



The adaptive benefit of hatching asynchrony in wild zebra finches

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The evolutionary consequences of parent–offspring conflict have received considerable attention, yet the extent to which parent–offspring conflict influences life history traits remains uncertain. In particular, it is unclear whether hatching patterns are parental strategies to manipulate competitive dynamics among offspring, or whether they are instead consequences of physiological or ecological variables affecting the payoffs of adjusting the onset of incubation. Here we describe an experiment in which we manipulated the hatching pattern of wild free-living zebra finches. We examined the consequences of hatching pattern on parental feeding behaviour and sibling competition, with the aim of identifying selective pressures that underlie differing hatching patterns. Increasing hatching asynchrony reduced the overall quantity of food that parents delivered and the equitability of its distribution among nestlings compared with synchronous broods. However, for each unit of food received, the begging intensity of nestlings from asynchronous broods was lower. As a consequence, the growth rate of first-hatched nestlings in asynchronous broods was significantly greater than those in synchronous broods, and there was no significant difference in growth rate between last-hatched nestlings in asynchronous broods and nestlings from synchronous broods, even though they received less food overall. The reduced scramble competition and energy wasted on begging behaviour in asynchronous broods supports the sibling rivalry hypothesis, suggesting an adaptive function for hatching asynchrony in wild zebra finches.

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Family conflicts over the level and distribution of parental care occur because offspring are selected to demand a higher level of resources than the parent may want to provide in the context of their own long-term interests (Trivers 1974). One mechanism through which avian parents are able to gain greater control over their offspring and manipulate the distribution of resources among their brood, is through the formation of size hierarchies created by the asynchronous hatching of nestlings (Magrath 1990). A high degree of hatching asynchrony can appear to be maladaptive in some species, as the resulting competitive disadvantage of the younger and smaller offspring can reduce the number and condition of surviving nestlings (Magrath 1990; Stoleson & Beissinger 1995; Stenning 1996). However, as parental incubation behaviour largely determines the degree of brood hatching asynchrony (Lack 1947), then we may expect hatching patterns to reflect an optimal strategy for parents. Indeed, the selective feeding by parents of last-

hatched crimson rosella, *Platycercus elegans*, nestlings suggests that a reduced growth and survival of younger nestlings is not an inevitable consequence of hatching asynchrony (Krebs 2001).

There are two broad sets of hypotheses attempting to explain the incidence and variation of hatching asynchrony in avian species (Stoleson & Beissinger 1995). The first set views age and size hierarchies among nestlings as an adaptive parental strategy: for example, through brood reduction in poor ecological conditions (Lack 1954; Huxell 1972; Hahn 1981; Slagsvold & Lifjeld 1989). The second set of hypotheses instead views the early onset of incubation by parents as adaptive, with the asynchronous hatching of nestlings then being an inevitable consequence of this (Ricklefs 1969; Clark & Wilson 1981; Arnold et al. 1987; Cresswell & McCleery 2003).

The sibling rivalry hypothesis states that parents create asynchronous broods to reduce sibling competition among nestlings and manipulate food distribution during harsh conditions (Hahn 1981). The preferential feeding of the older first-hatched nestlings would then allow parents to carry out a more energy efficient form of brood reduction, by having the smaller last-hatched nestlings die first (Lack 1947, 1968). The size hierarchy among nestlings established by asynchronous hatching has been shown to reduce scramble competition among nestlings, and it has been hypothesised that reducing sibling competition may also be beneficial to both the parents and the

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offspring by reducing the energy wasted on begging behaviour (Hahn 1981). Extensive work has been carried out to try and identify the cost of begging, which is a requirement for models describing nestling begging either as an honest signal of need (Godfray 1991, 1995), or scramble competition, where parents instead passively feed the nestlings presenting the greatest stimulus (Parker et al. 2002). Initial work suggested that the energetic cost of begging behaviour was relatively low (Chappell & Bachman 2002), but increased begging has now been shown to reduce growth rates (Kilner 2001; Rodríguez-Gironés et al. 2001) and immunity (Moreno-Rueda 2010), increase predation rates (McDonald et al. 2009), and increase the risk of falling out of the nest (Bize & Roulin 2006). In the tree swallow, *Tachycineta bicolor*, for example, increased begging does not appear to affect the growth rate of nestlings (Leonard et al. 2003), but it does lead to increased predation (Leech & Leonard 1997) and increased total energy expenditure of nestlings (Leech & Leonard 1996). If hatching asynchrony reduced the overall amount of energy spent on begging and sibling competition, the parents would get a higher level of return on the food they bring to the nest in terms of offspring growth and development.

The zebra finch, *Taeniopygia guttata*, is a granivorous, socially monogamous passerine commonly used as a model system for the study of intrafamilial conflict (e.g. Royle et al. 2004, and parental effects reviewed in Griffith & Buchanan 2010). This species is typical of other small passerines with respect to hatching pattern, with broods showing variation in hatching times across a range, from several hours up to five days in both wild and captive conditions (Zann 1996; Rutkowska & Cichón 2005). However, the results from studies examining the consequences of hatching pattern on captive domestic populations have been mixed, with no study directly examining how differing hatching patterns influence sibling competition and the distribution of food among nestlings. Furthermore, a recent study that manipulated hatching asynchrony in wild free-living zebra finches found no effect of hatching pattern on nestling mortality (Mainwaring et al. 2010). Identifying parental response to nestling begging behaviour, as well as the costs and benefits of parental care and sibling competition across differing hatching patterns, will provide valuable insight into the selective pressures underlying the variation in hatching pattern in this species.

We manipulated the hatching pattern of wild free-living zebra finch broods, examining the consequences of hatching pattern on parental provisioning behaviour, sibling competition, nestling begging behaviour and overall growth and survival. Furthermore, as nestlings within an asynchronous brood differ in size, we determined the relationship between nestling size and the quantity of seed transferred in a single parental regurgitation, to understand how nestling size asymmetry contributes to equitability in food distribution and to permit accurate measurements of parental response to nestling begging.

METHODS

Hatching Pattern Experiment

Study species and site

Wild zebra finch populations breeding in nestboxes at the Fowlers Gap Arid Zone Research Station, New South Wales, Australia (31°05'S, 141°45'E) were used in this study, from September to November 2008. Nestboxes were located at Saloon Tank (31°03'90''S, 141°50'60''E) and West Mandelman (31°01'S, 141°50'E; see Griffith et al. 2008 for more information on this study site).

Monitoring breeding attempts and setting up treatments

Empty nestboxes were checked every 3 days, but once nest building was initiated the boxes were checked daily. For 20 nests, we

removed eggs on the day they were laid and replaced them with dummy eggs made from white modelling clay. Each egg was placed into an artificial incubator on the day it was laid (Brinsea Octagon 20, DX auto turn; Brinsea Products, Winscombe, U.K.) and maintained at 37.7 °C and 60% (range: 50–70%) humidity. Nests were randomly assigned to either a synchronous or asynchronous hatching pattern treatment. On hatching, nestlings were weighed and individually marked by cutting the down on either their head, back or flanks and randomly assigned to either a synchronous or asynchronous treatment nest other than that of their genetic parents, with a maximum of two genetic siblings in each brood. Cross-fostering nestlings controlled for any intrinsic differences between broods, and although this design did reduce the level of relatedness between nestmates, this effect was equal across both treatments. Synchronous broods contained nestlings that hatched within an 18 h period of one another (as defined by Slagsvold 1990). Asynchronous nests initially had two or three nestlings assigned to them and then a further two or three assigned to them 36–48 h later. The mean mass of nestlings when placed into the synchronous treatment nests was 0.67 g ± 0.09 (SD); range 0.45–0.91 g. The mean mass of nestlings when placed into the asynchronous treatment nests was 0.68 g ± 0.07; range 0.50–0.86 g. However, when the second group of nestlings was added 36–48 h later, the mean mass of the nestlings from the first group was 1.97 g ± 0.29; range 1.16–2.92 g. A further eight clutches were left to hatch naturally in the nest in order to obtain the natural hatching pattern (hatching spread = 18.0 ± 6.4 h, $N = 8$). However, when these clutches hatched, the nestlings were subject to the same experimental conditions and procedures described above, with cross-fostering occurring across groups (i.e. between incubator-hatched nestlings and in-nest-hatched nestlings). Nestling mass at hatching did not significantly differ between nestlings that hatched in the incubator and nestlings that hatched in the nest (t test: $t_{100} = 0.631$, $P = 0.429$). A total of 28 nests was included in this study: 12 with a synchronous hatching pattern and 16 with an asynchronous hatching pattern. There was no significant difference in brood sizes between treatments (GLM: hatching pattern: $F_{1,26} = 0.1$, $P = 0.809$).

To obtain data on parental feeding behaviour, broods were filmed when the oldest nestling in the nest was between 7 and 9 days old, by attaching an infrared camera (colour CCD camera HK-C3, Handykam, Hayle, U.K.) to the inside of the nestbox lid and connecting it to an external hard drive (Archos 605, 160 GB memory). Cameras were placed in nestboxes 24 h before filming to allow birds to habituate to the presence of the camera. Videos were programmed to record for 8 h; however, owing to the sensitivity of the hard drives and batteries to the hot field conditions, recordings varied from 3 to 8 h per nest, with a mean of 5.01 h ± 2.16 SD ($N = 28$). Overall, 28 nests were filmed, providing a total of 133 h, with no significant difference in duration of recording between treatments (t test: $t_{26} = 0.404$, $P = 0.531$). Nestlings were individually identified on camera by marking them with one to three dots of nontoxic white correction fluid, either on their head or back. Markings lasted for a full day of filming but faded after 24 h, when nestlings were still identifiable by the pattern of down trimming. When nestlings were 12 days of age, they were weighed, had their right tarsus measured and were ringed.

Quantifying parental care

For each parental visit to the nestbox, entry time, duration of time in the box, parental behaviour, parental sex and nestling begging behaviour (see below) were recorded by direct observation of the video playback in real time (using Videolan's, VLC 1.0.3 media player). Parents gave multiple feeds to different nestlings within a single feeding visit to the nest, so the number of individual feeds (defined by the lowering of the parents beak to make contact with a nestling's mouth, followed by several heaving motions as food is transferred), the number of regurgitations given at each individual

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