ORIGINAL PAPER

Does experimentally simulated presence of a common cuckoo (*Cuculus canorus*) affect egg rejection and breeding success in the red-backed shrike (*Lanius collurio*)?

Piotr Tryjanowski[1,2] · Artur Golawski[3] · Mariusz Janowski[1] · Tim H. Sparks[1,4]

Abstract

Providing artificial eggs is a commonly used technique to understand brood parasitism, mainly by the common cuckoo (*Cuculus canorus*). However, the presence of a cuckoo egg in the host nest would also require an earlier physical presence of the common cuckoo within the host territory. During our study of the red-backed shrike (*Lanius collurio*), we tested two experimental approaches: (1) providing an artificial "cuckoo" egg in shrike nests and (2) additionally placing a stuffed common cuckoo with a male call close to the shrike nest. We expected that the shrikes subject to the additional common cuckoo call stimuli would be more sensitive to brood parasitism and demonstrate a higher egg rejection rate. In the years 2017–2018, in two locations in Poland, a total of 130 red-backed shrike nests were divided into two categories: in 66 we added only an artificial egg, and in the remaining 64 we added not only the egg, but also presented a stuffed, calling common cuckoo. Shrikes reacted more strongly if the stuffed common cuckoo was present. However, only 13 incidences of egg acceptance were noted, with no significant differences between the locations, experimental treatments or their interaction. Analysis of breeding success revealed significant differences between the locations, between experimental treatments and their interaction, which suggests a strong location effect. The red-backed shrike is an efficient rejector of foreign eggs. It would be interesting to see how similar tests affect hosts that have much higher rates of brood parasitism and egg acceptance.

Keywords Acceptance rate · Arm race · Co-specific mobbing · Eggs · Experimental design · Brood parasitism

Introduction

Breeding parasitism reduces the reproductive success of hosts; thus, hosts have evolved anti-parasitic strategies (Dawkins and Krebs 1979; Rothstein and Robinson 1998). The most widespread and effective anti-parasitic behaviour is egg rejection, and the ejection of a foreign egg in some species occurs in more than 90% of clutches (Honza et al. 2007; Soler et al. 2017), but a wide range of rejection rates have been documented (Lovászi and Moskát 2004). Hosts can also reject a parasitic egg by deserting the clutch, but the frequency of this defence mechanism is usually many times lower than egg ejection (Moskát and Honza 2002; Servedio and Hauber 2006; Schulze-Hagen et al. 2009). Defending the nest by mobbing is also an important anti-parasitic strategy used by many species (Welbergen and Davies 2009; Gloag et al. 2014; Carmody et al. 2016; Ma et al. 2018). Exceptionally, defence mechanisms occur also at the nestling stage, for example by the large-billed gerygone (*Gerygone magnirostris*) ejecting nestlings of the little bronze-cuckoo (*Chrysococcyx minutillus*) (Sato et al. 2010). Thus, the defence mechanism at the nestling stage may evolve when host defence at the egg stage is evaded by the parasite.

The antiparasite adaptations of many hosts towards common cuckoo (*Cuculus canorus*) have been studied (Schulze-Hagen et al. 2009; Møller et al. 2011). Despite many publications, some behavioural aspects of hosts

✉ Piotr Tryjanowski
  Piotr.Tryjanowski@gmail.com

1 Department of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71c, 60-625 Poznan, Poland

2 Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 16500 Prague 6, Czech Republic

3 Faculty of Natural Science, Siedlce University of Natural Sciences and Humanities, Prusa 14, 08-110 Siedlce, Poland

4 Museum of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

towards parasites are still not well understood. The interaction between hosts and brood parasites are often described as the arm race hypothesis (Langmore et al. 2003; Moskát 2005). However, the host's response to adding an artificial egg imitating that of a parasite coincidentally with the use of a dummy common cuckoo and its call has been rarely studied, and the results are not conclusive. Some authors (e.g. Bartol et al. 2002) argue that the sight of the common cuckoo at the nest may increase egg rejection rate by the great reed warbler (*Acrocephalus arundinaceus*), but this is mainly affected by the degree of mimicry of the parasitic egg. On the other hand, Trnka and Grim (2014), in studies of the same species, argue that differences in host behavioural types, rather than host egg discrimination ability, may predict rejection rate of the egg. It is worth debating whether experiments with more stimuli (e.g. an egg plus dummy birds plus calls) are definitely much closer to the real biological situation (Moksnes et al. 1991; Krüger 2007; Trnka and Grim 2014). Hence, the main aim of the current study was to check how two experimental approaches adding an artificial egg to the host nest either (1) alone, or (2) accompanied by a dummy common cuckoo and call, may change the behavioural reaction of the host and influence egg acceptance/rejection rates. We chose the red-backed shrike (*Lanius collurio*) which used to be a frequently used host of the common cuckoo in Europe (Makatsch 1955). Moskát and Fuisz (1999) reported that up to 5% of the population of this species was parasitized by common cuckoo in the Czech Republic, Germany and Ukraine, but subsequently several years of rapid decline have been noted in its parasitism rate (Lovászi and Moskát 2004; Adamík et al. 2009). In the current study we also checked how strongly male and female red-backed shrikes reacted to the artificial presence of common cuckoo in their territory.

Material and methods

Study area

Fieldwork was conducted in the 2017 and 2018 breeding seasons at two study locations, one in eastern and one in western Poland. The study area in eastern Poland at Podlasie (P) near Siedlce (3 km^2; 52°12′N, 22°17′E) was dominated by meadows and pastures divided by barbed wire fences into small fields; single bushes and trees were also present. Part of the research area was situated along a railway line with plenty of shrubs suitable as shrike nesting sites. The breeding densities here reached up to 19 pairs/km^2 (Antczak et al. 2009). The study in western Poland was conducted in an agricultural landscape in Wielkopolska (W) near Odolanów (51°34′N, 17°40′E) and was selected because it had already been the subject of previous studies

(Hromada et al. 2008; Trjanowski and Morelli 2015). The study location (380 km^2) is an extensively used agricultural landscape and comprises a mosaic of meadows and pastures (44%), arable fields (42%), midfield woodlots of different ages (6%), plus scattered trees and discontinuous linear habitats, mainly consisting of mixed rows of trees and shrubs (see details in Hromada et al. 2002).

Experimental design

Nests of shrikes were found by systematic searches of their typical nesting habitats: woodland edges, single trees and shrubs. For the experiment we used active nests in which female shrikes had just laid eggs or had started incubation. We randomly divided all detected nests into two groups. In the first group ($n = 66$, P:30, W:36) we added one artificial egg imitating a common cuckoo egg. Common cuckoos normally remove a host egg during parasitism, but Davies and de L Brooke (1988) have shown that removal does not affect the probability of rejection by European hosts so we did not remove a shrike egg. The artificial common cuckoo egg was added either during the laying period (at least one host egg already present) or early incubation period (days 1–5 of incubation) of the host, because shrikes eject cuckoo eggs with similar intensity during these two periods (Moskát and Fuisz 1999). We used a filled, hard plastic egg, 19×13 mm, which was within the dimensions of shrike eggs (Tryjanowski et al. 2004; Golawski and Mitrus 2018). Using online photos as a reference, we painted artificial eggs using coloured markers to resemble common cuckoo eggs laid in shrike nests (Fig. 1). In the second group of nests ($n = 64$, P:28, W:36), in addition to adding an artificial egg, a dummy common cuckoo (stuffed birds, grey morphs) was also used. The posture of the dummy birds (one stuffed bird per study area; perched bird with folded wings) was consistent in both study areas because the posture of a predator influences the response by birds (Sealy et al. 1998, but see also Marton et al. 2021). At the same time, the male common cuckoo call (for example, described here: Tryjanowski et al. 2018a) was played from an mp3 player located under the dummy common cuckoo. Because we planned to observe the behaviour of the shrikes in relation to the dummy, it had to be placed in a clearly visible place, so the dummy was placed 7 m away from the nest on a 1.5-m-high pole, this was also a reason to work with the male common cuckoo call, and we made observations from ca. 30 m away. Each session (presentation of dummies) lasted 5 min. During each session, we investigated aggressive behaviour of shrikes towards the dummy common cuckoo. We used the voice of the male common cuckoo as in the field, when males call much more and are then probably better known to red-backed shrikes than the generally much less

Fig. 1 A complete clutch of the red-backed shrike with an added artificial egg (lighter colour)

frequently calling females which also behave secretly. We recorded the response behaviour of shrikes on a 4-point scale for each sex: (0) no aggression; (1) weak reaction, bird responds slightly, but does not approach and does not fly in the direction of the dummy; (2) bird responds intensively, approaching and flying in the direction of the dummy; and (3) shrike physically attacks and pecks at the dummy common cuckoo (similar to the method used by Tryjanowski and Goławski 2004; Polak 2019). According to Rasmussen et al. (2012), eggs accepted for 5 days are also likely to be accepted for the remainder of the incubation so we inspected the nest after five days to record the fate of the previously placed artificial egg. Shrike responses were categorized as either acceptance or rejection of the cuckoo egg. Rejections included both egg ejections and nest desertions (according to Moskát and Honza 2002). Nest success or failure was determined by the presence or otherwise of at least one fledgling. Because red-backed shrikes in Poland have low philopatry (Tryjanowski et al. 2007), there was very little probability of experimenting on the same individual in the two successive years. In both study areas we did not find any naturally parasitised broods of shrikes by common cuckoos, and generally they have a very low parasitism rate in Poland (Kuzniak 1991; Wesołowski and Mokwa 2013). We also noted larders in shrike territories as an indicator of bird and territory quality (Hromada et al. 2008; Morelli et al. 2015). During the experiment we did

not observe the desertion of any red-backed shrike nest as a consequence of our presence.

Statistical analyses

Nonparametric methods were used to compare the 4-point behaviour scores (see above). Spearman rank correlation was used to compare male and female scores within a pair; Mann Whitney tests were used for unpaired data (i.e. behaviour scores for the two experimental approaches) and Wilcoxon tests for paired data (male vs. female within a pair). Binary logistic regression was used to compare the binary variables (egg acceptance no/yes; breeding success no/yes) between locations, the two experimental approaches ("dummy", "egg") of the study and their interaction. Covariates were added to the model; behavioural responses were as described above, but we also noted larders in shrike territories, and because they were so rare (see also Morelli et al. 2015) we coded this as a binary value: 0—no larder found and 1—larder found. The same type of analysis was used to compare breeding success (binary response: 0—failure, 1—success) between locations, the two experimental approaches and their interaction, and whether the birds accepted the artificial egg or rejected it. The analysis was carried out in SPSS 21.0 (IBM SPSS Statistics for Windows 2012). Only results with a probability of $\alpha \leq 0.05$ were regarded as statistically significant.

Results

Behavioural reactions towards the common cuckoo for the "dummy" part of the study were detected for 73% of male and for 48% of the female red-backed shrikes. There was a significant correlation between behaviour scores for male and female birds within a pair during the "dummy" part of the study ($r_s = 0.541$, $P < 0.001$), and the male behaviour scores were significantly higher than female scores (Wilcoxon test, $P < 0.001$). This remained true for the Wielkopolska records ($P < 0.001$) when considered separately but not for the Podlasie records ($P = 0.140$; Fig. 2). Behaviour scores at Wielkopolska during the "dummy" part of the study were significantly higher than at Podlasie (Mann Whitney test, $P = 0.008$) for male birds, but this was not confirmed for female birds ($P = 0.130$; Fig. 2). In four cases, shrikes mobbing the dummy common cuckoo were supported by barred warbler *Sylvia nisoria*.

There were only 13 incidences of egg acceptance, while egg ejections were found for 115 clutches and nest desertions for two clutches. The binary logistic regression model for egg acceptance revealed no significant differences between the locations ($P = 0.117$), between the two experimental approaches ($P = 0.186$), or their interaction ($P = 0.125$; Fig. 3). Despite this, and with caveats on small sample size, the effect of the dummy appeared to increase acceptance at Podlasie, but to reduce it at Wielkopolska. Extending this model to include male behaviour score as a covariate was not significant ($P = 0.478$).

Breeding success was recorded for 61 (47%) of the 130 nests. The binary logistic regression model for breeding success revealed significant differences between the locations ($P = 0.049$), between the two experimental approaches ($P = 0.003$) and their interaction ($P = 0.003$; Fig. 4). The effect of the dummy appeared to reduce nesting success at Podlasie, but to increase it at Wielkopolska. Extending this model to include male behaviour score as a covariate was not significant ($P = 0.980$). An alternative covariate of presence of a larder was also not significant ($P = 0.105$). However, a third option, of whether the egg was accepted, was a significant addition ($P = 0.027$), with lower success associated with egg acceptance.

Discussion

The red-backed shrike reactions to the calling dummy common cuckoo were clear. Male red-backed shrikes were more aggressive towards the dummy common cuckoo than females, although the behaviour across breeding pairs was correlated, as described in other studies (Tryjanowski and Golawski 2004; Polak 2016; Syrova et al. 2016). Moreover, during the experiment we also observed the barred warbler expressing antagonistic behaviour towards the dummy common cuckoo/call together with the red-backed shrikes. Both species often share similar habitats and territories, are known to mob common cuckoos (Tryjanowski et al. 2018b) which are predators in their territories (Polak 2016), and sometimes express this aggressive behaviour simultaneously

Fig. 2 Stacked percentage bar chart showing behaviour codes for the "dummy + egg" part of the study at the two locations (P Podlasie; W Wielkopolska) and for female and male birds. Scale: 0—no aggression; 1—weak reaction from a distance; 2—bird responds, approaching and flying in the direction of the dummy common cuckoo; 3—bird responds intensively, with physical attack towards the dummy common cuckoo. Sample sizes are 28 for Podlasie and 36 for Wielkopolska. See text for details of statistical significance
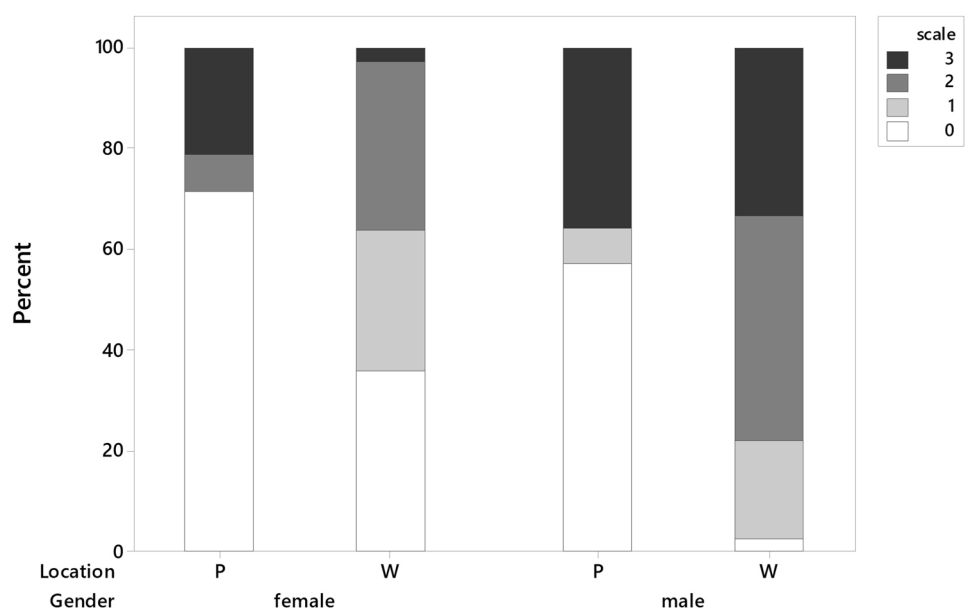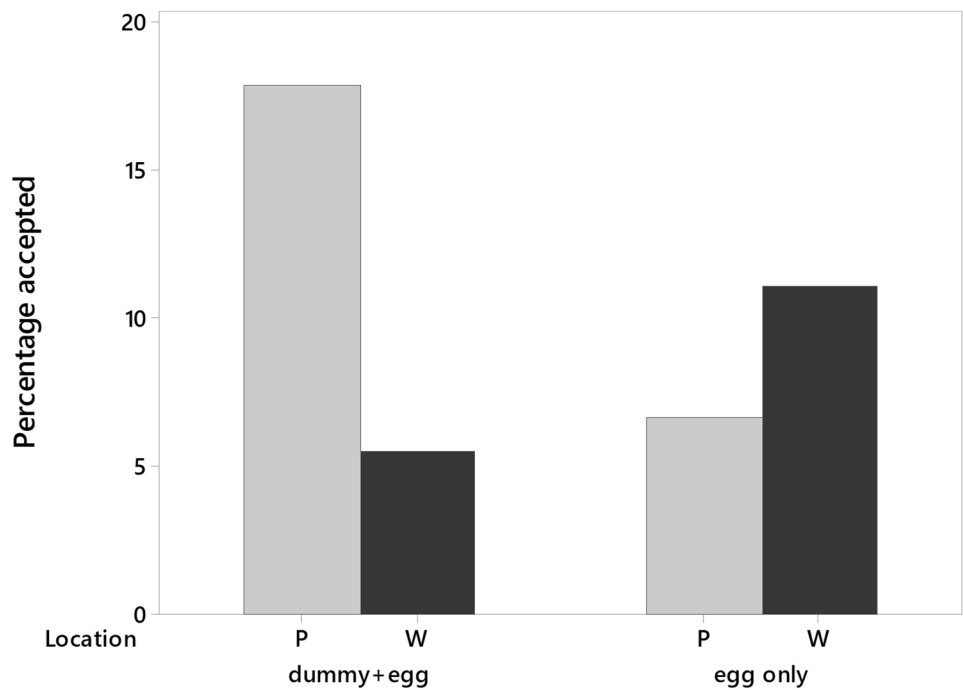
Fig. 3 Percentage of egg-additions accepted for the two locations (P Podlasie; W Wielkopolska) and for the "dummy + egg" and "egg only" parts of the study. Sample sizes for the four bars are, from left to right, 28, 36, 30 and 36. See text for details of statistical significance


(Polak 2016, 2019). Perhaps the barred warbler recognized the alarm calls of red-backed shrike in response to common cuckoos, as shown in *Acrocephalus* warblers (Yu et al. 2019).

Shrikes recognised and mobbed dummy common cuckoos, and we would have assumed that these added stimuli would affect vigilance, but this did not translate into a significant effect on egg rejection rate. Possibly, shrikes did

not associate the presence of the dummy common cuckoo with the addition of an egg to the nest. On the other hand, the red-backed shrikes had very effective egg recognition and consequently a low artificial cuckoo egg acceptance, similar to other studies on the red-backed shrike—common cuckoo brood parasitism system (Moskát and Fuisz 1999; Lovászi and Moskát 2004). However, we have to note that the current

Fig. 4 Percentage of nest success for the two locations (P Podlasie; W Wielkopolska) and for the "dummy + egg" and "egg only" parts of the study. Sample sizes for the four bars are, from left to right, 28, 36, 30 and 36. See text for details of statistical significance
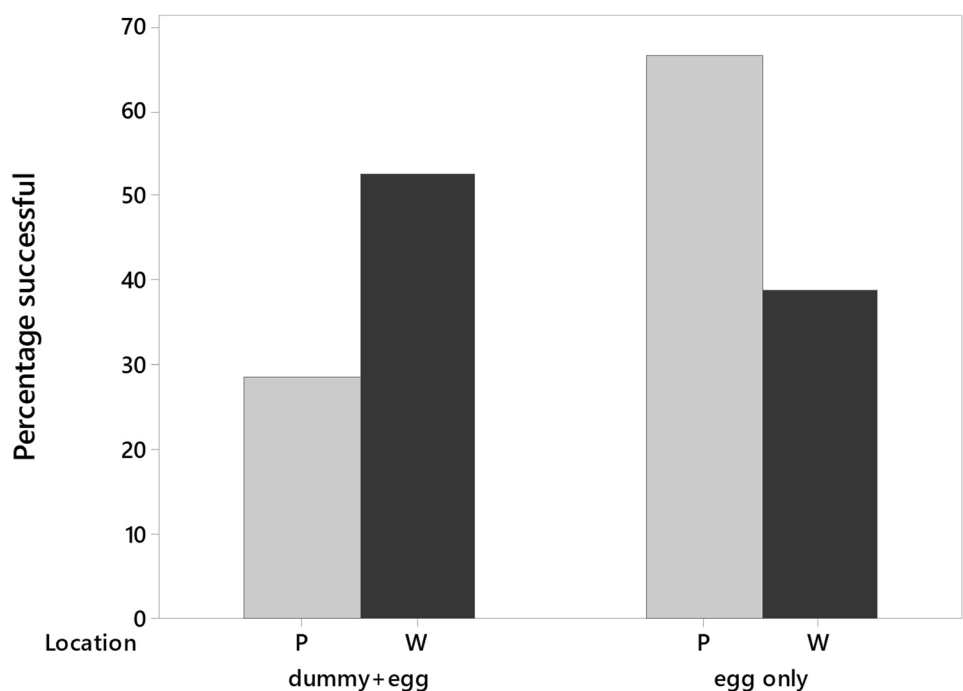
situation is probably quite novel from an evolutionary perspective. Half a century ago (and hence many shrike generations) the red-backed shrike was an important host for common cuckoo in Poland (Kuzniak 1991; Wesołowski and Mokwa 2013). However, more recently, this phenomenon is much less frequent in Central Europe (Lovászi and Moskát 2004; Adamík et al. 2009).

Surprisingly, the most significant effect in our study of responses of red-backed shrike towards common cuckoo was that in breeding success between the studied locations. Differences in red-backed shrike success are partially related to local conditions such as food supplies and weather effects (Kuzniak 1991; Antczak et al. 2009; Golawski and Golawska 2019). However, there was also a visible effect arising from common cuckoo presence. In other studies, differences were also noted between local populations, which can be related to host and brood parasite densities, their behaviour and a realised arm race strategy created during co-existing generations in the past (Moskát 2005; Krüger 2007; Trnka et al. 2012; Trnka and Grim 2014).

The present study tested the arm race theory, in particular the red-backed shrike—common cuckoo system, but it would be interesting to see how similar tests affect hosts that have much higher rates of brood parasitism and egg acceptance, for example *Acrocephalus* warblers (Dyrcz and Halupka 2006; Schulze-Hagen et al. 2009; Trnka and Grim 2014). Observations have confirmed different mobbing rates against common cuckoo between host species (Moksnes et al. 1991; Schulze-Hagen et al. 2009; Welbergen and Davies 2009; Tryjanowski et al. 2018b), which could be a key to understanding the issue of how different species recognise common cuckoo presence, their brood parasite behaviour and, in consequence, big inter-specific differences in brood-parasitism.

Author contribution PT and TS conceived the study. PT, AG and MJ designed and constructed the experimental setup and data collection procedures. PT, AG, MJ and TS collected the data and performed statistical analyses. PT and AG interpreted the results and wrote the manuscript. All authors gave final approval of the publication.

Declarations

References

Adamík P, Hušek J, Cepák J (2009) Rapid decline of common cuckoo *Cuculus canorus* parasitism in red-backed shrikes *Lanius collurio*. Ardea 97:17–22. https://doi.org/10.5253/078.097.0103

Antczak M, Golawski A, Kuzniak S, Tryjanowski P (2009) Costly replacement – how do different stages of nest failure affect clutch replacement in the red-backed shrikes *Lanius collurio*? Ethol Ecol Evol 21:127–136. https://doi.org/10.1080/08927014.2009.9522501

Bartol I, Karcza Z, Moskát C, Røskaft E, Kisbenedek T (2002) Responses of great reed warblers *Acrocephalus arundinaceus* to experimental brood parasitism: the effects of a cuckoo *Cuculus canorus* dummy and egg mimicry. J Avian Biol 33:420–425. https://doi.org/10.1034/j.1600-048X.2002.02945.x

Carmody LC, Cruz A, Chace JF (2016) Brood parasitism defense behaviors along an altitudinal gradient in the American robin (*Turdus migratorius*). Open Ornithol J 9:39–49. https://doi.org/10.2174/1874453201609010039

Davies NB, de Brooke ML (1988) Cuckoos versus reed warblers: adaptations and counteradaptations. Anim Behav 36:262–284. https://doi.org/10.1016/S0003-3472(88)80269-0

Dawkins R, Krebs JR (1979) Arms races between and within species. Proc R Soc B 205:489–511. https://doi.org/10.1098/rspb.1979.0081

Dyrcz A, Halupka L (2006) Great reed warbler *Acrocephalus arundinaceus* and reed warbler *Acrocephalus scirpaceus* respond differently to cuckoo dummy at the nest. J Ornithol 147:649–652. https://doi.org/10.1007/s10336-006-0097-x

Gloag R, Keller L-A, Langmore NE (2014) Cryptic cuckoo eggs hide from competing cuckoos. Proc R Soc B Biol Sci 281:20141014. https://doi.org/10.1098/rspb.2014.1014

Golawski A, Golawska S (2019) Weather and predation pressure: the case of the red-backed shrike (*Lanius collurio*). Acta Zool Acad Sci Hung 65:371–379. https://doi.org/10.17109/AZH.65.4.371.2019

Golawski A, Mitrus C (2018) Weather conditions influence egg volume repeatability in clutches of the red-backed shrike *Lanius collurio*. Zool Stud 57:e2. https://doi.org/10.6620/ZS.2018.57-02

Honza M, Pozgayová M, Procházka P, Kadlec E (2007) Consistency in egg rejection behaviour: responses to repeated brood parasitism in the blackcap (*Sylvia atricapilla*). Ethology 113:344–351. https://doi.org/10.1111/j.1439-0310.2007.01340.x

Hromada M, Antczak M, Valone TJ, Tryjanowski P (2008) Settling decisions and heterospecific social information use in shrikes. PLoS One 3(12):e3930. https://doi.org/10.1371/journal.pone.0003930

Hromada M, Tryjanowski P, Antczak M (2002) Presence of the great grey shrike Lanius excubitor affects breeding passerine assemblage. Ann Zool Fenn 39:125–130. https://doi.org/10.2307/23735820

IBM SPSS Statistics for Windows (2012) Version 21.0. IBM Corporation, Amrock

Krüger O (2007) Cuckoos, cowbirds and hosts: adaptations, trade-offs and constraints. Phil Trans R Soc B 362:1873–1886. https://doi.org/10.1098/rstb.2006.1849

Kuzniak S (1991) Breeding ecology of the red-backed shrike *Lanius collurio* in the Wielkopolska region (Western Poland). Acta Ornithol 26:67–84

Langmore NE, Hunt S, Kilner RM (2003) Escalation of a coevolutionary arms race through host rejection of brood parasitic young. Nature 422:157–160. https://doi.org/10.1038/nature01460

Lovászi P, Moskát C (2004) Break-down of arms race between the red-backed shrike (*Lanius collurio*) and common cuckoo (*Cuculus canorus*). Behaviour 141:245–262. https://doi.org/10.1163/156853904322890843

Ma L, Yang C, Liu J, Zhang J, Liang W, Møller AP (2018) Costs of breeding far away from neighbors: isolated host nests are more vulnerable to cuckoo parasitism. Behav Process 157:327–332. https://doi.org/10.1016/j.beproc.2018.07.017

Makatsch W (1955) Der Brutparasitismus in der Vogelwelt. Neumann Verlag, Radebeul and Berlin

Marton A, Fülöp A, Bán M, Hauber ME, Moskát C (2021) Female common cuckoo calls dampen the mobbing intensity of great reed warbler hosts. Ethology 00:1–8. https://doi.org/10.1111/eth.13126

Moksnes A, Korsnes L, Lampe PHC (1991) Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. Behaviour 116:64–89. https://doi.org/10.1163/156853990X00365

Morelli F, Bussière R, Golawski A, Tryjanowski P, Yosef R (2015) Saving the best for last: differential usage of impaled prey by red-backed shrike (*Lanius collurio*) during the breeding season. Behav Process 119:6–13. https://doi.org/10.1016/j.beproc.2015.07.006

Moskát C (2005) Common cuckoo parasitism in Europe: behavioural adaptations, arms race and the role of metapopulations. Ornithol Sci 4:3–15. https://doi.org/10.2326/osj.4.3

Moskát C, Fuisz TI (1999) Reactions of red-backed shrikes *Lanius collurio* to artificial cuckoo *Cuculus canorus* eggs. J Avian Biol 30:175–181. https://doi.org/10.2307/3677127

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. https://doi.org/10.1046/j.1474-919X.2002.00085.x

Møller AP, Saino N, Adamik P, Ambrosini R, Antonov A, Campobello D, Stokke BG, Fossøy F, Lehikoinen E, Martin-Vivaldi M, Moksnes A, Moskát C, Røskaft E, Rubolini D, Schulze-Hagen K, Soler M, Shykoff JA (2011) Rapid change in host use of the common cuckoo *Cuculus canorus* linked to climate change. Proc R Soc Lond B 278:733–738. https://doi.org/10.1098/rspb.2010.1592

Polak M (2016) Comparative breeding ecology, nest survival, and agonistic behaviour between the barred warbler and the red-backed shrike. J Ornithol 157:747–758. https://doi.org/10.1007/s10336-016-1336-4

Polak M (2019) Nest concealment and nest defence by two passerines: effect of protective nesting association. Zool Stud 58:e15. https://doi.org/10.6620/ZS.2019.58-15

Rasmussen JL, Sealy SG, Guigueno MF, Elliott KH (2012) Infrequent ejection of artificial bronzed cowbird (*Molothrus aeneus*) eggs by the clay-colored thrush (*Turdus grayi*) in Costa Rica. Ornitol Neotrop 23:33–41

Rothstein SI, Robinson SK (1998) The evolution and ecology of avian brood parasitism: an overview. In: Rothsteinand SI, Robinson SK (eds) Parasitic Birds and Their Hosts. Studies in Coevolution, Oxford University Press, Oxford, pp 3–56

Sato NJ, Tokue K, Noske RA, Mirami OK, Ueda K (2010) Evicting cuckoo nestlings from the nest: a new anti-parasitism behaviour. Biol Lett 6:67–69. https://doi.org/10.1098/rsbl.2009.0540

Schulze-Hagen K, Stokke BG, Birkhead TR (2009) Reproductive biology of the European cuckoo *Cuculus canorus*: early insights, persistent errors and the acquisition of knowledge. J Ornithol 150:1–16. https://doi.org/10.1007/s10336-008-0340-8

Sealy SG, Neudorf DI, Hobson KA, Gill SA (1998) Nest defense by potential hosts of the brown-headed cowbird. In: Rothstein SI, Robinson SK (eds) Parasitic Birds and Their Hosts. Studies in Coevolution, Oxford University Press, Oxford, pp 194–211

Servedio MR, Hauber ME (2006) To eject or to abandon? Life history traits of hosts and parasites interact to influence the fitness payoffs of alternative antiparasite strategies. J Evol Biol 19:1585–1594. https://doi.org/10.1242/jeb.040394

Soler M, Ruiz-Raya F, Roncalli G, Ibáñez-Álamo JD (2017) Relationships between egg-recognition and egg-ejection in a grasp-ejector species. PLoS One 12:e0166283. https://doi.org/10.1371/journal.pone.0166283

Syrova M, Němec M, Veselý P, Landova E, Fuchs R (2016) Facing a clever predator demands clever responses - red-backed shrikes (*Lanius collurio*) vs. Eurasian magpies (*Pica pica*). PLoS One 11:e0159432. https://doi.org/10.1371/journal.pone.0159432

Trnka A, Grim T (2014) Testing for correlations between behaviours in a cuckoo host: why do host defences not covary? Anim Behav 92:185–193. https://doi.org/10.1016/j.anbehav.2014.04.006

Trnka A, Požgayová M, Procházka P, Prokop P, Honza M (2012) Breeding success of a brood parasite is associated with social mating status of its host. Behav Ecol Sociobiol 66:1187–1194. https://doi.org/10.1007/s00265-012-1372-x

Tryjanowski P, Golawski A (2004) Sex differences in nest defence by the red-backed shrike *Lanius collurio*: effects of offspring age, brood size, and stage of breeding season. J Ethol 22:13–16. https://doi.org/10.1007/s10164-003-0096-9

Tryjanowski P, Golawski A, Kuzniak S, Mokwa T, Antczak M (2007) Disperse or stay? Exceptionally high breeding-site infidelity in the red-backed shrike *Lanius collurio*. Ardea 95:316–320. https://doi.org/10.5253/078.095.0214

Tryjanowski P, Morelli F (2015) Presence of cuckoo reliably indicates high bird diversity: a case study in a farmland area. Ecol Indic 55:52–58. https://doi.org/10.1016/j.ecolind.2015.03.012

Tryjanowski P, Sparks TH, Kuczyński L, Kuźniak S (2004) Should avian egg size increase as a result of global warming? A case study using the red-backed shrike (*Lanius collurio*). J Ornithol 145:264–268. https://doi.org/10.1007/s10336-004-0035-8

Tryjanowski P, Morelli F, Osiejuk TS, Møller AP (2018a) Functional significance of cuckoo *Cuculus canorus* calls: responses of conspecifics, hosts and non-hosts. PeerJ 6:e5302. https://doi.org/10.7717/peerj.5302

Tryjanowski P, Morelli F, Kwieciński Z, Indykiewicz P, Møller AP (2018b) Birds respond similarly to taxidermic models and live cuckoos *Cuculus canorus*. J Ethol 36:243–249. https://doi.org/10.1007/s10164-018-0554-z

Welbergen JA, Davies NB (2009) Strategic variation in mobbing as a front line of defense against brood parasitism. Curr Biol 19:235–240. https://doi.org/10.1016/j.cub.2008.12.041

Wesołowski T, Mokwa T (2013) Cuckoo's *Cuculus canorus* hosts and timing of breeding in Poland: analysis of ringing and nest records' data. Ornis Polonica 54:159–169

Yu J, Lu H, Sun W, Liang W, Wang H, Møller AP (2019) Heterospecific alarm-call recognition in two warbler hosts of common cuckoos. Anim Cogn 22:1149–1157. https://doi.org/10.1007/s10071-019-01307-9