Hatching asynchrony as a bet-hedging strategy – an offspring diversity hypothesis

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Many birds begin to incubate before their clutch is full, which results in the chicks hatching at different times. I propose that hatching asynchrony could serve as an adaptive parental strategy to produce phenotypic variation in the offspring through asymmetric sibling competition. Producing diverse offspring that follow variable life history strategies might be a risk-spreading strategy in spatially and temporally variable environments.

In many bird species incubation begins before the clutch is full. Many hypotheses have been put forward to explain the evolution and maintenance of hatching asynchrony, but so far none of them has received strong support or rejection (reviewed by Magrath 1990, Stoleson and Beissinger 1995). The only points on which there is agreement seem to be that there may be numerous factors involved and that these factors are likely to vary among taxa and environments (Stoleson and Beissinger 1995, Stenning 1996). The advancement may have been slow because the hypothesis promoting most research on hatching asynchrony, the “brood reduction hypothesis” (Lack 1954), considered only the number of fledged chicks in relation to the degree of synchrony. Only quite recently has interest turned to the quality of the offspring along with quantity, which seems to be a promising approach (Amundsen and Slagsvold 1991, 1996, 1998, Forbes et al. 1997, 2002). In particular, it has been suggested that hatching asynchrony assures that at least some of the offspring are of good quality (the offspring quality assurance hypothesis, Amundsen and Slagsvold 1991).

I would like to expand the ideas developed so far by proposing that hatching asynchrony could serve as an adaptive parental strategy not only to assure high quality of few offspring but also to produce phenotypic variation in the offspring. Producing diverse offspring through asymmetric sibling competition might serve as a form of bet-hedging (risk-spreading) strategy (Slatkin 1974) in environments that are temporally and spatially variable. In the following, I will first briefly describe how hatching asynchrony could produce differential offspring. Second, I will discuss why this possibility may have been overlooked in the past and point out some recent work that give reason to change the current way of thinking. Along with that, I will put forward two examples of how hatching asynchrony might produce variation in life history traits that are known to be important in birds. Third, I will discuss some other recent findings that also could be interpreted as means for the parents to produce variation in the offspring. Finally, I will briefly discuss possible methods for exploring the idea that hatching asynchrony might serve as a bet-hedging strategy to produce diverse offspring.

Asymmetric sibling competition and differential development of chicks

Hatching asynchrony creates a size hierarchy among chicks of altricial birds in the nest (Lack 1954, Mock and Parker 1997). Often the largest chicks have an advantage in getting food in scramble competition or through direct monopolisation of the food items (reviewed by Mock and Parker 1997, Glassey and Forbes 2002). Individuals in different positions in the size hierarchy may therefore get variable amounts of food or nutrients (Glassey and Forbes 2002), while growth and developmental program are normally age-dependent (Schlichting and Pigliucci 1998). It has been repeatedly documented that variation in external conditions during growth and development produces phenotypic differences (Roff 1992, Stearns 1992) and has a considerable impact on vertebrate life histories (Price 1998, Lindström 1999). Differences in the amount or quality of food among chicks at certain developmental stages are therefore likely to make the chicks within a brood to develop differentially and invest differentially in certain functions in e.g. physiology (Saino et al. 2001) or morphology...
hatching asynchrony insuring that at least some of the offspring are of good quality (Amundsen and Slagsvold 1998).

Despite the promising first results, there may be some limitations for estimating recruitment from fledgling-mass dependent functions. Although it is a general finding in avian ecology that fledging body mass predicts future local recruitment probability (reviewed by Martin 1987), even the most extensive population studies are inevitably restricted to small geographical areas (Newton 1998). The local recruitment measured in the study population might therefore often be an inadequate measure of offspring survival and parental fitness, as in most cases only a fraction of the true survivors are within the reach of the researchers to capture in the restricted study area (Lambrechts et al. 2000). The characteristics of the dispersing individuals are rarely known, but some exceptions make the case in point. In a study on great tits it was found that fledging body mass predicts also natal dispersal from the birthplace (J.M. Tinbergen, pers. comm.). In one restricted study area the pattern was the usual, higher fledging body mass indicating higher recruitment probability to the local population. However, when recaptures of individuals from other, more remote, study areas were included in the analysis, the emerging pattern in recruitment was quite different. There were no more differences in recruitment as a function of fledging body mass, as the individuals with lower body mass at fledging had dispersed further away from their birthplace. Longer natal dispersal distances of lighter individuals may result from competitive inferiority (Verhulst et al. 1997), which could suggest that they will have lower future survival or reproductive success than philopatric individuals. However, this is not always the case, as sometimes survival even improves with increasing dispersal distance (Altwegg et al. 2000). These results indicate that the use of recruitment estimates would need to be corrected for probability of dispersal or else the importance of high body mass may be over-estimated. Higher variation in body masses of fledglings in asynchronous than in synchronous broods (Slagsvold et al. 1995, Forbes et al. 2002) suggests that individuals from asynchronous broods might have more variation in dispersal distances. There are also direct observations that hatching rank affects natal dispersal from the birthplace (Altwegg et al. 2000, Forero et al. 2002).

The timing of breeding is another important avian life history trait that can be affected by conditions experienced in the nest of birth. Another study on great tits showed that contrary to previous thinking, early start of breeding within one breeding season did not assure that the highest food demand of the brood would be met in optimal conditions (Nager and van Noordwijk 1995, Nager et al. 2000). Often the best breeding success was achieved by breeding in the middle of the breeding

Risk-spreading in space and time: dispersal and timing of breeding

One shortcoming of research on hatching asynchrony, as well as on many other avian life history traits, has been that even long-term experimental studies are likely to lack sufficient data and statistical power for definitive conclusions even if the results would be meaningful in evolutionary sense (Slagsvold et al. 1995, Amundsen and Slagsvold 1996). This is especially true for such essential measures as recruitment of the young to the breeding population or lifetime reproductive success of the parents, which would be more meaningful fitness-estimates than fledgling numbers (Newton 1989, Mock and Forbes 1994, Amundsen and Slagsvold 1996). Amundsen and Slagsvold (1996) suggested that this problem could be circumvented using fledgling-mass-dependent recruitment functions to estimate recruitment from asynchronous and synchronous nests. They presented such an analysis on the recruitment probability of great tit Parus major fledglings to the local breeding population and showed that the recruitment probability was less variable for fledglings from asynchronous than synchronous nests (Amundsen and Slagsvold 1998). This result led them to suggest that hatching asynchrony could be a bet-hedging strategy to assure higher geometric mean of fitness over the generations. In particular, they suggested that this is the result of

Since environmental conditions vary in space and time and breeding success depends on when and where an individual breeds (Newton 1998), parents can through hatching asynchrony produce offspring that for instance disperse over variable distances, lay their eggs at variable times, follow different life history strategies through their lives or are adapted to different environments. In this way, parents could diversify the outcome of their investment and make it more probable that at least some of their offspring are successful in life (Cohen 1966, Hamilton and May 1977, reviewed by Philippi and Seger 1989, Meyers and Bull 2002). These offspring are not necessarily the ones that hatch first. It is noteworthy that although the mortality of last-hatched nestlings is generally higher in asynchronous broods, the mean body mass of fledglings is higher in asynchronous than in synchronous broods (Amundsen and Slagsvold 1991). This indicates that the middle-rank or even low-rank nestlings are not necessarily starving (Slagsvold et al. 1995, Forbes et al. 2002), but sometimes the death of a last-hatched nestling may be unavoidable and allows easy brood reduction (Forbes et al. 2002).
Sibling competition and other ways to produce variation in the offspring

I suggest here that hatching asynchrony and the resulting asymmetric sibling competition produces phenotypic variation in the offspring. Another way of producing offspring diversity could be to produce genetically variable offspring through extra-pair fertilisations (Birkhead and Møller 1992). Furthermore, there is also increasing evidence that female birds induce within-brood variation in their offspring already through differential allocation of resources like hormones, nutrients, or immune factors, to eggs (reviewed by Schwabl and Lipar 2002). In some studies this kind of allocation has been attributed to “within-brood favouritism”, the idea being the same as in the offspring quality assurance hypothesis (Reed and Vleck 2001, Saino et al. 2002). On the contrary, some other studies have suggested such allocation patterns to compensate, for example, the supposed negative effects of hatching asynchrony (Schwabl 1993, Royle et al. 2001) or smaller size in sexually size dimorphic species (Anderson et al. 1997). Because the patterns are contrasting, it might be worth consideration that also these differential maternal effects could be useful in producing variation in offspring without being direct favouritism. However, in general the maternal effects through allocation into eggs seem to have much less effect on chick characteristics and performance than sibling competition through hatching asynchrony (Mock and Parker 1997, Christians 2002, Glassy and Forbes 2002, but see Badyaev et al. 2002). It might be interesting to examine whether the degree of hatching asynchrony is higher in species exhibiting low frequency of extra-pair fertilisations or low within-brood variation in allocation to eggs. This could elucidate how common it is for birds to produce diversity in offspring.

Final remarks

The aim of this paper is not to claim that bet-hedging would be the total explanation for the evolution of hatching asynchrony instead of all other factors; there are probably a number of factors involved (Stoleson and Beissinger 1995, Forbes et al. 2002). Furthermore, the ideas presented here are in close congruence with the offspring quality assurance hypothesis (Amundsen and Slagsvold 1991, 1996, 1998). Hatching asynchrony can be an effective way to produce offspring that are of “good quality” in the traditional sense (have a high probability of recruiting to local population), and offspring that will disperse and follow variable life history strategies. The difference between the ideas is that while Amundsen and Slagsvold (1998) suggested that hatching asynchrony ensures a safe bet for the parents by enhancing the success of the first-hatched young, I suggest that the purpose is to ensure a safe bet by producing diverse young, some of which will succeed. These are not always the ones that hatch first. The implication of the new idea for empirical research is that when the conditions for future breeding vary in time and space, we should change the perspective and consider offspring variability in multidimensional space instead of focusing on “quality” on only one scale.

Indirectly the “offspring diversity hypothesis” presented here could be tested by relating the degree of hatching asynchrony to environmental variation in phylogenetic comparison, or preferably, in comparison of different populations of the same species. The prediction is that the degree of hatching asynchrony increases with increasing environmental variation, but this prediction holds for many other hypotheses, too. If hatching asynchrony was to produce phenotypic variation as in a risk-spreading strategy, we should find the geometric mean of fitness higher for producing asynchronous broods than synchronous broods (Philippi and Seger 1989). This was already found for the great tits (Amundsen and Slagsvold 1998) with the limitation that dispersal could not be controlled for. A first step might be to assess the effects of hatching rank and degree of asynchrony on offspring recruitment and number and quality of grand-offspring when dispersal is accounted for. In order to make definitive conclusions this should be done through careful experimentation to control for possible condition-dependent parental effects on hatching patterns (Amundsen and Slagsvold 1998). Sex-specific effects of hatching order on fitness parameters make the picture even more interesting (Slagsvold 1990, Badyaev et al. 2002, Forbes et al. 2002, Forero et al. 2002), but also more complicated. The experimental design should take into account sex ratio, laying order, a possible interaction between sex and laying order, and genetic variance within a brood. Therefore it might be useful to manipulate the degree of hatching synchrony by experimentally advancing or delaying the onset of...
incubation (Howe 1976) instead of swapping chicks between nests when the primary interest is on hatching spread per se. This approach would help to avoid inflation of within-brood variances in offspring traits due to genetic effects, and the sex ratio or laying-order related variation would not be distorted. These kinds of experiments with subsequent follow-up of individual life histories are difficult to accomplish with wild populations, but they might offer the best way to advance our understanding on which factors really are important in the evolution and maintenance of hatching patterns.

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References


