size because last-hatched young were relatively small when all eggs had completed hatching. Nestlings that were small at hatch completion grew slowly and exhibited a reduced probability of survival, suggesting that house sparrows begin incubation too early to maximize growth and survival of hatched offspring. These results suggest that timing of incubation neither maximizes embryo survival nor maximizes posthatching growth and survival. Instead, early incubation appears to be a trade-off between maintaining both embryo survival and growth and survival of late-hatched offspring. Thus, house sparrow females likely time incubation as an adaptive strategy to maximize the number of embryos that survive the incubation and nestling periods to fledge.

Hatching asynchrony occurs when siblings of the same cohort hatch at different times (Clark & Wilson, 1981). Although forms of asynchrony occur in diverse taxa, including mammals (Fraser, Thompson, Ferguson, & Darroch, 1979), reptiles (Chapple, 2005; Duffield & Bull, 1996), lamnoid sharks (Gilmore, 1993) and insects (Smiseth, Ward, & Moore, 2006), hatching asynchrony has been studied primarily in birds. Birds lay at most one egg per day and in nearly all species, embryonic development is driven by parental incubation (Clark & Wilson, 1981). Instead of beginning incubation after all eggs are laid, most species initiate incubation before clutch completion, which may cause eggs to hatch over one or more days.

Hatching asynchrony was first described over a half century ago as an adaptive strategy that enables parents to selectively feed young based on size and maximize offspring production when food is abundant, but also quickly reduce the brood to a manageable size when food is limiting (Lack, 1947; Ricklefs, 1965). By beginning incubation before all eggs are laid, females increase the variation in offspring size at hatching, and as a consequence often increase the variation in offspring growth and survival. The increased variation in growth and survival caused by hatching asynchrony is thought to be maintained in most altricial passerines because it increases the number of high-quality young that survive to breed (Lack, 1954, 1966). The brood reduction hypothesis was one of the first attempts to explain the adaptive significance of hatching asynchrony, which has since spawned over a dozen similar hypotheses (reviewed in Magrath, 1990; Stoleson & Beissinger, 1995). Many of these hypotheses focus on how parents regulate timing of hatching

* Correspondence: Robert A. Aldredge, Avon Park Air Force Range, 28 South Blvd., Avon Park, FL 33825, U.S.A.
E-mail address: robert_aldredge@fws.gov.

https://doi.org/10.1016/j.anbehav.2017.09.022

to maximize the number or quality of hatched young that fledge. Collectively, they are called adaptive hatching pattern hypotheses and although many hypotheses have been proposed, none have clear experimental support that is applicable to the diversity of species that begin incubation prior to clutch completion (Stoleson & Beissinger, 1997). Studies that test these hypotheses often experimentally create variation in offspring size within nests by exchanging nestlings between nests to simulate synchronously and asynchronously hatching clutches (Magrath, 1990; Stoleson & Beissinger, 1995). These studies predict that synchronously hatching clutches will (1) produce fewer offspring that survive to fledge, (2) produce lower-quality (e.g. smaller or lighter) offspring at or near fledging, or (3) produce offspring that exhibit lower postfledging survival (Stoleson & Beissinger, 1997). Overall, hatching asynchrony may increase posthatching growth and survival in environments or years when food is limiting (Amundsen & Slagsvold, 1998; Forbes, Glassey, Thornton, & Earle, 2001; Hebert & McNeil, 1999; Magrath, 1989; Podlas & Richner, 2013; Wiebe & Bortolotti, 1994), but this probably does not explain why most birds begin incubation prior to clutch completion, especially in species or populations that exhibit high levels of posthatching survival (Arnold, Rohwer, & Armstrong, 1987; Clark & Wilson, 1981). Furthermore, tests of the adaptive hatching pattern hypotheses often fail to account for the effects of incubation behaviour on embryo survival (Viñuela, 2000).

Recent evidence suggests that prolonged exposure of undeveloped embryos (i.e. unincubated eggs) increases the risk of embryo mortality (the egg viability hypothesis; Arnold et al., 1987; Veiga, 1992). Among those risks, exposure to pathogens (Cook, Beissinger, Toranzos, Rodriguez, & Arendt, 2003; Godard, Wilson, Frick, Siegel, & Bowers, 2007; Shawkey, Firestone, Brodie, & Beissinger, 2009) and suboptimal climatic conditions, including ambient temperature (Hebert, 2002; Webb, 1987), rainfall and humidity (Beissinger, Cook, & Arendt, 2005), are most commonly cited. Although species and populations may differ in the amount of exposure that increases embryo mortality, experimental (Arnold, 1993; Arnold et al., 1987; Beissinger et al., 2005; Stoleson & Beissinger, 1999; Veiga & Viñuela, 1993; Veiga, 1992; Viñuela, 2000; Walls, Hepp, & Eckhardt, 2011; Wang, Firestone, & Beissinger, 2011) and observational (Aldredge, LeClair, & Bowman, 2012; Sockman, 2008; Wang & Beissinger, 2009) evidence shows that females can reduce embryo mortality (hatching failure) by beginning incubation before clutch completion, which decreases the length of exposure for undeveloped embryos. Hatching failure can increase in as few as 2 days of exposure, which is the time required to lay a three-egg clutch in many species (Beissinger et al., 2005). Overall, embryo mortality appears to increase when eggs are exposed to environments where humidity is high or ambient temperatures are greater than physiological zero (24–27 °C) for prolonged periods prior to incubation. This early loss of offspring can have important consequences for parental fitness.

I experimentally manipulated when females could begin incubation to test predictions of the egg viability and adaptive hatching pattern hypotheses in the house sparrow, *Passer domesticus*. The house sparrow, like many temperate breeding passerines, typically lays clutches of four to six eggs and displays semi-asynchronous hatching (from a few hours to up to 3 days; Anderson, 2006). In addition, the house sparrow was the first passerine shown to exhibit declining egg viability with increased exposure prior to incubation (Veiga, 1992). Thus, the house sparrow is an appropriate species to manipulate the primary mechanism used by passerines to regulate patterns of hatching asynchrony and examine predictions of both the egg viability and adaptive hatching pattern hypotheses. I compared patterns of embryo survival and posthatching growth and survival between control clutches in which incubation began naturally before the last egg was laid and experimental clutches in which incubation began once all eggs were laid. If females time incubation to maximize embryo survival (i.e. the egg viability hypothesis is correct), then hatching success should be lowest in early-laid eggs even in control nests because these eggs would experience increased exposure prior to incubation. But hatching success should be even lower in experimentally synchronized nests because early-laid experimental eggs experience longer exposure than early-laid control eggs in nests with natural onset of incubation (i.e. naturally asynchronous nests). If females time incubation to maximize posthatching growth and survival (i.e. the adaptive hatching pattern hypotheses are correct), then naturally asynchronous nests should either produce more fledged young or more high-quality young at fledging compared to experimentally synchronized nests.

In most altricial species, early incubation influences posthatching growth and survival primarily by increasing the variation in offspring size at hatching (Clark & Wilson, 1981). Because young in experimentally synchronized clutches also exhibit some variation in size caused by asynchronous hatching (Harper, Juliano, & Thompson, 1993), I also examined how timing of incubation influenced variation in offspring size at hatching and then whether this variation was associated with differences in posthatching growth and survival. To quantify variation in offspring size, I used the mass difference (in grams) between an individual chick and the heaviest nestling in the brood 1 day after the first egg hatched, which provides a direct and ecologically relevant estimate of a nestling's mass relative to its nestmate(s) when all eggs in a clutch had completed hatching (hereafter referred to as hatch completion; only one of 229 nestlings hatched 2 or more days after the first hatched egg). The heaviest nestling in the brood had no mass difference (0 g), and a large mass difference indicated that a nestling was relatively light at hatch completion. I predicted that naturally asynchronous nests would contain more relatively light nestlings at hatch completion. In addition, I predicted that if early incubation is an adaptive behaviour to maximize the number of high-quality young that fledge, then nestlings from asynchronous nests should grow better (e.g. increase mass faster and become larger prior to fledging) than nestlings from experimentally synchronized nests. However, the increased growth associated with hatching asynchrony may be apparent only in environments or years when food availability is low or only in the largest, earliest-hatched young.

Although both the egg viability and adaptive hatching pattern hypotheses attempt to explain why, ultimately, early incubation occurs, they are not mutually exclusive. Indeed, it is possible that naturally asynchronous nests exhibit both reduced embryo survival in early-laid eggs and reduced growth and survival of late-hatched young caused by hatching asynchrony. Such a result would suggest that early incubation does not support either hypothesis but likely occurs as a trade-off between maintaining both embryo survival and posthatching growth and survival (Aldredge, Boughton, Rensel, Schoech, & Bowman, 2014; Sockman, 2008; Stoleson & Beissinger, 1995).

METHODS

I studied a population of house sparrows near Yanceyville, North Carolina, U.S.A. (36.41°N, 79.34°W) during the breeding seasons (late March–late June) of 2013 and 2014. This population has been studied since 2009 and contains approximately 35 wooden nestboxes, half to two-thirds of which are occupied at some point during a single breeding season. In 2013 and 2014, I checked nests daily from nest completion (nest lined) to the day the female laid the last egg (clutch completion). When a female laid the first egg of her first clutch, I randomly assigned the nest either to an