

**THESES
OF THE
DOCTORAL DISSERTATION**

**FACTORS CONTRIBUTING TO THE ACCEPTANCE / REJECTION
OF PARASITIC EGGS IN THE GREAT REED WARBLER
*ACROCEPHALUS ARUNDINACEUS***

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BACKGROUND AND OBJECTIVES

About 1% of extant bird species are so called 'obligate brood parasites' that is, they lay their eggs into other birds' nests. Brood parasitic cuckoos (Cuculiformes) and their diverse host species are among the oldest host-brood parasite systems (having evolved first more than 10 million years ago; Davies 2000). Co-adaptations appearing as a result of mutual selection pressures of host and parasite involve a wide range of intricately connected components. As many earlier studies have shown, co-adaptations can emerge and be observed on a relatively short (micro-evolutionary) time scale, while on the long run these often add up to speciation (Krüger et al. 2009), and thus be termed as co-evolution.

The host-brood parasite system in the focus of our research group, the common cuckoo (hereinafter: cuckoo; *Cuculus canorus*) and the great reed-warbler (hereinafter: GRW; *Acrocephalus arundinaceus*) is characterized by the following attributes:

1. The presence of perches (habitat type) greatly affects the risk of parasitism (Moskát & Honza 2000).
2. Egg mimicry is highly developed in the Hungarian GRW population, with host eggs being somewhat more elongated than cuckoo eggs (Moskát & Honza 2002).
3. The GRW has a number of defence mechanisms to evade successful parasitism (nest guarding, aggression, egg recognition). Egg recognition

is a complex process that is affected by a number of cues and factors from genetic background to environmental stimuli as well as cognitive and physical abilities of the host individual (for a review see Honza & Cherry 2017, Manna et al. 2017).

4. Following egg recognition (discrimination), the GRW either accepts or rejects the parasitic egg by (a) desertion, (b) ejection or (c) burial (Moskát & Honza 2002).
5. 'Egg colouration' includes both the background colour of the shell as well as its maculation (darker spots, blotches and streaks).
6. Colouration is more consistent on the blunt end of the egg, so the host pays more attention to this throughout the discrimination process (Polačikova et al. 2010).
7. In case of a successful parasitic event, the cuckoo chick hatches first (Birkhead et al. 2011) and evicts all nest-mates (eggs or chicks) within 2 days. For this reason, cuckoo parasitism drastically reduces host fitness.
8. The rate of parasitism within the GRW population on the Hungarian Plain is exceptionally high (Moskát & Honza 2002).
9. Cuckoo parasitism thus exerts a remarkable pressure both at the individual and the population level.

The objective of my field experiments and comparative study was to map out certain components of the egg discrimination process and the impact those components have on host decision (of accepting or rejecting an egg).

The components studied were:

- I. the asymmetry of egg shape (Zölei et al. 2012)
- II. interaction of the level of discordancy and within-clutch diversity (Moskát et al. 2014)
- III. reduced clutch size following a parasitic attempt (Moskát et al. 2010)
- IV. long-term trends in the rate of parasitism and rate of rejection (Zölei et al. 2015)

MATERIAL AND METHODS

The channel-side reed-beds in the Upper Kiskunság provide appropriate nesting habitat for the GRW. Our team has searched the reed-beds annually since 1998 to locate GRW nests. Most studies required naturally unparasitized nest so that parasitism could be imitated experimentally by artificial eggs and among controlled conditions. Egg discrimination studies were carried out for 5-6 consecutive days with daily nest controls as earlier experience made it obvious that the majority of hosts makes the rejection / acceptance decision within this period (Moskát & Honza 2002).

- I. According to earlier studies, hosts inspect mostly the blunt egg pole. To refine these tests, we placed an artificial egg in 5-egg GRW clutches by exchanging 1 host egg. The shape of the artificial eggs differed among the 3 experimental groups. Group I received an experimental egg with two sharp poles (2SP), Group II with two blunt poles (2BP) and Group III

received a plasticine egg of a normal (asymmetric) shape. All artificial eggs were of the same colouration and mass.

- II. The two main mechanisms of egg discrimination are memory (partly based on an inherited template) and comparison (discordancy). In order to test whether the proportion (majority or minority status) of the focal egg type affects discrimination or it is mostly the level of discordancy between the focal egg and a template, we used a 6-group experimental design. Minority and majority clutches consisted of manipulated and natural eggs, with the level of discordancy increasing from 'similar' (blue experimental egg) across moderately discordant (green egg) to discordant (orange egg). The experimental groups contained the following combinations of eggs: 1. 1 green+4 normal, 2. 1 green+4 blue, 3. 1 green+ 4 orange, 4. 1 orange+4 natural, 5. 1 orange+4 blue, 6. 1 orange+ 4 green.
- III. Data gathered since 1998 showed that 18% of hosts desert the nest after successfully ejecting a parasitic egg. Desertion and ejection may both be antiparasitic defences, but ejection is also a mechanism connected to nest sanitation (the removal of foreign objects; Moskát et al. 2003). In this study we tested the potential background of an apparently superfluous defence. We experimentally parasitized 3 and 5-egg GRW clutches by exchanging 2 host eggs for 2 non-mimetic eggs. In another experimental group, we solely reduced clutch size by 2 eggs without

introducing the parasitic eggs. In the control group, we immediately replaced the 2 host eggs upon host reaction to the non-mimetic eggs.

IV. The exceptionally high rate of parasitism in the Hungarian Plan makes an intriguing case of the 'sustainability' of parasitism. By comparing our own data with those gathered in the 1940s by Béla Molnár, we looked for changes in the rate of parasitism and the rate of rejection at the population level.

THESES AND CONCLUSIONS

- I. 100% of 2BP eggs were rejected by the host. Normal (asymmetric) eggs were rejected in 70% of the cases while only 50% of 2SP eggs were rejected. These results show that the blunt pole plays a more important role in egg discrimination role even in the lack of variance in colouration. The recognition of 2SP eggs presents the host with a greater challenge.
- II. Orange and green experimental eggs resulted in multiple ejection. The level of discordancy from the template affected the strength of host reaction. Blue experimental eggs induced similar reactions as natural GRW eggs. Thus, the majority egg type within a clutch affects the antiparasitic reaction.
- III. The host may desert the nest following a successful ejection if clutch size is reduced to a critical level. This reaction to clutch reduction is also typical without parasitic attempt. In the control group, the replacement of the own eggs greatly reduced the probability of desertion (to 25%).

With this experiment, we also proved that the decision to desert is only made after egg rejection (ejection) is carried out and is thus based on the assessment of the effective clutch size. In case of a clutch reduced to or less than a critical size, a replacement clutch appears to be the optimal decision for the GRW.

IV. As it became evident from our analysis, neither the rate of parasitism, nor the rate of rejection has changed from the 1940s to 2008. A potential explanation for the maintenance of such unusually high rates is the heterogeneity of the habitat and the immigration of naïve individuals into the local subpopulation.

PUBLICATIONS AS PART OF THE DISSERTATION

- I. Zölei A, Hauber ME, Geltsch N & Moskát C 2012: Asymmetrical signal content of egg shape as predictor of egg rejection by great reed warblers, hosts of the common cuckoo. *Behaviour* 149: 391-406
- II. Moskát C, Zölei A, Bán M, Elek Z, Tong L, Geltsch N, Hauber ME 2014: How to spot a stranger's egg? A mimicry-specific discordancy effect in the recognition of parasitic eggs. *Ethology* 120: 616-626
- III. Moskát C, Rosendaal E, Boers M, Zölei A, Bán M & Komdeur J 2010: Post-ejection nest-desertion of common cuckoo hosts: a second defence mechanism or avoiding reduced reproductive success? *Behav Ecol & Sociobiol* 65: 1045-1053

IV. Zölei A, Moskát C, Bán M 2015: No change in common cuckoo parasitism and great reed warblers' egg rejection after seven decades. *J of Avian Biol* 46: 570-576

Further publications relevant to the dissertation:

Moskát C, Avilés JM, Bán M, Hargitai R & Zölei A 2008: Experimental support for the use of egg uniformity in parasite egg discrimination by cuckoo hosts. *Behav Ecol & Sociobiol* 62: 1885–1890

Moskát C, Bán M, Zölei A, Barta Z, Geltsch N, Hauber ME 2012. Foreign egg recognition in multiple brood parasitism: how to confuse hosts? – Abstract. 14th Biennial meeting of the International Society for Behavioral Ecology, Lund, Sweden

Zölei A, Bán M & Moskát C 2015: Long-term dynamics of common cuckoo and great reed warbler populations in Central Hungary: are avian hosts threatened by their brood parasites? Student Conference on Conservation Science, Tihany, Hungary, 1-5th September 2015

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- Moskát C, Székely T, Kisbenedek T, Karcza Z & Bártol I 2003: The importance of nest cleaning in egg rejection behaviour of great reed warblers *Acrocephalus arundinaceus*. *J Avian Biol* 34:16–19
- Moskát C & Honza M 2000: Effect of nest and nest site characteristics on the risk of cuckoo *Cuculus canorus* parasitism in the great reed warbler *Acrocephalus arundinaceus*. *Ecography* 23: 335-341
- Moskát C & Honza M 2002: European cuckoo *Cuculus canorus* parasitism and host's rejection behaviour in a heavily parasitized great reed warbler *Acrocephalus arundinaceus* population. *Ibis* 144:614–622