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Chick Development and Asynchroneous Hatching in the Zebra Finch (*Taeniopygia guttata castanotis*)

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The mode of hatching in birds has important impacts on both parents and chicks, including the costs and risks of breeding for parents, and sibling competition in a clutch. Birds with multiple eggs in a single clutch often begin incubating when most eggs are laid, thereby reducing time of incubation, nursing burden, and sibling competition. In some songbirds and some other species, however, incubation starts immediately after the first egg is laid, and the chicks thus hatch asynchronously. This may result in differences in parental care and in sibling competition based on body size differences among older and younger chicks, which in turn might produce asynchronous development among siblings favoring the first hatchling, and further affect the development and fitness of the chicks after fledging. To determine whether such processes in fact occur in the zebra finch, we observed chick development in 18 clutches of zebra finches. We found that there were effects of asynchronous hatching, but these were smaller than expected and mostly not significant. Our observations suggest that the amount of care given to each chick may be equated with such factors as a camouflage effect of the down feathers, and that the low illumination within the nest also complicates the determination of the hatching order by the parents.

Key words: hatching asynchrony, development, parental care, sibling competition, zebra finch, chick down feathers

INTRODUCTION

The development of avian chicks is controlled by the parents in a variety of ways. In some species, during egg production mothers are able to control, e.g., the volume of the egg yolk, which is necessary for nutrition of the embryo, or the hormone level of individual eggs. It has also been shown that in some cases the size of the eggs depends on the order of laying, the first egg being bigger than the following, etc. There are also cases where the last egg layed is the biggest one. These strategies can be seen as to install some rank order between the chicks (some of the chicks are more fit than the others and have a higher chance to survive) and to optimize the parental investments in some way, to guarantee the survival of the maximum number of offspring and to keep the costs of rearing to a minimum (Lack, 1968; Slagsvold, 1986; Williams, 1994; Adkins-Regan et al., 2013; Deeming and Reynolds, 2015).

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Control of the offspring development continues after hatching. Many birds, including nearly all precocial species, wait to the start of incubation until the last egg is laid. By this strategy, the offspring hatch synchroneously because the embryo cannot start to develop without incubation. This may have a direct advantage for parents because the period where they have to care for food is shorter compared with the strategy of most avian species (Lack, 1968) to begin incubation after laying the first egg or at least before laying the last one. Starting incubation before the last egg is laid leads to asynchronous hatching of the offspring, the amount of asynchrony depending on the time of the incubation start. This strategy clearly confers an advantage for the early hatching chicks (Leonard and Horn, 1996; Glassey and Forbes, 2002) as they are bigger than their younger nestmates and may more easily receive food from their parents because of their bigger beaks and greater ability to compete for the best places during feeding. Likewise, early hatching chicks are the first to develop begging calls. All this may even more increase the difference in the amount of food that is provided to each individual nestmate, the younger being

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less fed than the older chicks, which in turn may reduce the probability of survival of the younger. Besides the brood reduction theory, proposing the idea that asynchronous hatching helps to adjust the number of offspring according to the availability of food (Lack, 1954), other explanations (more than 10 hypotheses) have been raised, including life history consequences for parents and offspring, or effects on predation (Hussell, 1972; Clark and Wilson, 1981; Magrath, 1990; Mock and Parker, 1997, 1998; Slagsvold et al., 1995; Stoleson and Beissinger, 1995).

The most extreme consequences of asynchronous hatching have been reported in raptors, egrets, and other shore birds (Lack, 1968; Magrath, 1990; Tingay and Katzner, 2010). In several species, the older chicks kill the younger ones if food availability is not sufficient to nourish all offspring (Gargett, 1978; O'Conner, 1978; Mock, 1984; Fujioka, 1985a; Drummond et al., 1986; Simmons, 1988; Mock et al., 1990). For example, siblicide occurs regularly in eagles, where only the first hatching chick survives, even though two or, in rare cases, three eggs are laid. The second one only has a chance if the first dies, and the third only if both of its elder siblings die. In black eagles (*Aquila verreauxii*), it has been observed that in only one of 200 observed cases did a second fledgling survive (Simmons, 1988). In some egrets and boobies, which lay between two and five eggs, the two eldest siblings attack and often kill the younger ones (Mock, 1984; Fujioka, 1984, 1985a, b; Mock, 1987; Mock et al., 1990). For the great egret (*Ardea alba*) and the cattle egret (*Bubulcus ibis*), it has been observed that the parents do not intervene when the elder offspring kills the younger one (Mock, 1984; Fujioka, 1985a). In passerines, such drastic events have not been described. However, as already mentioned above, there are differences in the magnitude of asynchrony. Most passerines hatch synchronously, but there are also cases of strongly asychronous hatching (Lack, 1968; Clark and Wilson, 1981; Slagsvold, 1986; Magrath, 1989).

To manipulate the treatment of the nestlings depending on the sequence of hatching deserves attributes that allow the parents to identify the position of the young chicks within the hatching order. One such distinguishing attribute could be the size of the young, at least in species that grow rapidly and have a relatively short nestling period. Another attribute could be the mouth markings which have been shown to enhance the parent's effort of feeding (Immelmann et al., 1977). It has been established that mouth markings differ between species and thus might help parents to avoid feeding nonconspecific young in cases where different species occupy the same biotope (Payne, 1977; Goodwin, 1982) and also to detect parasitic intrusions (Davies, 2000; Tanaka and Ueda, 2005). However, it has not yet been shown that mouth markings are used for individual recognition of siblings. Body size, which differs according to age, or differences in the development of the down feathers and the adult plumage are often used by ornithologists to determine the hatching order of nestlings, but whether these parameters are used by the parents is not known as yet.

Zebra finches (*Taeniopygia guttata castanotis*) begin incubating when the first egg is laid, and the chicks hatch asynchronously. This asynchronous hatching has been described in the wild as well as in captivity, and it has been shown that the asynchrony is bigger in the aviary than in the wild (Immelmann, 1962; Amundson and Slagsvold, 1991; Zann and Rossetto, 1991; Zann, 1996). It is as yet not known which of the above hypotheses may be suitable to explain why zebra finches belong to the few passerine species exhibiting strong hatching asynchrony.

The strategies of the parents to control offspring development are similar to those of other birds, control of egg yolk volume has been shown as well as that of the hormone level of individual eggs (Williams et al., 2005; von Engelhardt et al., 2006; Adkins-Regan et al., 2013). Likewise, the strategies that chicks employ to increase the probablity of receiving food are comparable to those of many other species, including strong gaping and effective mouth markings as well as begging calls (Immelmann et al., 1977). If there is sufficient food, as is the regular case in captivity, chicks do not die from a lack of nutrition. This may indicate that the effort of the parents to create a rank order between the offspring is only an emergency program that is in most cases is not necessary, or it could indicate that the effect of ranking the offspring into more and less survivable individuals is attenuated by some behavioral or morphological traits of the offspring (Zann, 1994, 1996).

To develop a clearer understanding of such possible traits, we observed the development of zebra finch chick plumage and appearance qualitatively, measured the weight development of the chicks to determine whether the older chicks have weight advantages over the younger ones. We also provide additional data concerning zebra finch post-hatch development, which may contribute to a better understanding of the mechanims and consequences of asynchronous hatching, and we speculate on the role of mouth markings on the feeding behavior of the parents.

MATERIALS AND METHODS

The observations were performed at two places, the Ethology department of the University of Bielefeld, Germany, and the RIKEN research center at Wako, Japan. At both places, zebra finch pairs were housed in cages (size in Bielefeld, 82 × 40 × 30 cm (w/h/d) which could be separated into two equal compartments, size at RIKEN 37 × 42 × 44 cm (w/h/d)) on the actual natural light - night cycle, approximately 14L:10D. There was unlimited access to food (egg food, minerals, seed mixture for finches) and water. A nest box (14 × 14 × 14 cm (w/h/d)), entrance size 7 × 14 cm) was provided in Bielefeld, a spherical "pot nest" (13 × 15 cm (diameter/depth)) at RIKEN.

Nesting material like coconut fibers were also provided. Despite the two types of nesting aids, the nest construction was not different between the Bielefeld and the RIKEN experiments. The birds in most cases constructed a roofed nest with a small circular entrance. Because the results of our observations did not differ between the two rearing conditions, we do not present the data separately.

The pairs in most cases began to build a nest shortly after the nest boxes and the nesting material was provided. Egg laying and incubation started after finishing the nest, and the young were hatching after about 12 days of incubation. From that time on, we checked and recorded the development and the weight of the birds every day. These checks were made around 5–6 pm, as there is an activity peak of the parents at that time and the chance to disturb them at the nest was minimal. The parents were separated from the nestbox, photos were taken from each single chick and the whole clutches, and we touched the beak of each chick and recorded

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whether it responded with gaping or an other response. Thereafter, the weight of each offspring was determined. We did not make more measurements because we wanted to keep the development of the birds as natural as possible, and because the young birds are very fast loosing their temperature (Randall, 1943).

From one clutch, we took photos and videos (Canon IXY DIGITAL 2000 IS) of young birds transferred to an open nest to obtain additional information about their gaping and fear behavior. For the same purpose, we placed a small color video camera (Keiyo AVC666SN/F36) at the nest entrance of another clutch to record with digital video recorder (SONY GV-D1000) the nestling behavior without disturbance within the nest.

Differences in quantitative results were evaluated by a two way ANOVA (Excel statistics 2010 for Windows (SSRI, Social Survey Research Information Co. Ltd., Japan)) with age and rank order as factors, and individual differences in the data were tested by posthoc SCHEFFE-test. A non paired t-test was applied to the data concerning the comparison of the birth weights of chicks surviving until the end of the study and chicks which died before the study was finished.

RESULTS

Development from hatching to fledging

Our study is based on data from 63 zebra finch chicks reared in 18 clutches, that is on average 3.5 ± 1.3 hatchlings per clutch. Figure 1 shows an overview of the hatching days within each clutch, and also shows which of the birds died in the course of the study and which survived until the time when the youngest chick was 30 days old. The average time span of asynchronous hatching was 3.1±1.6 days. There could be 1–3 hatches on one day, the average number of hatches was 1.2.

Figures 2 and 3 illustrate the results of our qualitative assessment of zebra finch chick development. It turned out that the hatching rank order of the young birds could be determined on the basis of the shape, the size and the plumage of the young, even when more than one chick hatched at one day. However, it was necessary for this purpose to take the animals out of the nest (Fig. 2).

After hatching, the young birds for several hours remained in an almost embronic posture, the down feathers were still wet, and no begging calls were detected (Fig. 2A). During the day, the body was stretched, the downs became dry, but the skin remained wrinkled as it was at birth (Fig. 2B–D).

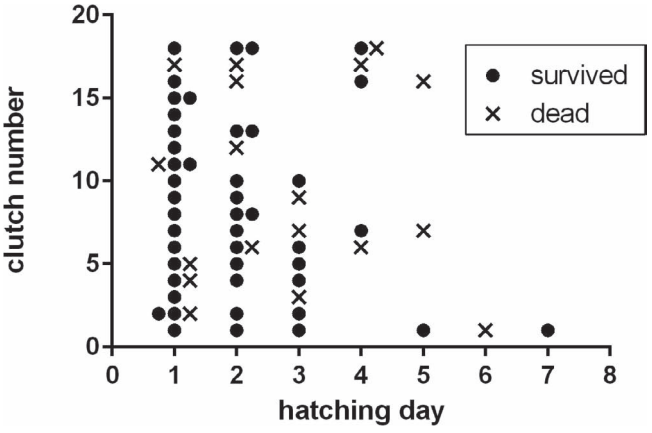


Fig. 1. Overview of the hatching days of the individual chicks within each of the 18 clutches (Y-Axis: Clutch 1–18) observed in this study. Filled circles indicate that the bird survived until the end of the study (when the youngest chick was 30 days old), "x" indicates that the bird died in the course of the study.

Although the birds were at this stage not able to roll themselves over using their wings, the first begging behavior (raising the head in an upright position and gaping) was observed. Thus, the neck muscles were obviously already strong enough to raise the head almost independent of the body position, and the birds were already able to determine the vertical, probably by perception of gravity. Gaping was not spontaneous, it was only shown after touching the rim of the beak. Later at the same day, wrinkles at the skin disappeared so that the skin was looking smooth and shining (Fig. 2C, D).

At three days, the first begging calls were uttered, but begging was not regularly accompanied by calls. Touching the beak at this age resulted in an enhancement of begging (gaping) behavior and of the utterance of begging calls. At day 5, the weight was around two grams. Growth was continuing steadily, the chicks got more and more fat especially round the neck and the rump (Fig. 2E, F). Gaping reactions to tactile stimuli became more reliable. Around day 6, stimuli from outside the nest, like handclapping or other vibration, sometimes inhibited begging, indicating that the acoustic and the somatosensory system was improving. Reactions to beak touching were somewhat reduced.

At day 8, the eyes began opening and the direction of gaping was no longer vertical, but was rather directed towards the nest entrance, probably because this was the direction from which light entered the nest. At day 10, the first feathers appeared, the chicks were able to move around, to roll over with help of their wings, the weight had increased to 6–8 g (Fig. 2G, H). Reactions to touching the beak disappeared. At day 12, the eyes were fully open and the birds began to attend to visual stimuli. At day 13, first fear reactions (moving away from the nest entrance) to outside noise could be seen. At day 15 (Fig. 2I, J), the downs were almost lost, and fear reactions to new stimuli increased. Weight was around 8.5 g. At day 18 (Fig. 2K, L), the down feathers were completely replaced by the new feathers. The distance call was uttered in the proper social context, meaning that it was uttered when the parents were not inside the nest and called, or appeared at the nest entrance. Fledging started, and continued until day 19. All chicks showed this developmental pattern regardless of the hatching order. Usually, the first fledglings returned to the nest until the youngest sibling had also fledged, in some cases we observed chicks resting in the nest until day 25 (Fig. 3F).

Determination of hatching order under normal dim light conditions

As already mentioned, the morphological and behavioral features described above could be related to the single chicks only if they were taken out of the nest. There were two reasons. First, zebra finches prefer closed nests, which are in their natural habitat located in tree burrows, or in nests built by weaver birds (Immelmann, 1962). The illumination within these nests is very low. Second, as demonstrated in Fig. 3, for about 14 days after hatching of the first chick, the single individuals were difficult to discern within the nest

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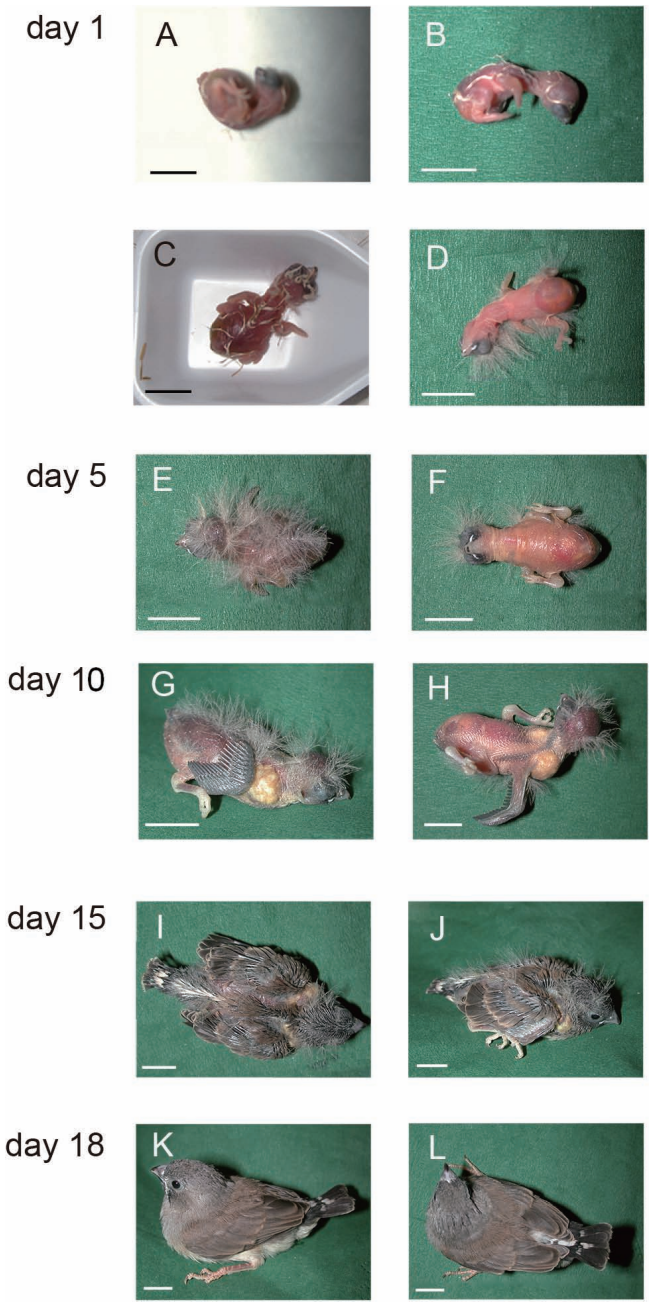


Fig. 2. Appearance of the zebra finch chicks at different ages, two images for each age except day 1 with four images . Note that there is in the first days a strong difference of plumage development between back and belly. Further description see text. Magnification bars: 1 cm.

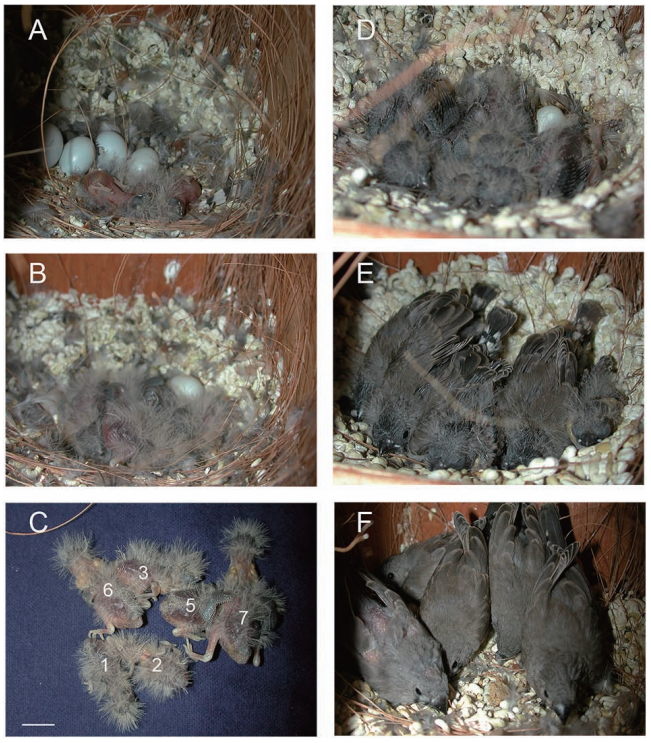


Fig. 3. **(A)**, **(B)**, **(D)**, **(E)** Young chicks of different ages within the nest. Note that the photos were taken with help of a flashlight. Normal light conditions within the nest are illustrated in figs. 4B and 4C. 3C, the same birds as in **(B)** outside the nest to illustrate the body size differences which are not visible in **(B)**. **(A)** three chicks, day 3/2/1, **(B)** six chicks, day 7/6/5/3/2/1, weights in grams: 3.93, 3.13, 3.08, 2.05, 1.55, 1.19 g. **(C)** same chicks as in **(B)**, the age of each individual chick is shown in the figure. **(D)** five chicks, day 11/10/9/7/5, **(E)** five chicks, day 17/16/15/13/11, **(F)** five chicks, day 25/24/23/21/19. Note that the four oldest birds in 3F had already left the nest, but returned until the youngest chick fledged. Magnification bar: 1 cm.

because the down feathers, which are mainly on the back of the birds, obscured the view to the body of the animals and let appear all the birds as one big mass (Fig. 3A, B, C). One has to keep in mind here that the photos of Fig. 3 were made with flashlight illumination; under “normal” light conditions the camouflage effect is even stronger (see Fig. 4B and C). Later on, when the older animals started growing adult feathers, the birds were more easy to separate from each other. In addition, the older birds started to align, the head pointing to the nest entrance (Fig. 3E). The younger birds also aligned, but often the head pointed away from the nest entrance. Finally, all birds including the youngest were aligned with the head towards the nest entrance.

Features which could probably help to identify the chicks even with dim light and at ages where the chick feathers obscured the body contours are the mouth markings which are of quite strong contrast at least under good illumination. Figure 4A shows young gaping nestlings transferred to an open nest for photography. In this case, with good illumination, the gaping beaks are clearly standing out against the background of the plumage. One can clearly identify the contrasting pattern of spots within the gape, and the white rim of the open beak. The mouth markings did not appear to be very different between ages, except that the white rim along the beak basis is slightly more visible in the younger chicks. However, the size of the open beak is quite different and corresponds with the age of the chicks, making the hatching order is quite easy to discern (see Fig. 4A).

Our photos taken under dim light illustrate that some of the features described above remained visible also in such condition. One is the bright white color of the flanges (the rim of the beak) which even in the dark is visible when the chicks are gaping (Fig. 4C with arrows). Also, if the beak is closed,

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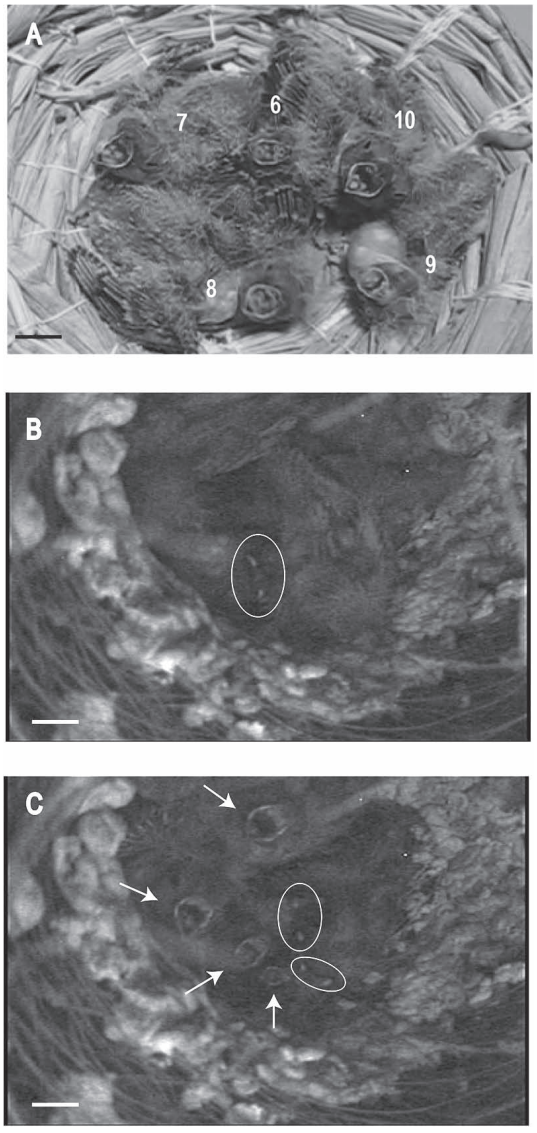


Fig. 4. The role of mouth markings for the recognition of zebra finch chicks within the nest. **(A)** Birds transferred into an open cup. Hatching order (numbers indicate the age) can be determined by beak size. **(B)** Birds in a closed nest, it is impossible to differentiate single individuals except when the head is raised. In this case, the white beak corners are visible (open oval). **(C)** The same nest with fledglings gaping (arrows) or raising the head without gaping (ovals). Now the individuals can be distinguished; but it is still difficult to put the birds into the correct hatching order. Magnification bars: 1 cm.

part of the white rim in the form of two white spots in the two corners of the beak are visible under dim light conditions, when the chicks are laying on the back and the beak is oriented upwards (Fig. 4B, C with open oval). These marks can also be seen by the parents, as they are often pecking at these spots, which results in a gaping response of the touched chick. Astonishingly, the mouth markings which are quite conspicuous under bright illumination (Fig. 4A) are not easy to discern with low illumination (Fig. 4B, C). Thus, under the more natural dim light conditions, it may be mainly the size of the open gape as defined by the white flanges,

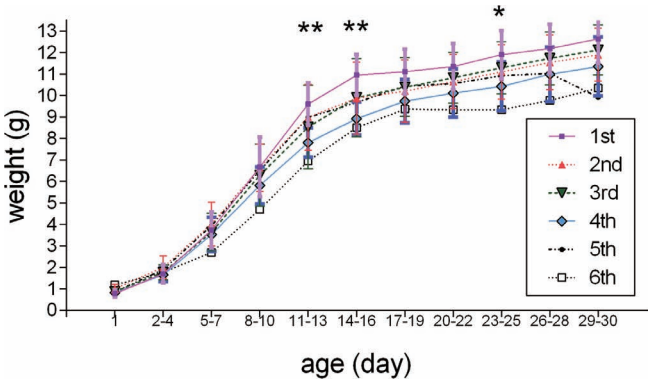


Fig. 5. Weight development of the chicks. "1st" to "6th" with different symbols: hatching order within the clutch. Means and SD's. *, $P \leq .05$, **, $P \leq .01$. Other explanations see text.

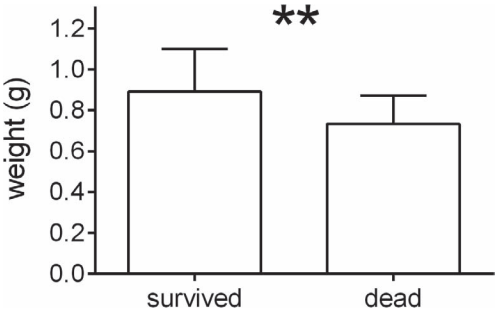


Fig. 6. Survival rate may depend on weight at birth. Means and SD's. **, $P \leq .01$.

and not the body size of the birds and/or the markings within the gape that help the parents to determine the hatching order of the young.

Weight development and survival rate

Figure 5 shows the weight development of the chicks of the different hatching ranks. We combined the measurements of three consecutive days to one data point to smooth the curve, and ranks five and six were not included into the statistical tests because of too low numbers. In general, the growth curve has a sigmoidal shape in all groups with a strong weight increase up to days 11–13, and a flattened slope thereafter. The 2way ANOVA indicated that the overall increase of weight with age was significant, and revealed significant differences due to the hatching order (ANOVA, f1 (hatch order) $F_{3,428} = 15.946$, $P < 0.0001$, f2 (age) $F_{10,428} = 501.296$, $P < 0.0001$). There was no interaction between factors (f1 $\times$ f2, $F_{30,428} = 0.91$, $P = 0.604$). The Scheffe's multiple comparison also revealed that the differences between a given rank (1–4) and the next were significant with the exception of the second to the third rank (1–2: $P = 0.028$, 1–3: $P = 0.004$, 1–4: $P = 0.000$, 2–4: $P = 0.002$, 3–4: $P = 0.023$, 2–3: $P = 0.918$). The chicks that hatched first showed a stronger growth than the others, the weight difference between the first and the fourth rank was significant at days 11–13 (simple main effect, Scheffe's posthoc test $P = 0.006$), days 14–16 ($P = 0.001$), and days 23–25 ($P = 0.038$).

Of the young birds, 27% died before day 30 when we

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stopped the observations. 14 of the 17 birds which died were less than seven days old, the other three died between day 15 and day 20. The latter showed a weight reduction from day 14 on. Interestingly, the probability to die depended on the weight of the chicks at the day of hatching. The mean weight of the birds surviving until day 30 was 0.89 ± 0.03 g, that of the birds which died until day 30 was 0.73 ± 0.03 g (means ± SD, Fig. 6) The difference was statistically significant (t-test, two sided, $P = 0.0071$). All birds that reached the age of 30 survived at least until day 100.

DISCUSSION

Our observations of zebra finch posthatch development support and extend those of previous reports. The onset of reactions to sensory stimuli was in a sequence of somatosensory–acoustic–visual, as described by Bischof and Lassek (1985). The present observations add some information about motor development of the hatchlings, again showing some sequence in development starting with the ability to gape, then to raise the head vertically, and finally to rotate the body with help of the wings, every step improving the begging display.

Clutch size and hatching time in our study was comparable to those obtained in other studies (Frith and Tilt, 1959; Skagen, 1988; Zann 1994, 1996). Variation may be due to food amount or diet (Williams, 1996), differences in social stimulation (Waas et al., 2005), geographic effects (Lack, 1968; Ricklefs, 1980) or effects of inbreeding (Forstmeier et al., 2007), but the clutch size in our study did not deviate enough from other studies to warrant discussion here.

The variability of hatching time (Fig. 1) was also comparable to previous studies (Immelmann, 1962; Skagen, 1988; Zann and Rossetto, 1991; Zann, 1996; Gilby et al., 2013). On average, one egg is layed each day, but the variability is big. Up to three chicks hatched in one day in our study (Immelmann (1962) even reports four chicks at one day), and there could also be gaps of two days between two hatches. The reason for this variability is not clear. Temperature may have some effect (Zann and Rosetto, 1991), but this idea is based on anecdotal material.

Our graphs demonstrate that the weight difference between the oldest and the youngest chicks was constantly visible from the 5- or 7-day age group to the end of our study, and on average, the first bird was the heaviest, the last one the lightest in all age groups. However, our posthoc tests show that these differences were only significant 11–13, 14–16, and 23–25 days after hatching. If one assumes that the parents actively work to keep or enhance the difference in weight by feeding more to the older birds, the quite big weight variation, which leads to the insignificance of the weight differences, may be partly due to difficulties of the parents recognizing the rank order of the younger chicks because of a camouflage effect of the down feathers which makes it almost impossible to differentiate the bodies of the young birds when they are in the nest (see Fig. 3). This may lead to the, for the younger chicks positive, effect that the parents made errors in the determination of the hatching sequence and thus on average the younger birds got more food than they would have got under better conditions for discrimintion of the rank order was. The down feathers are replaced by adult feathers around the time when the weight between the youngest and the oldest chicks is significant, 11–13 and 14–16 days, and it may thus be that for some days there is an additional trait which can be used by the parents to determine the hatching order and feeding preferentially the older chicks. This advantage may be eliminated when all chicks have developed adult feathers.

It might also be argued that parents attend most to the beaks of begging offspring, and that the gape marks should have much more impact on feeding than the body shape. Our observations, however, indicate that the gape marks are only vaguely visible under dim light conditions, and a determination of the hatching order by the estimation of the gape size with help of the white flanges of the beak is possible, but not absolutely certain. Thus, an additional trait like body size might be useful for the parents to evaluate the hatching order.

In any case, our study demonstrates that there is a weight advantage for the first chick, even if the difference to the fourth chick is not significant at 30 days. We have also evidence (not shown) that this weight difference persisted into adulthood. If so, one has to concede that the weight difference induced by asynchronous hatching may have an enduring effect, e.g. on the chance of the heavier bird to get a mate (Ikebuchi and Okanoya, 2006) or to produce bigger clutches (Haywood and Perrins, 1992), even if there might be a reduction of this advantage by the mechanisms described above.

Our observations show that the survival rate of the chicks did not depend on hatching rank. Instead, it is clear that weight at hatching affects the survival rate; chicks which died later on were significantly lighter than those surviving. It is difficult to speculate what the reasons for this relation may be. Most probably, lighter weight at birth can be seen as an indication of some problems in the condition of the mother at the time of egg production, for example hormonal status (Williams et al., 2005; von Engelhardt et al., 2006; Adkins-Regan et al., 2013), health problems, or disturbance of the egg laying process. This might have led to some congenital disorder which affected the survival of the light weight chicks because of immune system weakness, water loss, or other metabolic problems. Another explanation might be that, at least in inexperienced pairs, the parents of the first chick may have difficulties after hatching in switching from pure incubation to a mixture of incubation and feeding. After hatching, young birds can survive up to two days without feeding, by relying on the remaining store of egg yolk. If the parents do not start feeding during these two days, the young birds may die of starvation. However, such a scenario has not been descibed as yet and needs further examination.

To summarize, our observations revealed some effects of asynynchroneus hatching like a weight advantage, a corresponding increase of the beak size, and an increase in motor skills that all could have caused the parents to feed the older birds preferentially. On the other hand, we found factors which could obscure the determination of the hatching order and could lead to a more balanced feeding of the whole clutch, like the camouflage effect of the down feathers which obscured the size of the chicks' bodies, or the fact that the dim light within the nest made it difficult, but not fully impossible, to determine the gape size of the chicks and

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thus to determine the hatching order. Accordingly, measurable parameters such as death rate and weight differences were visible, but rarely significant. In conclusion, asynchronous hatching causes an advantage of the early born siblings in zebra finches, but this advantage may be partly reduced by factors which complicate the recognition of the hatching order by the parents. This in turn may enhance the chances of the younger siblings to survive and to gain weight. On the other hand, one has to take another scenario into account. If the parents simply feed the hatchlings as long as they appear to be hungry (attending, e.g., to the intensity of gaping), this might also lead to the constant weight differences between the younger and the older chicks which we observed. Further experiments are needed to decide beween these alternatives, and also to determine why the zebra finch is one of the few passerine species to exhibit asynchronous hatching.

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COMPETING INTERESTS

The authors have no competing interests to declare.

AUTHOR CONTRIBUTIONS

This study were conceived and designed by all authors. MI did all parts of this study. MI HB wrote the manuscript.

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