Final Report

"Resource use dynamics in an avian brood parasite: the effects of social structure, population fluctuation, and climate change"

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Introduction

Avian brood parasitism is among the most fascinating reproductive forms in nature. A bird species, the brood parasite, lay its egg into the nest of another bird species, the host, and leaves incubation, feeding and rearing to this genetically non-relative species. As hosts suffer from high costs of brood parasitism, in many cases they rear the brood parasitic chick, only, so they have no reproductive success at all. For this reason, they are forced to be adapted against brood parasitism (e.g., with recognition and rejection ability toward foreign eggs). Brood parasites also adapts to hosts, e.g., with laying mimetic eggs, to reduce the efficiency of hosts' antiparasitic defence. Adaptations at both sides results in the co-evolutionary arms race between brood parasites and hosts, showing text-book examples of adaptations (Davies 2000).

As only about 1% of the bird species are brood parasites (Stevens 2013), brood parasitism is not common, and, typically, it is difficult to study. However, in central Hungary there is a unique system, where the common cuckoo (*Cuculus canorus*) parasitizes, almost exclusively, the great reed warbler (*Acrocephalus arundinaceus*) in an unusually high rate (> 50%), and with a high rate of multiple parasitism (Zölei et al. 2015). This peculiar system offers a good chance to study brood parasitism, including several aspects of this ecologically and evolutionary important phenomenon, which cannot be studied where the density either of the brood parasite or the host is low, typically connected with low parasitism rate.

The aims of the project can be grouped into four categories:

(1) To reveal the social structure of brood parasites.
Although there is a wide range of publications related to brood parasitism, most studies focused on the antiparasitic behaviour of the hosts. However, the special life style of the brood parasites sets up the need of adaptations to this reproductive strategy. Although the common cuckoo is one of the most studied brood parasitic species, such studies are scarce, and almost lacking. We revealed the importance of acoustic signalling (sensu Maynard Smith and Harper 2003) in social organization of cuckoos, e.g., reducing aggression both in male and female cuckoos, and in cooperation between sexes (e.g., duetting).

(2) To understand space use, population structure, and territorial behaviour of a brood parasitic species.

New technical development (e.g., GPS tracking methods) let possible to follow the position of individual cuckoos more precisely than with the classical VHF telemetry. We revealed cuckoo space use and territorial behaviour using GPS telemetry in their breeding ground, which also revealed their main migration routes into their wintering areas and back to Hungary.

(3) To explore how acoustic signalling can control social behaviour in a species with small acoustic repertoire.
This topic is the consequence of our results revealed in points (1) and (2). The present study focused on the role of social structure of common cuckoos, and our results revealed the enhanced importance of acoustic communication in this host-brood parasite system. Consequently, we extended our research in this direction, especially in the 2-year extension of the project. We showed that this brood parasitic species with simple acoustic repertoire is able for high level of acoustic communication. We also analysed the potential effects of aberrant calls and syntax errors in their basic call types. We revealed that these acoustic errors cannot reduce signalling efficiency if the error occurs in a secondary element of the call. These results are useful for other bio-acoustical studies explaining high-level acoustic communication with simple repertoire in cuckoos, which are not able to learn new acoustic elements as songbirds (Brenowitz 1991). Despite this constraint, we showed that cuckoos evolved new call types with frequency and speed modulations.

(4) To reveal the potential effects of climate change on a host species and its brood parasite.
We could evaluate the potential effects of climate change on the great reed warbler hosts, and also on their brood parasite, the common cuckoo, using our present and previous data. We focused on the time of the start of breeding in the great reed warbler host, also considering the time of common cuckoo parasitism.

(5) *Others.*
We also investigated a few other questions related to cuckoo-host brood parasitism. For example, we analysed egg mimicry of cuckoo eggs and hosts’ ability to discriminate (recognize and reject) these eggs from the clutch with a new direction of models, the so-called visual modelling (e.g., Hanley 2017).

Main scientific results

We published 21 scientific papers from our results, including 2 reviews in a Springer thematic book about brood parasitism. The following list of results shows a few examples from our results, representing the most important novel findings.

(1) Social structure

(1/a) Are common cuckoo males territorial?

Previously it was questionable if cuckoos are territorial or not. We designed a playback experiment with common cuckoos’ advertisement calls for testing how resident males react to intruding strangers. We revealed that male common cuckoos formed and defended territories during their breeding season (although they could partly overlap each other), and attacked intruding conspecific males. Our playback experiments also revealed that territorial males can distinguish between neighbours and strangers, expressing higher aggression toward the stranger than toward their neighbours (Moskát et al. 2017a). We also revealed that both of the elements in the simple two-note call (“cu” and “coo”) was necessary to identify the neighbour/stranger status of an intruder (Moskát et al. 2018).

(1/b) Are common cuckoo females territorial?

For cuckoo females it was also unknown if they were territorial (Honza et al. 2002) or not (Vogel et al. 2002). In other words, cuckoos should mark and defend their resources, e.g., their laying areas with host nests, from concurrent females. We also applied a playback study for simulating territorial intrusions by conspecific females. We received intensive responses to playbacks by females. Females used their bubbling calls to reduce and avoid direct attack between individuals. A recent study revealed that females’ bubbling call was used in brood parasite-host relationship as an aggressive signal (mimicking the sparrowhawk’s call) toward the host (York and Davies 2017). We revealed that this call type is also used in conspecific relationships, both in male-female and female-female communications (Moskát and Hauber 2019). Later we continued studying the male-female relationship in details, and revealed duetting between males and females. Males use a three-note variant of their bisyllabic call for duetting, and females use their only one call type, the bubbling call for male-female communication (Moskát et al. 2021).

(1/c) Colour morphs of female common cuckoos

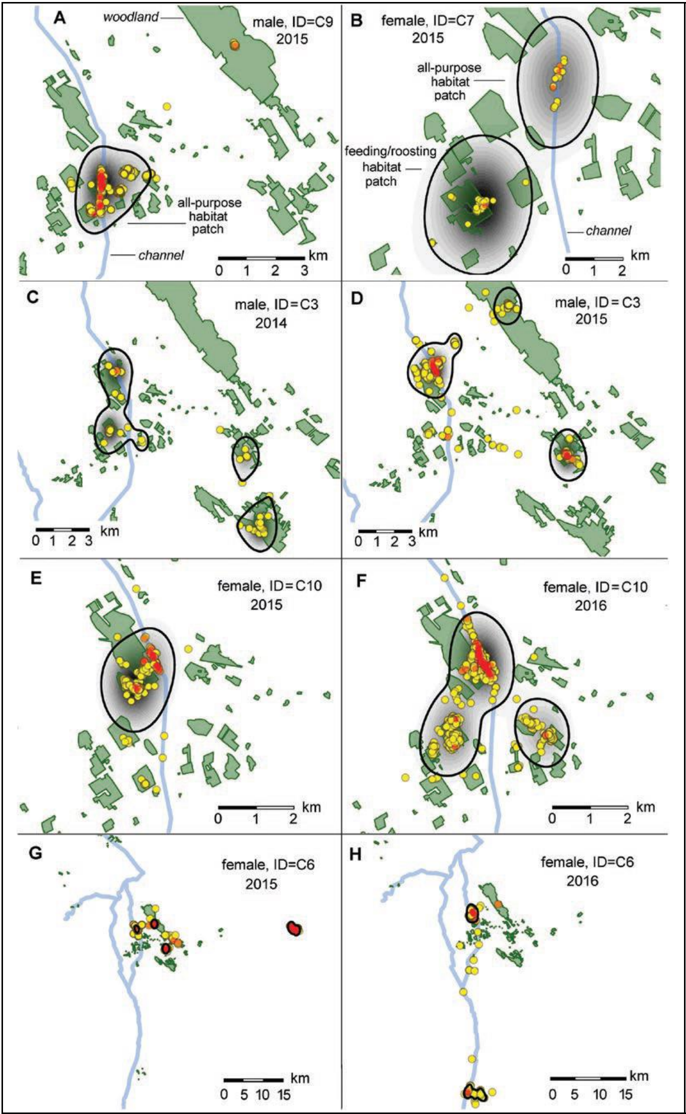
Theory suggests that the rare colour morph has an advantage over the common colour morph in a species. Male common cuckoos are always grey, but females have two colour morphs: the reddish-brownish (hepatic) form, and the grey variant. The hepatic form is typically rare in different populations of the common cuckoo, and it seemed to be more advantageous than the grey morph in many ways (Mappes and Linström 2012). The rare morph may lose its advantage where it is as common as the other morph. This hypothesis can only be tested in Hungary, where the frequencies of the two morphs are similar. In our detailed analyses we proved that the rare form really lost its advantage in our case. We tested aggression of female and male cuckoos toward a new female appeared in the territory, simulated by 3D artificial cuckoos printed by 3D printers, painted either grey or rufous, and accompanied with playback of cuckoo female calls. As we predicted, no significant differences were detected between the live cuckoos’ responses toward the two colour morphs in a field experiment. We concluded that dichromatism in female cuckoos evolved to serve one or more functions other than conspecific signalling (Moskát et al. 2020).

Colour variants of live common cuckoos (*Cuculus canorus*) and decoys used for model presentation experiments, including Eurasian collared dove (*Streptopelia decaocto*) used for a neutral control. Decoys: a: grey cuckoo, b: rufous cuckoo, c: collared dove; live common cuckoos: d: adult male, always grey; e: grey adult female, and a series of rufous adult females: f: brownish female; g: red-brown female; and h: bright orange-red female. Birds were caught by mist-netting at our study site in Hungary (Moskát et al. 2020 Sci Nat).

(2) Space use in common cuckoos

(2/a) Cuckoos' GPS tracking in their breeding area

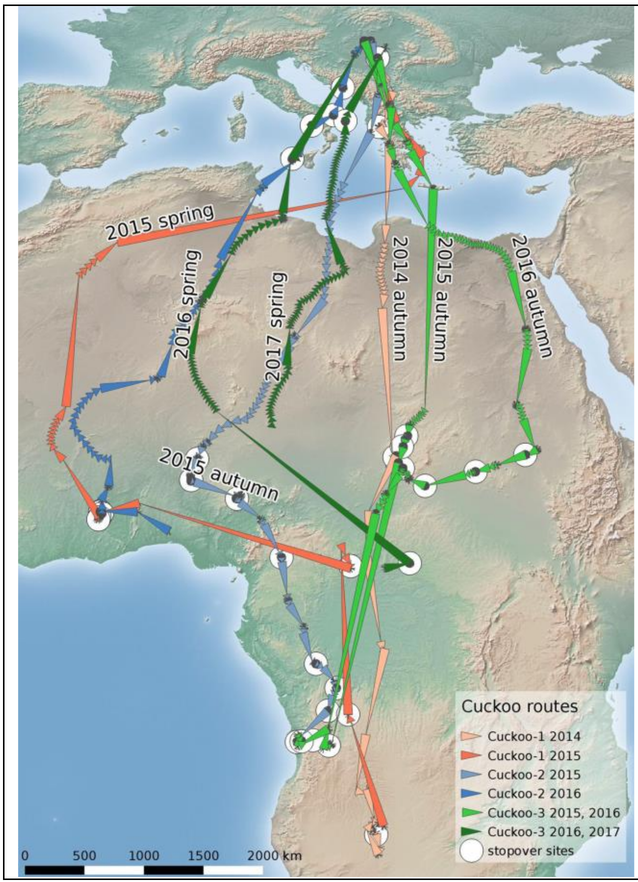
We used GPS tracking on male and female common cuckoos to reveal their daily and seasonal space use. We applied the non-satellite, UHF GPS tracking method, at the first time on this species (on 9 males and 6 females). As the male cuckoos are difficult to separate from females of the grey colour morph, at the beginning of the study we validated morphological parameters in respect to DNA sampling, based on the presence of the avian W chromosome (Moskát et al. 2017a). Our results revealed that some of the cuckoos showed bimodal habitat use (feeding and breeding habitats), but others used only one habitat type. Data were analysed by the minimum convex polygon and kernel density estimation methods. The latter proved to be better for territory size estimation, which varied in a wide range (1-17 km^2). Male and female home ranges often overlapped each other. We also revealed partly overlapping territories. We suggest future studies on the hierarchy of cuckoo individuals, which could control cuckoos' social organisation.



Examples of habitat and patch use by common cuckoos, where their hosts, great reed warblers, nest in the reedbeds of small channels. (Blue lines = channels, green patches = woodlands, white background = arable fields.) (A) An example of unimodal habitat use by a male cuckoo. (B) An example of bimodal habitat use by a female cuckoo. Home ranges of a male (C, D) and 2 female cuckoos (E, F) and (G, H) were from 2 consecutive years and estimated by the kernel density estimation (UD 85%) method (Moskát et al. 2019 Auk).

(2/b) *Cuckoos' GPS tracking in their migration routes and wintering areas*

We found a few cases of tagged cuckoos returned from their wintering grounds, and these data were suitable to localize their wintering areas in Africa, as well as their speed and the routes of their migrations (Bán et al. 2018).



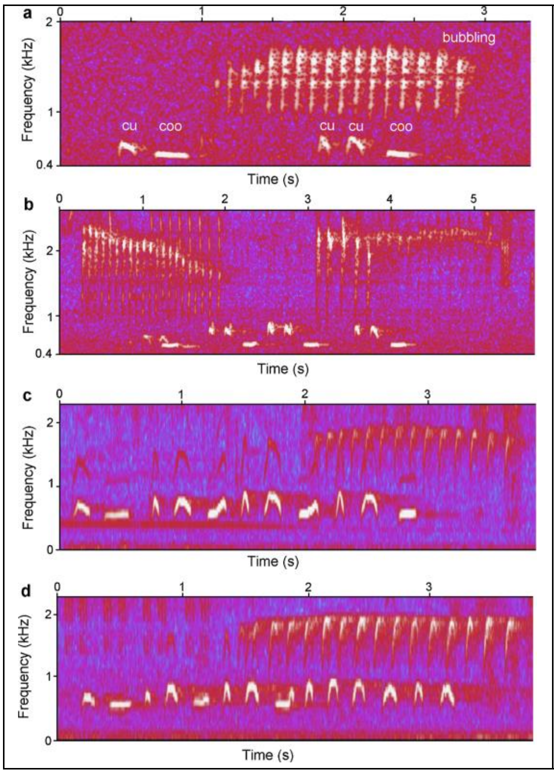
Loop migration of three adult common cuckoos from breeding grounds in Hungary to Africa and back. Colours indicate the autumn (lighter) and spring (darker) migration of the three common cuckoos: orange cuckoo 1 (male); blue cuckoo 2 (female); green cuckoo 3 (female, tracked in two consecutive years). Stopover sites are marked with white patches (Bán et al. 2018).

(3) Acoustic signalling in the common cuckoo

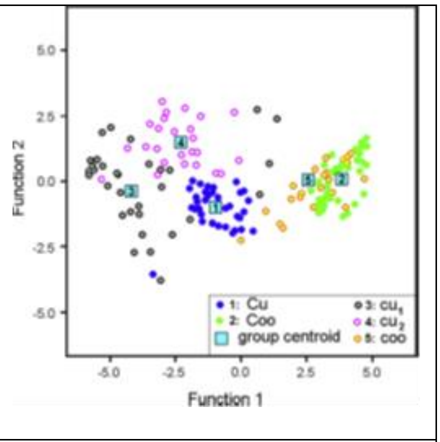
Our results in the present project revealed the importance of acoustic communication in social organization of the common cuckoo. It is a surprising result, as cuckoos' acoustic repertoire is very simple. Although males use a few different calls, females use only one multifunction call, the bubbling call. Despite many birds, including the passerines, cuckoos are known as vocal non-learners (see above). It means that cuckoos have genetically fixed (inherited) vocal elements, they cannot learn new songs or calls. Despite this constraint, their acoustic communication is effective, and we revealed how they enlarge their acoustic repertoire.

(3a) Cuckoos evolved a three-note variant of their two-note main call type

Despite cuckoos are vocal non-learners, we found that the three-note variant of their two-note call has got a new function. The two-note basic call ("cu-coo") is a used for advertising territories, but the three-note variant ("cu-cu-coo") has a different signalling value, it is used for communication with females. Male and female cuckoos often "duetting" with this call and females' bubbling call (Moskát and Hauber 2021). Not only the first note is repeated in the three-note call type, but it was uttered with higher speed, and the frequency of the first two elements were higher than in the basic two-note call type. This finding showed that even vocal non-learner species with simple repertoire can evolve new signals, despite of their constraints in their vocalization ability.



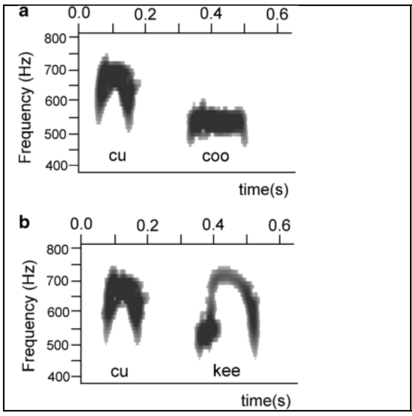
Spectrograms of female common cuckoos’ bubbling calls partly overlapping with males’ 3-note (“cu-cu-coo”) calls. (a) The bubbling call precedes the only 3-note call. (b) Two bubbling calls and four 3-note calls. (c) The 3-note calls precede the bubbling call. (d) A sequence of 3-note male cuckoo calls, starting with a normal 2-note (“cu-coo”) call, and followed by a bubbling call of a female (Moskát and Hauber 2021 Behav Process).



A plot of discriminant scores of the elements of 2-note and 3-note male common cuckoo calls generated by canonical discriminant functions. (Elements of the calls: “Cu” and “Coo” in the 2-note variant, and “cu1”, “cu2” and “coo” in the 3-note form; Moskát and Hauber 2021 Behav Process).

(3b) Aberrant calls in the cuckoo

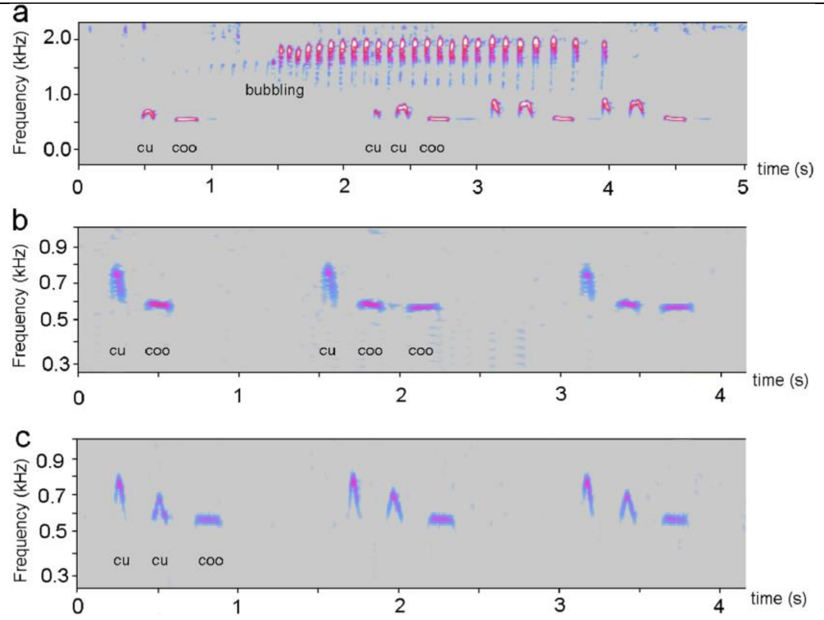
We found that some of the male cuckoos utter an aberrant version of their basic, two-note advertisement call. We showed by a playback experiment that this error did not reduce the signalling value of this call type, as it is located in the second note. We showed that in the advertisement call the first note has more importance than the second note. The first note alone may have the same communication efficiency as the whole two-element call (Moskát et al. 2021), but it has some relevance in individual recognition (Moskát et al. 2018).



Male common cuckoo (*Cuculus canorus*) calls: (a) a normal call (“cu-coo”) with the typical two notes; (b) an aberrant call (“cu-kee”) with the different second note (Moskát et al. 2021 Behav Ecol Sociobiol).

(3c) Syntax errors in cuckoo calls

Syntax rules play important roles in animal communication (Bolhuis et al. 2018). The syntax-semantics relationships are the basic of a language-type communication (Suzuki et al. 2019). We found several syntax errors in cuckoos’ calling sequences (e.g., repetition of an element, delete of an element, reversion of the order, etc.). We found that syntax errors only affect communication when it is related to the first note, as the second note has less importance. The only exception is the males' three-note call (see at point (3/a)), where the repetition of the first note was accompanied with elevated frequency and higher speed (Moskát and Hauber 2022).



Examples of male (and female) common cuckoo calls. (a) The natural forms of 2-note ("cu-coo") and 3-note ("cu-cu-coo") calls of males, together with a female-specific bubbling call also indicated on the sonogram. (b) A "cu-coo" call and the first two calls in a series of "cu-coo" calls with a syntactic error, where the second note is repeated (the "coo" element, i.e. "cu-coo-coo"). (c) A normal "cu-coo" call and calls from a series of "cu-cu-coo" syntax errors. A proportion of (b,c) were uttered by the same individual cuckoo. Note that the natural 3-note call in (a) is normal (natural), but the 3-note call in (c) differs from it in several respect (see more details in the text): it specifically suffers from a syntactic error, where the first note of the normal "cu-coo" call ("cu") is repeated. In (c) the decreasing frequencies of the first two "cu" elements are a unique case, showing that cuckoos are capable of frequency modulation (typically, the second note is about as high as that of first element; Moskát and Hauber 2022 Sci Rep).

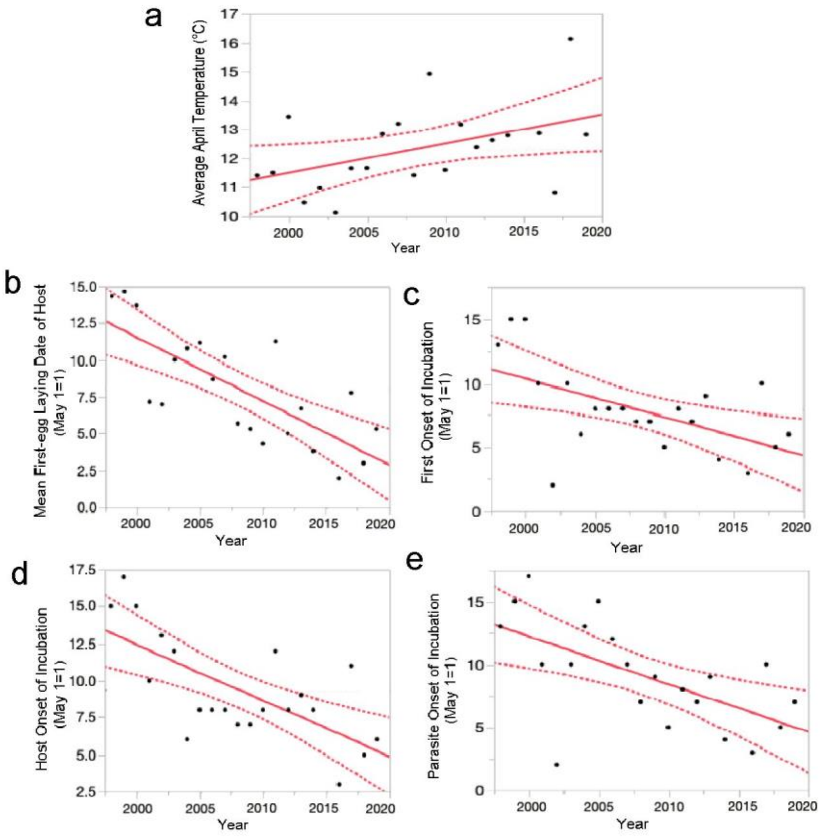
(3/d) Interspecific effects (brood parasite-host communication)

Common cuckoo females' bubbling call has multiple functions: territory advertisement, male-female conspecific communication (see above) and it is an aggressive signal toward the host. The bubbling call mimics a raptors' (the sparrowhawk *Accipiter nisus*) call, and this hawk-like call increased the success of parasitism by diverting host parents' attention away from the clutch and towards their own safety in the reed warbler (*Acrocephalus scirpaceus*; York and Davies 2017). For example, it delayed returning to the nest. We also played bubbling calls to great reed warblers, a much greater and more aggressive host than the reed warbler (32 g and 12 g body masses of the great reed warbler and the reed warbler, respectively). We found that bubbling calls dampened the aggression of this greater Acrocephalus warbler, so this hawk-like effect of the bubbling call seems to be general (Marton et al. 2020).

Interestingly, we also revealed that not only hosts could utilize the acoustic signals of the cuckoo, but cuckoos also can utilize hosts' aggressive calls when they are searching for host nests (Marton et al. 2019).

(4) Effects of climate change

Recent climatic changes affect bird populations, especially their reproductive success. Unfortunately, long-term data on these changes are limited. We analysed a local breeding site's weather changes in Central Hungary and shifts in the reproductive timing of two interacting long distance migratory bird species in a 22-year-long data set. Some weather and all of our breeding phenology metrics of host great reed warblers and common cuckoos showed strong statistical patterns, with spring temperatures increasing and host and parasite laying dates becoming earlier with advancing years. However, temporally decoupled weather metrics did not consistently predict host or brood parasitic reproductive onsets. This suggests that breeding site weather change does not cause the ongoing advancement in the reproductive timing of these avian hosts and their brood parasites (Hauber et al. 2021).



Increasing mean April daily temperatures (a) near our study site in Central Hungary and changes in the host's and parasite's breeding metrics (b-e), across the 22-year duration of our study, as function of advancing years. The plots depict the mean slopes and their 95th percentile confidence intervals (Hauber et al. 2021 Ethol Ecol Evol).

(5) Others

Just recently a new set of models has been developed to evaluate parasitic egg mimicries (visual modelling; Hanley et al. 2017). We applied these models to our host-brood parasite relationship. We experimentally parasitized host clutches with model eggs painted along a colour gradient. Our analyses revealed that chromatic and achromatic just-noticeable differences (JNDs) along the colour gradients affect egg rejection rates, but we found no such effect by maculation. Directional egg colour discrimination shown here and in a suite of recent studies on other host species may shape the cognitive decision rules that hosts use to recognize foreign eggs and affect the course of evolution in parasitic egg mimicry (Abolins-Abols et al. 2019).

We also studied how multiple parasitism reduces hosts' egg rejection ability. Although rejection rates in single parasitism were positively related to the perceptual distance between own and foreign eggs in the nests, rejection thresholds were more permissive (error prone) both with greater proportions of foreign eggs per clutch and/or when the suite of foreign eggs was perceptually more variable within the nest. These results suggest that parasites, through multiple parasitism, can partially overcome the evolution of hosts' recognition of mimetic parasite eggs (Manna et al. 2019).

We also synthesized our knowledge on brood parasite-host relationships, based on the present and previous projects, in two review papers (Manna et al. 2017, Moskát et al. 2017b).

Conferences

We presented some of our most important results at scientific conferences. For example, at international conferences: ISBE (International Society for Behavioural Ecology) 2018, Minneapolis, USA (poster), ESA (the Ecological Society of America) 2018, New Orleans, USA (talk), IOC (International Ornithological Congress) 2018, Vancouver, Canada (speed talk and poster), European Ornithological Conference 2019, Cluj-Napoca, and BOU (British Ornithologists' Union) 2022 conference (planned oral presentation). We also presented our results at Hungarian meetings and conferences: Udvardy Memorial Meeting 2017, DAB, Debrecen (oral presentation), Conference of the Hungarian Ethological Society 2021, online (plenary talk).

References

Abolins-Abols M, Hanley D, Moskát C, Grim T, Hauber ME 2019. Anti-parasitic egg rejection by great reed warblers (*Acrocephalus arundinaceus)* tracks differences along an eggshell color gradient. Behav Process 166: 103902.

Bán M, Moskát C, Fülöp A, Hauber ME 2018. Return migration of Common Cuckoos (Cuculus canorus) between breeding grounds in Hungary and wintering grounds in Africa as documented by non-PTT GPS technology. J Ornithol 159: 337–344.

Bolhuis JJ, Beckers GJL, Huybregts MAC, Berwick RC, Everaert MBH 2019. Meaningful syntactic structure in songbird vocalizations? PLoS Biol. 16: e2005157.

Brenowitz EA 1991. Evolution of the vocal control system in the avian brain. Semin Neurosci 3: 339–407.

Davies NB 2000. Cuckoos, cowbirds and other cheats. T and A D Poyser.

Hanley D, Grim T, Igic B, Samaš P, Lopez AV, Shawkey MD, Hauber ME 2017. Egg discrimination along a gradient of natural variation in eggshell coloration. Proc R Soc B Biol Sci 284: 201625920.

Hauber ME, Elek Z, Moskát C 2021. Advancing onset of breeding dates in brood parasitic common cuckoos and their great reed warbler hosts over a 22-year period. Ethol Ecol Evol 33: 553-560.

Honza M, Taborsky B, Taborsky M, Teuschl Y, Vogl W, Moksnes A, Røskaft E 2002. Behaviour of female common cuckoos, *Cuculus canorus*, in the vicinity of host nests before and during egg laying: a radiotelemetry study. Anim Behav 64: 861–868.

Manna TJ, Moskát C, Hauber ME. 2017. Cognitive decision rules for egg rejection. pp. 437-448. in Soler M (ed) Avian brood parasitism: behaviour, ecology, evolution and coevolution. Springer Int Pub, Cham, Switzerland.

Manna TJ, Moskát C, Tong L, Bán M, Aidala Z, Low J, Hauber ME 2019. Multiple parasitism reduces egg rejection in the host (*Acrocephalus arundinaceus*) of a mimetic avian brood parasite (*Cuculus canorus*). J Comp Psych 133: 351–358.

Mappes J, Lindström L 2012. How did the cuckoo get its polymorphic plumage? Science 337: 532.

Marton A, Fülöp A, Bán M, Hauber ME, Moskát C 2020. Female common cuckoo calls dampen the mobbing intensity of great reed warbler hosts. Ethology 127: 286–293.

Marton A, Fülöp A, Ozogány K, Moskát C, Bán M 2019. Host alarm calls attract the unwanted attention of the brood parasitic common cuckoo. Sci Rep 9: 18563.

Maynard Smith J, Harper D 2003. Animal signals. Oxford Univ Press.

Moskát C, Hauber ME 2019. Sex-specific responses to simulated territorial intrusions in the common cuckoo: a dual function of female acoustic signaling. Behav Ecol Sociobiol 73: 60.

Moskát C, Hauber ME 2021. Male common cuckoos use a three-note variant of their “cu-coo” call for duetting with conspecific females. Behav Process 191: 104472.

Moskát C, Hauber ME 2022. Syntax errors do not disrupt acoustic communication in the common cuckoo. Sci Rep 12: 1568.

Moskát C, Bán M, Fülöp A, Bereczki J, Hauber ME 2019. Bimodal habitat use in brood parasitic common cuckoos (*Cuculus canorus*) revealed by GPS telemetry. Auk 136: 1–12.

Moskát C, Elek Z, Bán M, Geltsch N, Hauber ME 2017a. Can common cuckoos discriminate between neighbours and strangers by their calls? Anim Behav 126: 253–260.

Moskát C, Hauber ME, Louder MIM 2017b. The evolution of nest sharing and nest mate killing strategies in brood parasites. pp. 475-492. in Soler M (ed) Avian brood parasitism: behaviour, ecology, evolution and coevolution. Springer Int Pub, Cham, Switzerland.

Moskát C, Hauber ME, Ruzicková J, Marton A, Bán M, Elek Z 2020. Female-female aggression and male responses to the two colour morphs of female common cuckoos. Sci Nat 107: 28.

Moskát C, Hauber ME, Bán M, Fülöp A, Geltsch N, Marton A, Elek Z 2018. Are both notes of the common cuckoo’s call necessary for familiarity recognition? Behav Process 157: 685–690.

Moskát C, Taylor DM, Hauber ME 2021. Effective conspecific communication with aberrant calls in the common cuckoo (*Cuculus canorus*). Behav Ecol Sociobiol 75: 7.

Stevens M 2013. Bird brood parasitism. Curr Biol 23 (20): R909-R913.

Suzuki TN, Wheatcroft D, Griesser M 2019. The syntax–semantics interface in animal vocal communication. Philos Trans R Soc B. 375: 20180405.

Vogl W, Taborsky B, Taborsky M, Teuschl Y, Honza M 2004. Habitat and space use of European cuckoo females during the egg laying period. Behaviour 141: 881–898.

York J, Davies NB 2017. Female cuckoo calls misdirect host defences towards the wrong enemy. Nat Ecol Evol 1: 1520–1525.

Zölei A, Bán M, Moskát C 2015. No change in common cuckoo *Cuculus canorus* parasitism and great reed warblers ’ *Acrocephalus arundinaceus* egg rejection after seven decades. J Avian Biol 46: 570–576.