



The adaptive function of hatching asynchrony: an experimental study in great tits



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In many bird species offspring hatch over hours or days, which leads to an age and size hierarchy within broods. The function of hatching asynchrony is much debated, and it has been suggested that the induced size hierarchy among offspring may be an adaptive maternal mechanism for maximizing reproductive output under variable environmental conditions. The best known hypothesis to explain the adaptive value of hatching asynchrony, the 'brood reduction' hypothesis, holds that a size hierarchy among offspring allows for a quick adaptive adjustment of brood size to unpredictable feeding conditions and thus benefits parents. To test the consequences of hatching asynchrony on offspring growth and food provisioning we experimentally manipulated the onset of incubation of eggs within broods of great tits, *Parus major*, to induce either synchronous or asynchronous hatching, and then manipulated brood size after hatching to simulate favourable, control or harsh conditions. We did not find a difference in offspring mortality between asynchronous and synchronous broods under any of these conditions. In harsh conditions, nestling mass and size were reduced in asynchronous broods compared to synchronous ones. The opposite pattern occurred under control conditions. Although our results showed that induced hatching asynchrony alters offspring phenotype, they do not provide strong support for the brood reduction hypothesis as a mechanism to explain hatching asynchrony.

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Environmentally induced parental effects include a large range of factors that influence offspring phenotype (Lacey 1998). They are the product of the interaction of a parental genotype with the environment as expressed in the offspring (Mousseau & Fox 1998). Such cross-generational effects have been observed in both animals (Bernardo 1996) and plants (Galloway 1995, 2005). They are based on a variety of transmission pathways, and are potentially powerful means for producing phenotypic variants among offspring that are well adapted to the prevailing or future conditions (Marshall & Uller 2007). Many animals produce more than one offspring at a time, which poses the interesting evolutionary problem of how births should be spaced to maximize reproductive success. Asynchronous birth is a common phenomenon (e.g. amphibians: Ryan & Plague 2004; reptiles: While et al. 2007; insects: Smiseth & Morgan 2009; sharks: Farrell et al. 2010), and has been extensively studied because the incubation pattern of eggs, as a parental effect, can influence hatching patterns and thus competitive hierarchies among offspring. Most studies have been conducted on altricial bird species (e.g. Clark & Wilson 1981; Magrath 1989; Mock &

Parker 1997; Mainwaring et al. 2012), probably because birds offer excellent models to study such parental effects since embryos develop outside the parent's body and hence facilitate manipulation of incubation patterns, hatching order and other stages of offspring development (Bernardo 1996; Groothuis & Schwabl 2008).

Avian parents may control hatching patterns because, in birds, embryonic development typically starts when eggs are actively incubated (Drent 1975; Wiebe et al. 1998). Most birds lay one egg per day, and incubation may begin at any time during the laying sequence (Blackburn & Evans 1986; Bortolotti & Wiebe 1993). Incubation of eggs before the completion of the clutch (Clark & Wilson 1981; Slagsvold 1985; Magrath 1990) leads to hatching asynchrony and in turn to a pronounced age-based competitive hierarchy in which the younger offspring typically face reduced growth (Stokland & Amundsen 1988; Nilsson & Svensson 1996; Rosivall et al. 2005) and increased mortality before or after fledging (Magrath 1990; Forbes et al. 1997; Vinuela 2000). Thus, the differential onset of incubation and hence hatching asynchrony induced by parents (Drent 1975; Wiebe et al. 1998) will also determine offspring growth (Cotton et al. 1999; Clotfelter et al. 2000; Mainwaring et al. 2010) and survival (Forbes et al. 1997; Vinuela 2000), and may have long-term consequences for nestlings (Forbes 2009; Mainwaring et al. 2012). Moreover, it has been

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shown previously that the degree of asynchrony can be adjusted to the availability of food (Slagsvold & Lifjeld 1989; Nilsson 1993; Wiebe & Bortolotti 1994; Fleming et al. 1997; Eikenaar et al. 2003; but see Kontiainen et al. 2010; Parejo et al. 2012). Thus, by varying the onset of incubation, mothers may adjust offspring growth via asynchronous hatching in anticipation of the conditions expected during brood rearing (Magrath 1990; Wiebe & Bortolotti 1994; but see Wiehn et al. 2000), and thereby may also enhance their own probability of survival and future reproduction (Mock & Forbes 1994; Horak 1995; but see Stoleson & Beissinger 1997; Szollosi et al. 2007).

Many hypotheses have been proposed to explain why females start incubation before clutch completion (reviewed in Nilsson 1993; Stenning 1996). Some hypotheses suggest that the size hierarchy established by hatching asynchrony increases the fitness of both the parents and early hatched offspring. Among these, the best known and the most debated is the brood reduction hypothesis proposed by Lack (1947), which states that hatching asynchrony is advantageous in unpredictable environments. When food is plentiful, all offspring can fledge independently of hatching patterns (Forbes 1990; but see Amundsen & Slagsvold 1991). However, when food is scarce, later hatched offspring might be outcompeted by the older, earlier hatched siblings, and in turn quickly starve to death. Although under unfavourable food conditions hatching asynchrony might be detrimental for last-hatched offspring, it may have no or very small effects upon the early hatched nestlings. If parents invest the saved energy to rear the remaining nestlings, brood survival and nestling condition at fledging may be enhanced. Higher body mass and size of nestlings have been repeatedly shown to predict their subsequent survival and thus might be a good proxy for parental fitness (Pettifor et al. 2001). Moreover, if parents save resources by early elimination of some nestlings, those resources could also be invested in their own survival and future reproduction (e.g. Mock & Ploger 1987; Mock & Forbes 1994).

In the majority of empirical studies, two weak trends seem to emerge: first, synchronous broods produce more fledglings than asynchronous broods, and second, asynchronous broods produce heavier nestlings at fledging than synchronous broods (reviewed in Amundsen & Slagsvold 1991, 1998). Studies testing the adaptive significance of hatching asynchrony have shown that the relationship between the prevailing breeding conditions and the benefits of hatching patterns is complex (Forbes 1994; Amundsen & Slagsvold 1996; Szollosi et al. 2007; but see Magrath 1989). Although some experimental studies showed that asynchronous broods are more productive when food is scarce (Magrath 1989; Wiebe & Bortolotti 1994; see also Theofanellis et al. 2008), others have shown that nestlings from asynchronous broods suffered equally under both good and bad conditions compared to synchronous broods (Szollosi et al. 2007), and brood reduction occurred even when food was plentiful (Amundsen & Slagsvold 1991; Parejo et al. 2012). Since the number of starving offspring is sometimes greater than the number of offspring at a competitive disadvantage (e.g. Howe 1978; Horak 1995), it has been suggested that hatching asynchrony may not be essential for facilitating brood reduction (Clark & Wilson 1981). In addition, some studies found that partial brood starvation occurred in both asynchronous and synchronous broods (Howe 1976; Horak 1995; Kontiainen et al. 2010), suggesting some other factors were involved in nestling death, such as sibling despotism (Forbes 1994; Mock & Forbes 1994). Finally, there is some evidence that partial brood reduction increases future female survival (Horak 1995) or parental condition (Slagsvold & Lifjeld 1989), suggesting some advantages for parents rearing asynchronous broods. Other studies, however, found that parental survival is independent of hatching patterns (Stoleson & Beissinger 1997; Szollosi et al. 2007).

The aim of the present study was to test the effects of hatching asynchrony on offspring quality, rates of food provisioning and length of the nestling period as predicted by the brood reduction hypothesis. To this end, we performed a field experiment in a free-living population of great tits, *Parus major*, in which we simultaneously manipulated the onset of incubation and the rearing conditions for both parents and offspring by changing brood size. By removing eggs from the nest and returning them for incubation either simultaneously or sequentially, we created clutches that were incubated and hatched either asynchronously or synchronously. We measured the effects of experimentally induced hatching regimes (both asynchrony and synchrony) on average fledgling size, fledgling body mass and fledging mortality, as well as on parental effort and parental body condition in enlarged, control and reduced broods. We used brood size manipulation as a proxy for manipulations of food availability. It has been previously shown that brood size manipulation can successfully alter the food-provisioning rate to individual nestlings (Dijkstra et al. 1990; Martins & Wright 1993; Pettifor et al. 2001) and change the level of nestling competition (Neuenschwander et al. 2003), thus allowing an indirect but largely adequate test of the brood reduction hypothesis.

Based on the predictions of the brood reduction hypothesis, we expected hatching asynchrony and the resulting size hierarchy to be beneficial for parents under suddenly changing harsh conditions. Thus, under harsh conditions as induced by brood enlargement, we expected that hatching asynchrony should result in higher mortality in asynchronous broods owing to the death of the smaller, weaker nestlings compared to synchronous broods. In consequence, the average size and mass of nestlings in asynchronous broods should be greater than in synchronous broods after the death of the smaller, weaker nestlings, so that eventually asynchronous broods should fledge fewer but bigger nestlings than synchronous ones. On the other hand, under favourable conditions we expected hatching asynchrony to have neutral or negative effects, as proposed by Amundsen & Slagsvold (1991). In contrast, under control conditions, we expected either neutral or advantageous effects of hatching asynchrony.

METHODS

Biological Model

The great tit is a small resident passerine, a hole-nester that readily accepts artificial nestboxes for breeding and roosting. Great tits breed between March and July, and the start of breeding depends largely on spring temperature and the peak abundance of caterpillars (Nager & van Noordwijk 1992; van Noordwijk et al. 1995; Visser et al. 1998). Clutch size varies from four to 13 eggs (Slagsvold & Lifjeld 1990; Haywood & Perrins 1992). Only females develop a brood patch and hence incubate the eggs. Full incubation lasts on average 13 days and males provide food to the females during this period (Haftorn 1981). Hatching spread varies from 0 to 4 days, with a mean around 1.5 days (e.g. Haftorn 1981; Slagsvold et al. 1992; Amundsen & Slagsvold 1998; Tilgar & Mand 2006), and leads to a size hierarchy in which the last-hatched nestlings often die before fledging because of starvation (Horak 1995; Amundsen & Slagsvold 1998; Tilgar & Mand 2006). Although the role of hatching asynchrony in great tits has been widely studied and is still highly debated, its consequences for offspring phenotype and its adaptive function remain elusive. Some studies have suggested that increased hatching spread and lower fledging success of nestlings in clutches laid later in the breeding season might facilitate brood reduction if, as is likely, food is scarce late in the season (Barba et al. 1995; Cresswell & McCleery 2003). In

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