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Source: Journal of Vertebrate Biology, 70(1)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/jvb.20109

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Journal of Vertebrate Biology

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J. Vertebr. Biol. 2021, 70(1): 20109 DOI: 10.25225/jvb.20109

RESEARCH PAPER

# How strong are eggs of the common cuckoo *Cuculus canorus*?

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*The original version of this paper was written twenty years ago. Unfortunately, the lead author, Jaroslav (Slávek) Picman, passed away and the paper was subsequently 'put on the shelf'. I recently re-read the draft version of the paper again and, despite the great progress that has been made on the subject in recent years, I found that some of the original findings were of great interest and still largely unexplored. Consequently, I decided to revise and update the text, with the inclusion of recent literature, while still leaving much of the text in its original form as a tribute to the paper's lead author. (Preface by Marcel Honza)*

Received 30 September 2020; Accepted 19 November 2020; Published online 21 December 2020

**Abstract.** The common cuckoo *Cuculus canorus* is an obligate brood parasite that lays its eggs in the nests of small passerines. It has long been hypothesized that cuckoo eggs should be structurally stronger than host eggs or those of non-parasitic cuckoos to reduce chances of breakage during laying, to prevent accidental damage during incubation and/or to hinder their rejection through puncture ejection by the host. Therefore, we analysed selected characteristics of a sample of freshly laid eggs of the common cuckoo with two of its major hosts, the reed warbler *Acrocephalus scirpaceus* and great reed warbler *Acrocephalus arundinaceus*, and a sample of species with known puncture resistant eggs. We found that in puncture resistance tests cuckoo eggs tolerated on average 231 g. The cuckoo eggs were 3.3 and 2.5 times stronger than those of the reed warbler and great reed warbler, respectively. Greater shell thickness can explain only 17% of the total extra strength of the cuckoo eggs (125.97 g). When we controlled for the confounding effects of egg size (using a sample of eggs of normal strength from bird species of varying size), the common cuckoo eggs were 2.2 times stronger than expected for their size. Our results are consistent with the hypothesis that cuckoo eggs are structurally stronger and this trait probably represents an adaptation for a brood parasitic life style.

**Key words:** coevolution, brood parasitism, egg shell

## Introduction

One of the remarkable adaptations which has evolved during coevolution between obligate brood parasites (cuckoos and cowbirds) and their hosts is the strength of their egg shells. Since the pioneering work by Swynnerton (1918) who was the first to suggest that the thick egg shell of the common cuckoo *Cuculus canorus* (hereafter cuckoo) may function as a mechanism for preventing breakage by puncturing prior to rejection by the small hosts, several studies have been published. Studies by Lack (1968), Rahn et al. (1988), Picman (1989a), Picman & Pribil (1997) and Antonov et al. (2006) indicated that brood parasitic eggs are stronger. Similarly, Honza et al. (2001) without specifying quantitative data on cuckoo egg shell strength concluded that cuckoos possess

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several mechanisms to overcome the problems of hatching from a structurally strong egg. On the other hand, Brooker & Brooker (1991) recorded that *Cuculus* eggs are not stronger than those of their hosts. Swynnerton´s idea, later postulated as the "puncture resistance hypothesis" has been supported by some findings of Spaw & Rohwer (1987) and also by Antonov et al. (2006). This explanation seems to be logical as many smaller cuckoo hosts are known as puncture ejectors, i.e. those which first have to puncture the egg in order to carry it in the bill and remove it from the nest.

An alternative explanation is the "laying damage hypothesis" which states that the greater strength of the parasitic egg represents an adaptation to protect it from damage during laying (Lack 1968). Wyllie (1981) found indirect evidence for this assumption, when especially in the case of parasitism of cavity-nesters or hosts with domed nests, where they cannot enter to lay, some hosts eggs were damaged. However, when open nesters were tested, there was no evidence that egg damage was associated with laying of the parasites (Antonov et al. 2006, Lopez et al. 2018).

Another hypothesis is "the chick vigour hypothesis" whereby cuckoo chicks may decalcify a greater proportion of their eggshells during development, which facilitates hatching from an initially thicker shelled egg (Igic et al. 2017). Further, the "anti-bacterial protection hypothesis" explains the role of the shell as a barrier between the cuckoo embryo and microorganisms in the host nest (Antonov et al. 2012). Finally, Yang et al. (2018) proposed that unusually thick-shelled eggs may retain more heat for the developing embryo and thus contribute to the early hatching of parasite eggs.

The main aims of this study were to fill the gap in our knowledge relating to egg shell strength. More specifically we (1) determined strength of cuckoo eggs, (2) compared strength of cuckoo eggs with that of its major hosts and of selected bird species and (3) established whether egg shell thickness contributes to egg shell strength.

## Material and Methods

### Study species

Parasite: the cuckoo, is an obligate brood parasite that occurs in eight subspecies in most of Eurasia (Wyllie 1981, Cramp 1985). Although more than 125 bird species have been recognized as cuckoo hosts, only 11 are frequently parasitized (Moksnes & Røskaft 1995).

Host species: both the reed warbler *Acrocephalus scirpaceus* and great reed warbler *Acrocephalus arundiaceus* are among the most frequently used cuckoo hosts in Europe (Moksnes & Røskaft 1995). In our study area the frequency of parasitism in reed warbler nests was about 16% (Øien et al. 1998) and 33.8% in great reed warbler nests (Kleven et al. 2004).

### Egg collection

In late May and early June of 1999 we collected a total of 21 freshly laid cuckoo eggs (the stage of incubation was established using the floating method, see Hays & Lecroy 1971) from ten nests of great reed warblers and ten reed warblers around fishponds in the south eastern part of the Czech Republic. Along with each cuckoo egg we also collected one host egg (randomly selected from the host's clutch). All eggs were stored in a refrigerator (at 100% humidity to prevent water loss) for later analyses.

### Control eggs

To establish if cuckoo eggs are unusually strong, we compared them to eggs of two control groups: (1) their hosts (eggs of reed warblers and great reed warblers collected from the parasitized nests as mentioned above), (2) selected freshly laid eggs of non-parasitic species: bobolink (*Dolichonyx oryzivorus*), red-winged blackbird (*Agelaius phoeniceus*), yellow-headed blackbird (*Xanthocephalus xanthocephalus*; for details about collection see Picman 1989a). Also, the eggs of black-capped chickadee (*Poecile atricapillus*), cedar waxwings (*Bombycilla cedrorum*), purple finch (*Haemorhous purpureus*), common grackle (*Quiscalus quiscula*), mourning dove (*Zenaida macroura*), American robin (*Turdus migratorius*), yellow warbler (*Setophaga petechia*) and tree swallow (*Tachycineta bicolor*) collected in June 1988-1989 near Ottawa, Ontario, Canada.

### Egg measurements

For each egg we obtained the following data: length (L) and breadth (B; at the widest region of the egg), measured with electronic callipers (accuracy 0.01 mm). These measurements were used to calculate the shape index (S) for each egg as S = L : B and egg volume (V) using the following equation (see Spaw & Rohwer 1987): $V = 0.498\ LB^2$.

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Following these measurements, the strength of each egg was tested using a mechanical puncture tester (Picman 1989b). This device establishes the pressure (in grams) that has to be exerted by a steel punch (diameter at the tip 1.2 mm) to puncture the eggshell. If possible, three measurements were made for each egg, unless the egg cracked during the first or second test. These measurements were performed on the widest area of the egg and were approximately uniformly spaced. All strength measurements for a given egg were then averaged and the resulting value (henceforth puncture resistance) was used as an index of egg strength.

Eggshell thickness was measured using an electronic micrometre (accuracy 0.001 mm) by removing three small fragments (each around 1 × 1 mm) of the shell from the three areas where puncture tests were performed. The mean of the three values was used as an index of eggshell thickness in the widest area of the egg.

### Statistical analyses

We conducted statistical analyses at between-species and within-species levels. At the between-species level we used independent t-tests to compare the volume, shape, thickness and puncture resistance of the cuckoo eggs to the eggs of each host.

To establish if the cuckoo eggs are unusually strong, we conducted the following analysis. First, for a sample of control non-parasitic species we established a relationship between egg volume and puncture resistance using linear regression. From the resulting regression equation, we obtained the expected puncture resistance of the cuckoo eggs (by calculating puncture resistance of control eggs of the same size as cuckoo eggs). To determine if the observed and expected puncture resistance of the cuckoo eggs differed statistically, we compared the residual puncture resistance of the cuckoo eggs with that of the 13 control species using a one-sample t-test.

### Within-species analyses

To establish if the selected eggshell parameters had the predicted effects on cuckoo eggshell strength, we performed forward stepwise multiple regression, where the dependent variable was puncture resistance and the predictor variables were egg volume, egg shape, and eggshell thickness.

## Results

### Comparison of egg characteristics between the cuckoo and its hosts

Because our samples of cuckoo eggs laid in nests of reed warblers and great reed warblers did not differ in volume, shape, eggshell thickness or puncture resistance (Wilcoxon signed rank test with continuity correction; for all cases $P > 0.1$), in the following analyses all cuckoo eggs were pooled. A comparison between eggs of the cuckoo and the two hosts showed that the cuckoo eggs were larger than eggs of the reed warbler, but were similar in size to eggs of the great reed warbler (Table 1). The cuckoo eggs were similar in shape to eggs of the two hosts (Table 1). The cuckoo eggs did not differ from the great reed warbler eggs in shell thickness, but they were significantly thicker than those of the reed warbler (Table 1). Finally, the puncture resistance tests demonstrated that the cuckoo eggs tolerated 3.3 times greater pressure than those of the reed warbler and 2.5 times greater than the great reed warbler (Table 1).

### How much stronger are cuckoo eggs than would be expected for their size?

To establish the magnitude of increase in the outside strength of the cuckoo eggs, we compared

**Table 1.** Comparison of selected characteristics of the cuckoo eggs to those of the reed warbler and the great reed warbler. The cuckoo eggs were compared to eggs of each host with an independent t-test. Probability of each comparison shown in parentheses.

| | Egg characteristic cuckoo | Reed warbler | Great reed warbler |
|---|---|---|---|
| Shape (S) | 1.339 ± 0.045 | 1.345 ± 0.046 (0.77) | 1.359 ± 0.062 (0.37) |
| Volume (ml) | 3.071 ± 0.0262 | 1.790 ± 0.121 (< 0.001) | 3.128 ± 0.430 (0.7) |
| Puncture resistance (g) | 231.753 ± 0.02 | 70.411 ± 3.46 (< 0.001) | 91.042 ± 0.77 (< 0.001) |
| Thickness (mm) | 0.102 ± 0.031 | 0.0703 ± 0.0052 (0.017) | 0.0870 ± 0.0083 (0.129) |

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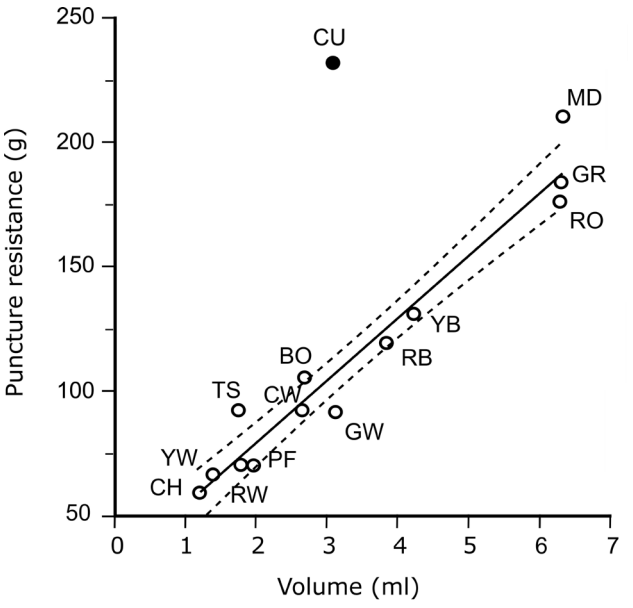



**Fig. 1.** Comparison of puncture resistance of eggs of the common cuckoo (CU) and 13 non-parasitic species (BO bobolink; CH black-capped chickadee; CW cedar waxwing; PF purple finch; GR common grackle; GW great reed warbler; MD mourning dove; RB red-winged blackbird; RO American robin; RW reed warbler; YB yellow-headed blackbird; YW yellow warbler; TS tree swallow). Dashed lines show 95% confidence intervals.

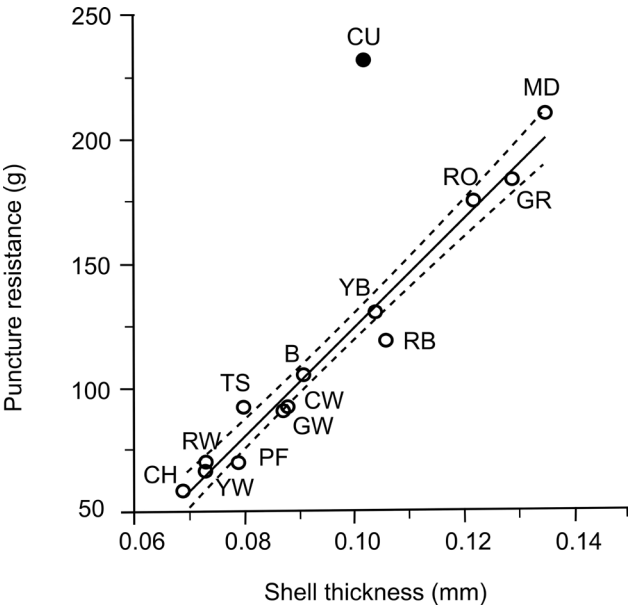



**Fig. 2.** Comparison of puncture resistance of eggs of the common cuckoo (CU) and 13 control non-parasitic species (species abbreviations as in Fig. 1) when the eggshell thickness is taken into consideration. Dashed lines show 95% confidence intervals.

their observed puncture resistance to their expected strength. Regression analysis revealed a highly significant relationship between puncture resistance (PR) and egg volume (VOL) for the control species (Fig. 1) that can be described by the following equation: PR = 28.861 + 25.046 * VOL (r = 0.973, ANOVA for the regression equation: F = 195.98, df = 1,11, $P < 0.001$). Based on this equation the expected puncture resistance of cuckoo eggs is 105.78 g. Consequently, the observed puncture resistance of the cuckoo eggs (231.75 g) is 2.2 times greater than that of non-parasitic species of similar size (one-sample t-test: t = 10.71, df = 12, $P < 0.001$).

### Do eggshell thickness affect the strength of cuckoo eggs?

To establish the magnitude of this contribution, we compared the observed puncture resistance of the cuckoo eggs to that expected for a control egg with eggshell of the same thickness as the cuckoo egg. There was a significant relationship between puncture resistance and eggshell thickness for the control species (Fig. 2) that can be described by the following regression equation: PR = –93.47 + 2168.17 TH ($r^2 = 0.974$, ANOVA for the regression equation: F = 410.43, df = 1,11, $P < 0.001$). From this equation we calculated that the expected puncture resistance of cuckoo eggs based on their eggshell thickness is 127.69 g. However, to estimate the magnitude of contribution of the greater eggshell thickness to the strength of cuckoo eggs, first we determined their extra strength (i.e. the difference between their observed strength and their expected strength based on their egg volume). This extra strength was 125.97 g (actual value: 231.75 g – expected value: 105.78 g, Fig. 1). Because the expected puncture resistance of cuckoo eggs based on their volume was 105.78 g, their greater eggshell thickness explained only 17% of their total extra egg strength (i.e. 127.69 – 105.78 = 21,91 g). Hence, most (104.06 g, or 83%) of the total extra strength of cuckoo eggs must be explained by another mechanism.

## Discussion

The first goal of our study was to test the hypothesis that the cuckoo should have unusually strong eggs. To determine how much stronger cuckoo eggs are than would be expected for their size, we compared them to a group of 13 control species. This analysis demonstrated that the cuckoo eggs are 2.2 times stronger than would be expected for their size. We believe, this is strong evidence that the hardness of the cuckoo shell makes its eggs less vulnerable to breakage. In addition, our finding concurs with the results of Picman (1989a), who found that brown-headed cowbird *(Molothrus ater)* eggs tolerated twice as much pressure than control eggs of non-parasitic *Icterids.* These findings are not only important in understanding brood parasite egg adaptations but should be taken also into account

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in the design of studies of rejection behaviour of cuckoo hosts. Using model hard-shelled eggs, which are impossible for the host to puncture (Bártol et al. 2002, Moskát et al. 2002, Honza et al. 2004) and similarly real eggs (Martín-Vivaldi et al. 2002, Procházka & Honza 2003, 2004) may be result in over/underestimation of the costs that hosts incur when confronted with real cuckoo eggs.

### The role of eggshell thickness for the unusual strength of cuckoo eggs

The volume and shell thickness of the cuckoo and great reed warbler eggs were very similar to those reported by Hargitai et al. (2010). We did not find any difference in egg shell thickness between two cuckoo races parasitizing the reed warbler and great reed warbler which is in line with findings by Igic et al. (2011) who compared micro-structural strength among three cuckoo host races. On the other hand, Spottiswoode (2010) reported a positive relationship between egg rejection frequencies and eggshell strength in five cuckoo host races in Great Britain. However, this finding may have been differentially affected by the particularly thin-shelled eggs of the cuckoo host race parasitizing the dunnock (*Prunella modularis*).

We found that cuckoo eggs have thicker shells than eggs of equivalent sized control species. This result is consistent with the finding of Brooker & Brooker (1991) who reported that the eggshells of parasitic *Cuculidae* (genera *Cuculus, Cercococcyx, Penthoceryx, Cacomantis, Chrysococcyx, Chalcites, Eudynamys, Scythrops, Tapera, Dromococcyx*) are no thicker than those of non-parasitic *Cuculidae*. Therefore, the greater eggshell thickness of the parasitic *Cuculidae* relative to that of passerines should be attributed to common ancestry rather than to a recent evolutionary adaptation associated with brood parasitism. Nevertheless, the greater strength of cuckoo eggs may partly be explained by their thicker eggshells, although as shell thickness accounts for only 17% of total extra egg strength, other egg characteristics such as shape and shell density must also be involved. This finding is supported in a recent study by Soler et al. (2019) who suggest that differences in eggshell microstructure contribute to making parasitic eggs more resistant to breakage than those of their hosts. Similarly, Igic et al. 2011 reported that cuckoo eggs exhibit greater microhardness, especially in the inner region of the shell matrix, relative to host and sympatric non-host species.

In addition, outside the parasitic cuckoos, unusually strong eggshells have been reported in several other species. Firstly, the brown-headed cowbird lays eggs that are 2.4 times stronger than would be expected for its size. The unusual strength of cowbird eggs also appears to be an adaptation to brood parasitism by reducing chances of puncture ejection by small hosts (Spaw & Rohwer 1987, Picman 1989a). The strength of cowbird eggs is a result of their more spherical shape and greater shell thickness (Picman 1989a). Although eggs of other parasitic cowbirds have not been subjected to the same tests for eggshell strength, their characteristics (more spherical shape and thicker shells compared to non-parasitic *Icteridae*) suggest that these species also lay unusually strong eggs (Picman 1989a). Secondly, the marsh wren (*Cistothorus palustris*, *Troglodytidae*) lays eggs that are 2.9 times stronger than would be expected for its size. The greater egg strength in this species is also achieved through thicker shells and more rounded shape and plays a role in reducing the chances of intraspecific egg destruction (Picman et al. 1996). Similar data also exist on the house wren *(Troglodytes aedon)*, another member of *Troglodytidae*, where unusual egg strength may play a similar role (J. Picman, unpublished data).

To conclude, we demonstrated that eggs of the cuckoo are unusually strong and that their structural strength is only marginally associated with their thickness. Future studies should look at the effect of other parameters like egg shell density and egg shape on strength.

## Acknowledgements

*This research was supported by a Natural Sciences and Engineering Research Council (NSERC) Operating Grant to J. Picman and by the Grant Agency of the Czech Academy of Sciences to M. Honza. Author contributions: J. Picman collected and analysed data, wrote first draft, M. Honza collected and analysed data, finalized draft.*

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