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# How to hatch from an egg of great structural strength. A study of the Common Cuckoo

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Brood parasitism represents a unique mode of avian reproduction that requires a number of adaptations. For example, to reduce chances of puncture ejection of their eggs by small hosts, brood parasites may have been selected for laying eggs of unusually great structural strength. However, great structural strength of eggshells should hinder hatching. The goals of our study were to establish if chicks of the Common Cuckoo *Cuculus canorus* have more difficulty with hatching out of their strong eggs than chicks of species with eggs of similar size, and whether they possess any mechanisms facilitating hatching. To achieve these goals, we compared hatching pattern and selected body characteristics of chicks of the Common Cuckoo with those of another altricial species with eggs of a similar size, the Great Reed Warbler *Acrocephalus arundinaceus*. Although the rate of pecking was similar in the two species, the Common Cuckoo chicks started pecking earlier in relation to their emergence and consequently required more time and a greater cumulative number of pecks for breaking open their eggs than did young Great Reed Warblers. The two species also differed with respect to the pattern of opening their shells; in contrast to the warbler chicks, which enlarged the original pip circularly, the cuckoo chicks opened the egg by systematically creating a long narrow slit until they emerged. Finally, our study of hatched young revealed several differences; the Cuckoo hatchlings were significantly heavier, had a longer forearm, and their egg tooth was located significantly farther from the tip of the beak. The edge used for cutting through the shell was also significantly longer than that of hatchling Great Reed Warblers. To conclude, our data suggest that hatching is more difficult for a Cuckoo than for a Great Reed Warbler and that Cuckoos possess several mechanisms to overcome the problems of hatching from a structurally strong egg.

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Avian eggs characteristically have hard calcareous eggshells whose main function is to provide mechanical protection for the developing embryo from outside pressures. Egg strength is highly species-specific because it represents a compromise between different selective forces such as the need for mechanical protection of an embryo, which favours great strength, and the necessity for the young to hatch without assistance from its parents presumably favouring low strength of an egg. There exists a highly significant relationship between egg strength and egg size (Ar et al. 1979, Picman et al. 1996). However, available data suggest that brood parasitic species of birds such as cuckoos and cowbirds lay eggs that are stronger than expected for their size (Spaw and Rohwer 1987, Picman 1989a, Brooker and Brooker 1991, Picman and Pribil 1997).

The Common Cuckoo *Cuculus canorus* is an obligate brood parasite that breeds across the Palearctic from western Europe to Japan (Cramp and Simmons 1985). This cuckoo species is known to have parasitized more than 125 passerine species, but only 11 of these are considered to be major hosts (Moksnes and Røskaft 1995, Wyllie 1981). Since Common Cuckoo parasitism characteristically reduces hosts' reproductive success to a very low level (Øien et al. 1998), there should be strong selection for host defences against parasitism. During the evolution of this brood parasitism system a number of adaptations and counter adaptations have evolved, described by Davies and Brooke (1989a, b) and Øien et al. (1995) as a co-evolutionary arms race between the Common Cuckoo and its hosts. The rejection of the brood parasite's egg(s) by the host is an important trait that may have selected for increased eggshell strength in the cuckoo, thus precluding rejection of cuckoo eggs by small hosts through puncture ejection. Alternatively or in addition, the extra strength could simply reflect a residual characteristic of the much larger cuckoo egg before it evolved its small size (Lack 1968, Spaw and Rohwer 1987, Picman 1989a, J. Picman and M. Honza unpubl. data). In addition, increased strength of the Common Cuckoo eggs should also prevent their breakage during laying (Lack 1968). The great strength of cuckoo eggs has recently been demonstrated in a study that showed that Common Cuckoo eggs are 2.2 times stronger against outside pressure than eggs of the same size laid by their passerine hosts (J. Picman and M. Honza unpubl. data). Similar evidence also exists for inside strength of eggs of this cuckoo species (J. Picman and M. Honza, unpubl. data). This suggests that the great structural strength of cuckoo eggshells should make hatching difficult for young Common Cuckoos. Therefore, there should be intense selection on Common Cuckoos for various adaptations facilitating hatching.

In this study we examine hatching-related adaptations in the Common Cuckoo and one of its major hosts, the Great Reed Warbler *Acrocephalus arundinaceus*. Our earlier studies have established that eggs of these two species are similar in size (t-test, $P > 0.05$; mean egg volume in ml $\pm$ SD: $3.071 \pm 0.026$ vs $3.128 \pm 0.43$ for Common Cuckoo and Great Reed Warbler, respectively, J. Picman and M. Honza unpubl. data). To measure the strength of eggs, we used a mechanical puncture-resistance tester (see Picman 1989b). Both the outside and inside strengths of eggs are substantially greater in the Common Cuckoo than in the Great Reed Warbler (J. Picman and M. Honza unpubl. data). Based on these findings we suggest that the Common Cuckoo chicks should: (1) experience greater difficulty during hatching and (2) possess specific mechanisms facilitating their hatching. More specifically, we propose the following predictions. First, the great inside eggshell strength should increase the effort required for both egg pipping and subsequent shell breakage during emergence. Therefore, we expect that Common Cuckoo chicks should start pecking earlier relative to their emergence and/or that they should exhibit a higher pecking rate than their hosts' chicks, which hatch from eggs of normal strength. Second, the necessity to break through the unusually strong eggshell could also result in several changes in the egg tooth used for puncturing and then breaking the shell open. For example, a strong shell may require an egg tooth that is larger and possibly also located closer to the forehead on the upper mandible (thereby presumably increasing its leverage). Third, we predict that natural selection has favoured long forearms and tarsi in cuckoo chicks, because both are presumably used in the final stages of hatching (stretching legs and spreading forearms should contribute to the opening of eggshell by forcing the shell apart; see e.g. Pettingill 1970). If this is true, then hatchling Common Cuckoos should have longer forearms than hatchling Great Reed Warblers.

## Methods

### Egg collection

We collected Common Cuckoo and Great Reed Warbler eggs between 15 May and 30 June 1999, in the south-eastern part of the Czech Republic, in pond areas near the villages of Lednice and Lužice (47° 40′ N, 16° 48′ E), about 40 and 60 km south and south-east of Brno, respectively. We searched the littoral vegetation surrounding fish ponds for nests. The vegetation consisted of common reed *Phragmites australis* and narrow-leaf cattail *Typha angustifolia* stands which provide suitable nesting sites for the two main Common Cuckoo hosts, the Great Reed Warbler and Reed Warbler *Acrocephalus scirpaceus*. We included only one egg from each female cuckoo. This was made possible because individual female Common Cuckoos lay eggs of an individual-specific appearance (Wyllie 1981). If a nest contained more than one cuckoo egg, we selected one that was different in appearance from those collected earlier. In this study we used only those eggs that were freshly laid or that had been incubated for a maximum of three days. If the stage of embryonic development was not precisely known, we estimated it by the floatation method (Hays and Lecroy 1971). Egg volume (ml) was calculated using Hoyt's (1979) formula: $\text{volume} = 0.507 \times \text{length} \times \text{breadth}^2$.

### Incubation

We artificially incubated a total of 25 Common Cuckoo and 25 Great Reed Warbler eggs of which 18 (72.0%) and 17 (68%) eggs hatched. Incubation took place in an incubator (Octagon 20, Brinsea, UK), with temperature ranging from 37.7° to 37.8°C and relative humidity (RH) from 55 to 65%. Eggs were turned automatically 24 times a day (once every hour). Two to three days before expected hatching, we transferred the eggs to another incubator (Octagon 10, Brinsea, UK), where we maintained the same temperature, but where we increased RH to 75–80%. The eggs were not turned in the second incubator. Both incubators were transparent and double-skinned. During the last two days prior to the expected hatching day, we listened for bill-pecking every two hours during the day and every four hours during the night. When we recorded the first bill-pecking, we placed a small, sensitive tie-clip microphone, SONY ECM T 140 (connected to a Marantz PMD 222 audio tape-recorder), in the incubator in such a way that it almost touched the egg. The bill-pecking was then recorded automatically on audio tape during 5-min intervals, with 30 min between consecutive recording sessions until chick emergence (emergence was defined as the time when the chick pushed the shell cap off and emerged from the egg; Hamburger and Oppenheim 1967). Just before the eggs began to hatch, we started video-recording the eggs using Sony CCD-TR 660 E Hi 8 video-cameras. Immediately after emergence, hatched chicks were euthanased by cold and then stored in 60% alcohol for later analyses of selected meristic traits. During the hatching process, we measured the time from the first pip on the shell to chick emergence. Only those eggs where the interval between the last examination and the first crack in the shell was shorter than 30 min were included in the following analyses. The half-time between the two events (last examination and the first crack) was then considered as the starting time for all calculations. It is known that certain stimuli to which developing avian embryos are exposed (e.g. click communication) may affect the timing of emergence and duration of the hatching process (e.g. Vince 1969, McMaster and Sealy 1998). Therefore, we incubated eggs that were at the same stage of embryonic development together. Since it is known that avian embryos are behaviourally responsive to light stimulation (Oppenheim 1968), we maintained a constant light regime throughout the incubation period.

## Egg measurements

To determine eggshell thickness, we obtained a small shell fragment (about 2 mm$^2$) with pincers from three randomly selected areas along the widest area of an egg and measured its thickness with a micrometer (accuracy 0.001 mm). Hatchling weight was obtained by removing the chick from alcohol, drying it for 5 min at 20°C, and then weighing it (accuracy 1 mg). For a comparative analysis of meristic traits between the Common Cuckoo and the Great Reed Warbler, we selected traits that are likely to play a role in hatching: length of culmen, forearm length, body length (measured from shoulder to tail), tarsus length, length and height of the egg tooth, and distance of the egg tooth from the tip of the beak (see Fig. 1). The selected traits of the emerged chicks were measured using the stereomicroscope system OLYMPUS and MicroImage software (accuracy 0.1 μm).

# Results

## Hatching pattern; egg-pecking

The first Common Cuckoo started to peck 16 h before it emerged, whereas the first Great Reed Warbler chick started to peck 7 h before its emergence. On average, the Common Cuckoo chicks started pecking earlier ($\bar{x} = 7.10 \pm 4.70$ (SD) h, $n = 18$) before their emergence than the Great Reed Warbler chicks ($\bar{x} = 4.15 \pm 4.01$ (SD) h, $n = 17$); see also Figs 2 and 3). The difference between the two species was statistically significant (t-test; $t = 0.55$, d.f. $= 43$, $P < 0.05$). The difference in the timing of egg pecking between the two species is further evident from the fact that 50% of Cuckoo chicks were pecking 8 h before their emergence versus 2.5 h for Great Reed Warbler chicks. However, chicks of the two species exhibited similar rates of pecking (36 and 37 pecks/min for Common Cuckoo and Great Reed Warbler, respectively; $t = 1.802$, d.f. $= 24$, $P > 0.05$) and in general also similar temporal patterns of pecking throughout the hatching period (see Fig. 2a and b). However, the examination of the temporal pattern of egg pecking revealed that the mean pecking rates of both species increased gradually to their peak

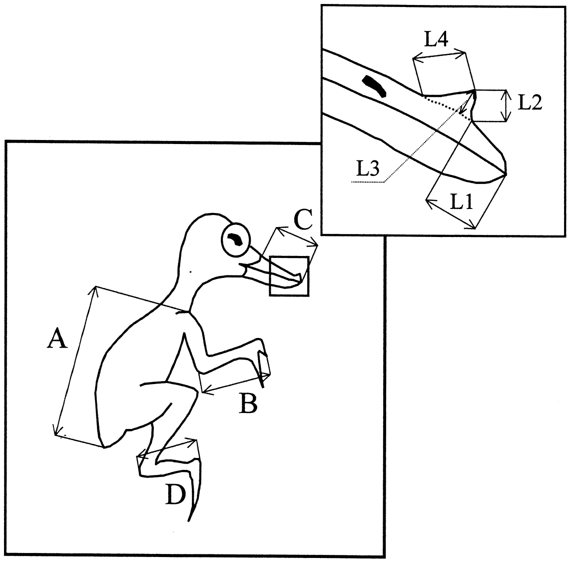

Fig. 1. Measurements of bird embryos. (A) shoulder to tail length; (B) forearm length; (C) culmen length; (D) tarsus length. The measurements on the egg tooth included distance from the front edge of the tooth to the tip of the beak (L1), length of the front edge of the egg tooth (L2), tooth height (L3) and length of the cutting (rear) edge of the tooth (L4).

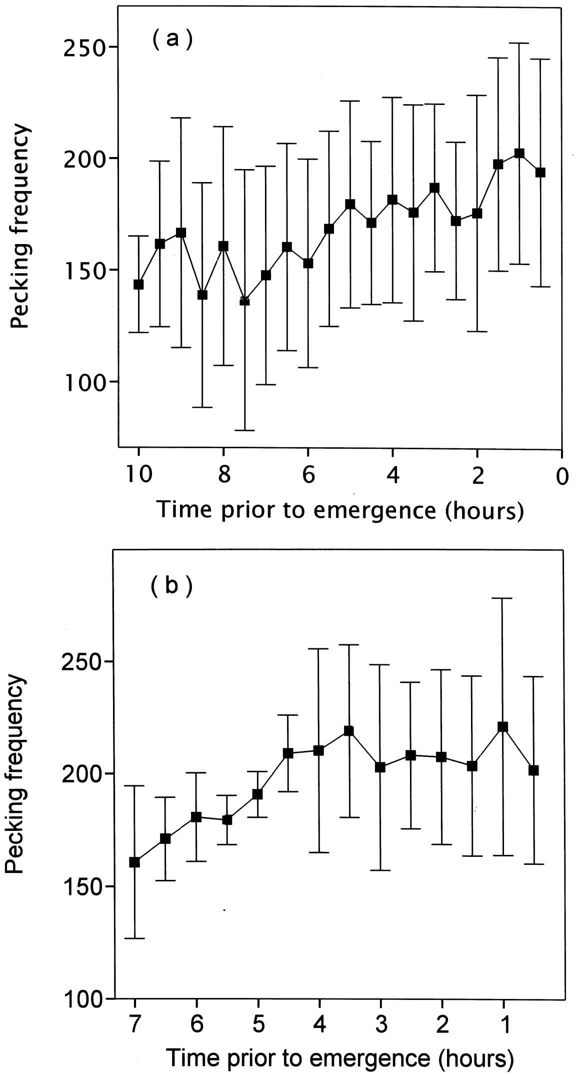

Fig. 2. Pecking frequency (number of pecks/5 min) of the embryos. Shown are means and S.D. Only intervals in which at least three embryos pecked are considered. The time between successive recording intervals was 30 min. (a) Common Cuckoo, (b) Great Reed Warbler.

levels, which were reached about 1.5 h and 1 h before emergence in the Common Cuckoo and Great Reed Warbler, respectively (Fig. 2a and b). This increase in pecking rate was statistically significant for both species (Generalized Linear Mixed Model, slope for Common Cuckoo = 4.086, d.f. = 13, t = 3.70, P = 0.0027; slope for Great Reed Warbler = 4.797, d.f. = 11, t = 4.55, P = 0.0008). Just before emergence, the mean pecking rates declined slightly for chicks of both species (Fig. 2a and b).

The total number of pecks made by the chicks of the two species reflects their different timing of initiation of pecking. Overall, hatching required a significantly higher total number of pecks by the Common Cuckoo chicks than by the Great Reed Warbler chicks (Fig. 3; Wilcoxon signed ranks test: Z = −9.43, P < 0.001). Finally, also as a result of the different timing of initiation of egg pecking, the hatching period (time between the first egg pip and chick emergence) was longer in the Common Cuckoo (416.66 ± 219.25 min) than in the Great Reed Warbler (119.66 ± 149.8 min; t-test; t = 3.36, d.f. = 16, P < 0.001).

## Hatching pattern; opening of the eggshell

The Common Cuckoo and Great Reed Warbler chicks exhibited species-specific patterns of opening the eggshell. The Common Cuckoo chicks first made a crack in the shell with the egg-tooth and then, by back-stretching the neck and using the long edge of the egg tooth (designated as L4 in Fig. 1) as a cutting device made a narrow slit approximately 1 mm wide. The average length of this slit immediately before emergence was 10.84 ± 2.79 mm (n = 13). In five (38.5%) chicks, we recorded a second pip located up to 2 mm from the original one. These chicks then continued breaking the egg from these holes as described above. In contrast to the cuckoo chicks, after having made the first crack in the shell, the Great Reed Warbler chicks were enlarging the original pip circularly (i.e. by increasing the diameter of the initial hole) until emerging when the mean (± SD) length and width of the opening

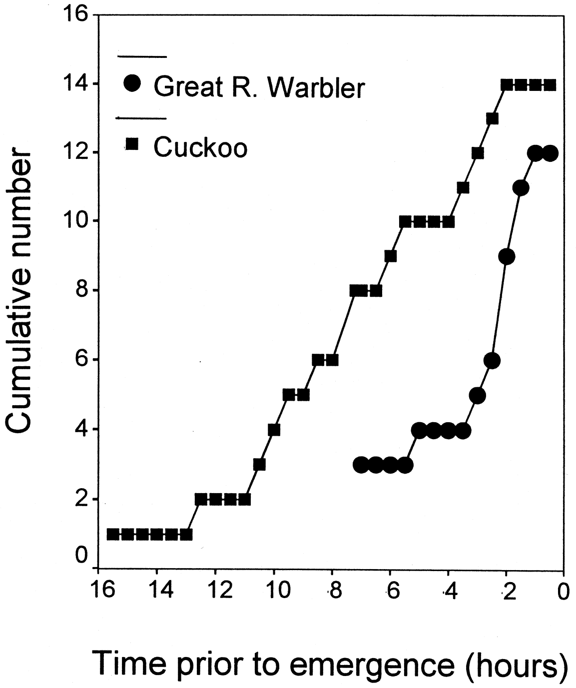

Fig. 3. Cumulative number of pecks by hatching embryos of the Common Cuckoo (■) and Great Reed Warbler (●) as recorded at 30-min intervals.

Table 1. Comparison of selected meristic traits (shown are means ± SD; sample sizes in brackets) between hatchling Common Cuckoos and Great Reed Warblers. The two species were compared by a two-tailed t-test.

| Characteristic | Cuckoo | Warbler | P |
|---|---|---|---|
| Nestling mass (g) | 2.557 ± 0.354 (16) | 2.159 ± 0.314 (16) | 0.002 |
| Length (mm) | 19.827 ± 0.810 (14) | 19.844 ± 0.639 (15) | 0.951 |
| Forearm (mm) | 9.420 ± 0.298 (14) | 7.746 ± 0.766 (15) | 0.000 |
| Tarsus (mm) | 8.057 ± 0.621 (14) | 8.526 ± 0.697 (15) | 0.068 |
| Bill length (mm) | 7.820 ± 0.408 (14) | 7.714 ± 0.465 (18) | 0.505 |
| Egg tooth*: | | | |
| L1 (mm) | 1.0354 ± 0.101 (14) | 0.773 ± 0.181 (18) | 0.000 |
| L2 (mm) | 0.317 ± 0.051 (14) | 0.338 ± 0.215 (18) | 0.736 |
| L3 (mm) | 0.249 ± 0.044 (14) | 0.222 ± 0.093 (18) | 0.327 |
| L4 (mm) | 0.622 ± 0.082 (14) | 0.515 ± 0.148 (18) | 0.018 |

* For measurements see Fig. 1.

was 4.06 ± 1.27 mm and 3.76 ± 1.05 mm ($n = 6$), respectively.

## Comparison of hatching-related mechanisms

Although the Common Cuckoo eggs had slightly smaller volume (3.069 ± 0.306 ml; $n = 22$) than the Great Reed Warbler eggs (3.105 ± 0.172 ml; $n = 25$), the difference between the two species was not statistically significant (t-test: $t = -0.505$, d.f. = 45, $P > 0.05$). In both species, egg volume was highly significantly positively correlated with hatchling mass (Great Reed Warbler: $r_s = 0.678$, $n = 17$, $P = 0.008$; Common Cuckoo: $r_s = 0.635$, $n = 18$, $P = 0.007$; Table 1, Fig. 4). A comparison of eggshell thickness showed that Common Cuckoo eggs had thicker shells (0.118 ± 0.009 mm; $n = 22$) than those of Great Reed Warblers (0.095 ± 0.007 mm, $n = 19$; t-test: $t = 8.44$, d.f. = 39, $P < 0.001$).

A comparison of hatchling characteristics showed that Common Cuckoos and Great Reed Warblers differed statistically significantly in four out of nine characteristics that we examined (Table 1). More specifically, the hatchling cuckoos were heavier, had longer forearms and egg tooth (designated as L4, Fig. 1), and their egg tooth was placed farther from the tip of the beak (or closer to forehead; see L1 on Fig. 1). Hatchlings of the two species did not differ in the remaining two egg tooth parameters and there was no significant difference in tarsus length between the two species (Table 1).

# Discussion

## Pecking effort

We predicted that, in comparison with Great Reed Warblers which lay structurally weaker eggs, Common Cuckoos should experience greater difficulty in hatching. This prediction was supported by the following observations: (1) relative to emergence, the Common Cuckoo chicks started pecking much earlier than the Great Reed Warbler chicks (resulting in a significantly longer hatching period in the Common Cuckoo chicks), and (2) the total number of pecks was greater for Common Cuckoos than for Great Reed Warblers. However, the rates of pecking (the number of pecks per unit of time) and the temporal pecking patterns (i.e. changes in pecking frequency during the course of the hatching period) were similar. A possible explanation for the similar temporal hatching patterns is that similar pecking behaviour among species may reflect common ancestry. This view is supported by the fact that the pecking rates of the two species we studied (36 pecks/min and 37 pecks/min for Cuckoo and Reed warbler, respectively) are relatively similar to the rates of bill-clapping (i.e. rapid opening of the upper and lower mandibles) by duck embryos (27 pecks/min) reported by Oppenheim (1972). These observations also

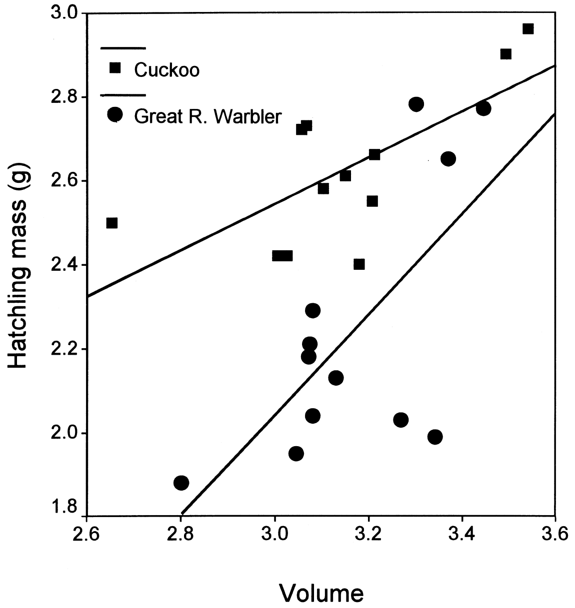

Fig. 4. Relationship between egg volume (ml) and nestling mass of the Common Cuckoo (■) and Great Reed Warbler (●).

suggest that there are physiological constraints on the frequency of egg pecking by avian embryos. Therefore, the greater hatching difficulty is more likely to be reflected in changes in the duration of hatching and thus in the total number of pecks rather than in the pecking rate.

## Eggshell opening

After an avian embryo has made the first pip-crack in the eggshell, there is a relatively long interval until it begins the final stage of hatching (Abbott and Craig 1960, Oppenheim 1970). Oppenheim (1972) found that the time interval between pipping and emergence varied among species from 15 h in the House Wren *Troglodytes aedon* to almost 41 h in the Northern Bobwhite *Colinus virginianus*. However, our results suggest that the time between pipping and emergence is shorter in the two species we studied. The observed variation among species could at least partly be caused by size-related differences in egg size and incubation period, variation in eggshell strength, and different conditions during hatching. For example, the discrepancy between our and Oppenheim's (1972) results could be explained by different humidity conditions in the two studies of hatching. While we kept relative humidity during the final stage of hatching between 75 and 80%, Oppenheim (1972) hatched chicks at 55–65%.

In any case, our results support our prediction that Common Cuckoos must use more effort to hatch than do Great Reed Warblers. Furthermore, the prediction that Common Cuckoo chicks should experience greater difficulty in hatching was supported by the observation that five (38.5%) chicks made an additional crack to the first one. In contrast, additional cracks were not made by Great Reed Warbler embryos. According to Oppenheim (1972), after avian embryos have made the initial crack in the shell, they usually do not make any additional cracks until emergence. Despite Oppenheim's finding (1972) that pre-hatching behaviour and hatching behaviour are similar in species representing all forms of birds (precocial, semi-altricial, altricial), some species appear to have a characteristic pattern of hatching as shown by the condition of their eggshells after hatching. For example, American Woodcock *Scolopax minor* and Willet *Catoptrophorus semipalmatus* split eggshell longitudinally, ripping open the seam rather than breaking the shell into pieces (Wetherbee and Barlett 1962). Furthermore, the Australian Brush-turkey *Alectura lathami* exhibits an unusual hatching pattern; for example, artificially incubated eggs fail to hatch if they are exposed to light. Further, instead of simply removing a shell cap, the chick breaks the entire shell into small pieces (Baltin 1969). Finally, in the Ostrich *Struthio camelus*, chicks essentially explode out of their strong-shelled eggs shattering the shell into many pieces (Sauer and Sauer 1966).

The hatching pattern of the Great Reed Warbler chicks conforms to the general hatching pattern described by Gill (1994) for most birds. However, the Common Cuckoo chicks exhibit a completely different pattern of breaking the shell, and we suggest that this could be the result of selection favouring adaptations facilitating hatching from structurally unusually strong eggs.

## Do Common Cuckoos possess any adaptations facilitating hatching?

The second goal of our study was to examine selected structural characteristics of Common Cuckoo and Great Reed Warbler hatchlings and establish if any of those in the Cuckoo could facilitate hatching from the species' strong eggs. Our analyses demonstrated that, immediately after hatching, the Common Cuckoo chicks are heavier, have longer forearms and somewhat longer tarsi than the Great Reed Warbler chicks, despite the fact that Common Cuckoo egg is somewhat (although not significantly) smaller. This, along with the fact that the incubation period of brood parasites is unusually short (O'Connor 1984), suggests that embryonic development is faster in this species than in the Great Reed Warbler.

The importance of the egg tooth for hatching has already been discussed by Clark (1961), and in our study we concentrated on the size and placement of this structure on the upper mandible. We found that the egg tooth had a longer cutting edge in Common Cuckoo chicks than in Great Reed Warblers, but the two species did not differ in the other two egg tooth parameters (height and length of the front edge). We hypothesize that (1) the placement of the egg tooth closer to the forehead in the cuckoo increases the amount of pressure that the chick can exert on the shell through pecking (due to increased leverage) and (2) that the longer upper edge of the egg tooth presents a longer cutting blade, which should also facilitate hatching from structurally strong eggs.

It is known that inorganic constituents of avian eggshells (mainly calcium carbonate) have higher specific mass than the organic constituents (matrix proteins and polysaccharides) and that they play a dominant role in determining eggshells strength (Romanoff and Romanoff 1949, Burley and Vadehra 1989). Since eggs of brood parasites are structurally much stronger than those of their hosts (Spaw and Rohwer 1987, Picman 1989a, J. Picman and M. Honza unpubl. data), their shells presumably contain greater amounts of calcium carbonate than would be expected for their size. This is supported by data showing a significantly greater thickness of eggshells of the Brown-headed Cowbird *Molothrus ater* (Picman 1989a) and a somewhat, although not significantly, greater thickness of shells of the Common Cuckoo (J. Picman and M. Honza unpubl. data). Furthermore, Common Cuckoo eggs have shells of unusually high density (Picman and Pribil 1997, J. Picman and M. Honza unpubl. data). These findings suggest that brood parasites must ingest large quantities of calcium to be able to form eggshells. Because much of the calcium that is needed for embryonic development (especially for the formation of skeleton) is derived from the eggshell, the rapid development may play an important role in a specialized pattern of decalcification that may, in turn, facilitate hatching.

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