Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2011, **80**, 508–518 doi: 10.1111/j.1365-2656.2010.01798.x

Constraints on host choice: why do parasitic birds rarely exploit some common potential hosts?

Tomáš Grim[1]*, Peter Samaš[1], Csaba Moskát[2], Oddmund Kleven[3], Marcel Honza[4], Arne Moksnes[5,6], Eivin Røskaft[5,6] and Bård G. Stokke[5,6]

[1]Department of Zoology and Laboratory of Ornithology, Palacký University, tř. Svobody 26, CZ–771 46 Olomouc, Czech Republic; [2]Animal Ecology Research Group of the Hungarian Academy of Sciences, c/o Hungarian Natural History Museum, H–1083 Budapest, Ludovika ter 2, Hungary; [3]National Centre for Biosystematics, Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway; [4]Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Květná 8, CZ–603 65 Brno, Czech Republic; [5]Department of Biology, Norwegian University of Science and Technology, NTNU, N–7491 Trondheim, Norway; and [6]Centre for Advanced Study, CAS, N–0271 Oslo, Norway

Summary

1. Why are some common and apparently suitable resources avoided by potential users? This interesting ecological and evolutionary conundrum is vividly illustrated by obligate brood parasites. Parasitic birds lay their eggs into nests of a wide range of host species, including many rare ones, but do not parasitize some commonly co-occurring potential hosts.

2. Attempts to explain the absence of parasitism in common potential hosts are limited and typically focused on single-factor explanations while ignoring other potential factors. We tested why thrushes *Turdus* spp. are extremely rarely parasitized by common cuckoos *Cuculus canorus* despite breeding commonly in sympatry and building the most conspicuous nests among forest-breeding passerines.

3. No single examined factor explained cuckoo avoidance of thrushes. Life-history traits of all six European thrush species and the 10 most frequently used cuckoo hosts in Europe were similar except body/egg size, nest design and nestling diet.

4. Experiments ($n = 1211$) in several populations across Europe showed that host defences at egg-laying and incubation stages did not account for the lack of cuckoo parasitism in thrushes. However, cross-fostering experiments disclosed that various factors during the nestling period prevent cuckoos from successfully parasitizing thrushes. Specifically, in some thrush species, the nest cup design forced cuckoo chicks to compete with host chicks with fatal consequences for the parasite. Other species were reluctant to care even for lone cuckoo chicks.

5. Importantly, in an apparently phylogenetically homogenous group of hosts, there were interspecific differences in factors responsible for the absence of cuckoo parasitism.

6. This study highlights the importance of considering multiple potential factors and their interactions for understanding absence of parasitism in potential hosts of parasitic birds. In the present study, comparative and experimental procedures are integrated, which represent a novel approach that should prove useful for the understanding of interspecific ecological relationships in general.

Key-words: antiparasite defence, co-evolution, host selection, interactive effects, parasite avoidance

Introduction

Resource use lies at the heart of ecological research. Common and easily accessible resources (prey for predators or hosts for parasites) should be, all other things being equal, used frequently (Jaenike 1990). Still, some apparently accessible and suitable resources remain unexploited. Absence of resource use can be explained by various factors, such as inconspicuousness or unpalatability (Ruxton, Sherratt & Speed 2004). Such avoidance of cryptic or aposematic prey is easily explained. In contrast, avoidance of common, conspicuous, easily accessible and nonaposematic resources presents a real ecological conundrum. Here, we combine comparative and experimental approaches to study a

---

*Correspondence author. E-mail: tomas.grim@upol.cz particularly striking example of nonuse of an apparently suitable resource.

Absence of brood parasitism in potential hosts was previously explained mostly by inaccessible nests and unsuitable diet for parasite chicks (Davies 2000). In general, little effort has been made to explain the absence (Peer & Bollinger 1997) or low rates of parasitism (Briskie, Sealy & Hobson 1990) in potential hosts of parasitic birds. Further, hypotheses on host avoidance have been tested almost entirely among North-American brown-headed cowbird *Molothrus ater* hosts (Briskie, Sealy & Hobson 1992; Sealy & Bazin 1995; Peer & Bollinger 1997; Mermoz & Fernandez 1999), whereas common cuckoo *Cuculus canorus* (hereafter: cuckoo) hosts have received marginal attention (Davies 2000; Honza *et al*. 2004). Importantly, most previous studies did not reach strong conclusions, as most of the potential factors usually remained untested. The few studies that claimed to explain the absence of cuckoo parasitism have focused on single-factor explanations, namely extremely high egg rejection rates (Procházka & Honza 2003; Honza *et al*. 2004; Lovászi & Moskát 2004; Stokke *et al*. 2004; but see Sealy & Bazin 1995; De Mársico & Reboreda 2008). Thus, previous studies remain inconclusive because they in principle cannot exclude the possibility that other factors (aggression against adult cuckoos, chick discrimination, etc.) contributed to the extinction of specific cuckoo races parasitizing these hosts. Previous studies also did not consider the possibility that some factors *per se* might not constrain brood parasitism, but that *interactions* between factors might be important (see also Weidinger 2002). For example, nest design alone or egg size alone might not constrain cuckoo eviction behaviour, but their combination may do so (i.e. cuckoos might be able to evict small eggs from large nests, or large eggs from small hosts nests, but not large eggs from large nests).

Common blackbirds *Turdus merula*; hereafter: blackbird, song thrushes *Turdus philomelos*, fieldfares *Turdus pilaris* and redwings *Turdus iliacus* breed at high densities in their respective habitats over most of Europe (BirdLife 2004). All four species build large and open conspicuous nests – in fact, thrush nests are by far the most conspicuous nests of any forest passerine. Thrushes are striking exceptions to the result reported by Soler, Møller & Soler (1999) where host population size was the best predictor of parasitism rate. For example, the blackbird is roughly as common as the four most frequently used cuckoo host species taken together (BirdLife 2004). However, the number of cuckoo eggs found in blackbird nests is almost 300 times lower than that among these common hosts (Moksnes & Røskaft 1995). Available data from other European thrushes (including the mistle thrush, *Turdus viscivorus*, and ring ouzel, *Turdus torquatus*) lead to similar conclusions – most hosts that are considered ‘rare’ are parasitized infrequently but still orders of magnitude more than thrushes (Moksnes & Røskaft 1995). As there are observations of thrushes rearing a young cuckoo up till fledging (Glue & Morgan 1972), the big puzzle is why thrushes are almost never parasitized by cuckoos despite their high abundance, very poor nest concealment and apparently appropriate body size.

An apparent absence of cuckoo parasitism in thrushes can reflect either real absence of parasitism and hence history of co-evolutionary interactions with the cuckoo (*primary unsuitability* because of host life-history) or well-developed host defences that evolved owing to either intra- or interspecific brood parasitism (*secondary unsuitability*; e.g. hosts prevent cuckoos from entering their nests or remove their eggs very fast). Primary unsuitability prevents any co-evolution between the parasite and potential hosts, whereas secondary unsuitability is caused by previous co-evolution between the two parties. Therefore, we first employed simple *exploratory* comparisons (i.e. without performing statistical tests, see Materials and methods) between all six extant European *Turdus* thrushes and the 10 most common cuckoo hosts in Europe (Table 1 in Moksnes & Røskaft 1995) to identify candidate traits that could explain absence of cuckoo parasitism in thrushes. We *a priori* rejected traits that are known to affect host selection by cuckoos (Soler *et al*. 1999), but are identical between common hosts and thrushes or even make thrushes more available for parasitism than regular hosts: (i) thrushes cannot escape cuckoo parasitism by their habitat selection because they breed in forest and woodland edges just like many regular cuckoo hosts; (ii) cuckoos do not parasitize hole nesters (with the single exception of the semi-hole nesting common redstarts *Phoenicurus phoenicurus*; hereafter: redstart; Rutila, Latja & Koskela 2002), but all thrushes are open-nesters just like most regular cuckoo hosts; and (iii) some passerines with well-hidden nests may, at least partly, avoid being parasitized, but there are no more conspicuous passerine nests in forests than those of thrushes. The rationale behind selecting the particular traits and logic behind our directional predictions (Table S1) is given in previous studies (references in Table S1).

After excluding some candidate traits, we tested experimentally whether cuckoos fail to parasitize *Turdus* species owing to thrushes being unsuitable at (i) egg-laying, (ii) incubation and/or (iii) nestling stages. We made three major types of experiments: (i) we presented stuffed dummies of the cuckoo and a common avian nest predator, the hooded crow *Corvus cornix*, at host nests to test host aggression and enemy recognition abilities, (ii) we introduced model eggs into potential host nests to test their egg discrimination abilities and (iii) by cross-fostering of host eggs and cuckoo nestlings between the nests of common hosts and thrushes, we attempted to disentangle the effects of nest architecture, egg size and presence of cohabiting host chicks on the performance of parasite nestlings.

Materials and methods

EXPLORATORY COMPARISONS OF LIFE-HISTORY TRAITS

First, we collated data on thrush and regular cuckoo host life-history traits from the literature (Perrins 1998; Soler *et al*. 1999). We compared possible deviations of traits between all European *Turdus* 'thrushes' ($n = 6$ species) and 'common hosts' ($n = 10$ most common hosts reported in Table 1 of Moksnes & Røskaft 1995).

There are both obvious similarities (e.g. large body size) and striking differences (e.g. aggression to intruders near the nest) between various thrush species (Fig. S1). Therefore, some thrushes are more similar to common hosts than other thrush species in our sample. This implies that a particular thrush species may, in principle, differ from other thrush species in the reasons why it is avoided by cuckoos (indeed, our results support this view). Pooling of data into 'thrushes' vs. 'common hosts' groups for statistical analyses of variance would mask such differences. Therefore, we simply plotted original species-specific data for thrushes vs. common hosts to investigate whether particular thrush species deviate from the common hosts in any life-history traits. The rationale for this comparison was not to test any hypothesis (note that we did not perform any formal statistical test in this part of the study), but was simply to identify traits for future experimental work. Clearly, if a *particular* life-history trait of a *particular* thrush species is within the range of that life-history trait in common cuckoo hosts, then it follows that the *particular* life-history trait is not responsible for the absence of cuckoo parasitism in that thrush species. This, of course, does not exclude the possibility that the same trait (with different quantitative value) precludes cuckoo parasitism in another thrush species.

From a statistical point of view, the present study does not suffer from pseudoreplication because we are interested in the specific difference between thrushes and regular hosts ('location differences', Hurlbert 1984). Our comparisons of life-history traits between thrushes and regular cuckoo hosts are heuristic. The comparisons (Table S1, Fig. S2) do *not* test a hypothesis; in contrast, their aim is to identify what factors are meaningful candidates for experimental tests.

GENERAL FIELD PROCEDURES

To increase the power of our tests, we included both our unpublished data and our own already published results (see below). From 1986 to 2009, we studied 1016 thrush nests in 12 localities in Northern and Central Europe (Appendix S1; see Moksnes *et al.* 1991; Grim & Honza 2001a; Moskát, Karcza & Csörgö 2003, for descriptions of those areas and field procedures). The host population was considered sympatric when the cuckoo was breeding in that particular area ($n = 6$). Other populations, mainly in urban areas, were considered allopatric ($n = 6$). Additionally, for eviction and cohabitation experiments with cuckoo chicks, we studied 185 nests of common hosts in the Czech Republic, Hungary and Finland (see Grim & Honza 2001b; Grim *et al.* 2009a; Moskát & Hauber 2010, for descriptions of those areas and field procedures).

Blackbird populations in towns show very high philopatry that has even led to striking and partly genetically determined differences in biology of urban vs. rural blackbirds (Partecke & Gwinner 2007). Because cuckoos generally avoid towns (Perrins 1998), urban populations can be regarded as allopatric (this is confirmed by the absence of any records of cuckoo parasitism in any passerines in our intensely studied urban populations). Data from Hungary show very high site fidelity in both town and countryside blackbird populations (96·0% of recoveries in the city for birds banded in Hungarian towns; T. Csörgö pers. comm.; 87·9% of recoveries in Hungarian countryside for birds banded there; Z. Karcza pers. comm.). Fieldfares also show high fidelity to their natal areas (84·9% recoveries within 6 km from original nest; Norman 1994). We predicted stronger anti-parasite defences in sympatry than in allopatry (Davies & Brooke 1989; Stokke *et al.* 2008).

We measured the nest cup inside diameter and inner depth with a ruler to the nearest millimetre. The index of nest cup steepness was calculated as the nest cup depth divided by the nest cup width (Grim *et al.* 2009a).

DUMMY EXPERIMENTS

Responses of thrushes to adult brood parasites were tested using stuffed dummies of the cuckoo and the hooded crow as a control. The reason for using hooded crow dummies was to determine whether the absence of aggression against a cuckoo dummy in preliminary experiments reflected an overall absence of aggression to any, even clearly dangerous, enemies near the nest. We used one or two (depending on availability) stuffed specimens for both the cuckoo and crow at each study site. Responses did not vary between the specimens; thus, we pooled the data (see also Grim 2005). The dummy was placed between 0·5 and 1·0 m from the focal nest, level with it and facing the nest rim. We observed the responses of nest owners for 10 min after the first parent appeared near the nest and became aware of the dummy. We scored responses on the following scale: (i) no reaction = host(s) observed the dummy but ignored it, (ii) distress calls = host(s) uttered distress/alarm calls, (iii) mobbing = host(s) performed dives or flights around the dummy and (iv) attacks = host(s) aggressively attacked the dummy with contact attacks (Moksnes *et al.* 1991). In cases of attacks, the dummy was immediately removed to avoid its destruction. As some responses were rare in some data sets, we pooled scores 1 and 2 as 'no aggression' and scores 3 and 4 as 'aggression' (Røskaft *et al.* 2002). If no birds arrived at the focal nest during a 30-min period after the dummy was placed near the nest, the response was scored as 'no reaction'. Excluding data from such experiments had no effect on the results from blackbirds (excluded $n = 5$), song thrushes ($n = 10$), fieldfares ($n = 1$) or redwings ($n = 4$).

Each nest was tested only once to avoid pseudoreplication, and only one kind of dummy (cuckoo or crow) was presented near each nest. Nest defence experiments were performed during egg-laying, incubation and young nestling stages when the adult cuckoo is a threat to hosts – female cuckoos prey upon host nestlings (Davies 2000), and accordingly, hosts do not differ in their responses to adult parasites across breeding stages (Grim 2005). At some nests, both egg and nest defence experiments were done. In such cases, an aggression experiment was performed after the egg discrimination experiment was finished.

EGG EXPERIMENTS

We tested the rejection abilities of thrushes with cuckoo-sized model eggs painted (i) immaculate blue to mimic eggs of the cuckoo gens parasitizing the redstart (Moksnes & Røskaft 1995) and (ii) brownish and densely spotted to resemble those of the meadow pipit *Anthus pratensis* (Moksnes *et al.* 1991). Redstart type models were similar to song thrush eggs (as for background colour) and clearly dissimilar to eggs of the other three host species. Pipit type models were dissimilar to eggs of all hosts. Models were made of plaster of Paris or hard plastic. Thrushes are grasp-ejecters; thus, the model material should not affect their egg rejection decisions (Honza, Kuiper & Cherry 2005).

We introduced the parasitic egg to the host nest during the egg-laying or incubation stages. In some of the experiments, one host egg was removed, but in the majority of the cases, no host egg was removed (removal of one egg has no effects on thrush responses; Davies & Brooke 1989). We made an effort to monitor experimental nests daily during a standard 6-day-period following experimental parasitism (Davies & Brooke 1989; Moksnes *et al.* 1991). Nests depredated before the 6-day-period finished were excluded from analyses. We scored three kinds of responses: acceptance, ejection and desertion. Desertion can largely be considered as a rejection response in thrushes because (i) parasitized nests are deserted more frequently than unparasitized nests (Grim & Honza 2001a) and (ii) hosts tested with nonmimetic eggs desert more often than those parasitized with mimetic models (Davies & Brooke 1989). Exclusion of deserted nests from analyses did not change our results and inferences.

CHICK CROSS-FOSTERING EXPERIMENTS

None of the thrush nests monitored in this study were naturally parasitized by the cuckoo. Therefore, we cross-fostered cuckoo hatchlings from *Acrocephalus* warblers to thrush nests to test their eviction and survival abilities. We did not introduce cuckoo eggs as that would result in an unnecessary waste because of egg rejection by hosts (see Results). This was also the reason we did not test whether there was decreased incubation efficiency of relatively smaller cuckoo eggs in the presence of larger thrush eggs. Although hatchability decreases with increasing clutch volume (Lerkelund *et al.* 1993; Tuero, Fiorini & Reboreda 2007), cuckoo females remove at least one host egg before laying their own (Davies 2000). This would result in decreased clutch volume and thus *improved* incubation efficiency. However, a cuckoo egg has a volume 1·4–2·0 times smaller than *Turdus* eggs which might decrease hatching success of the parasite (but see Tuero *et al.* 2007). Still, successful and increasing rates of cuckoo parasitism in azure-winged magpies *Cyanopica cyana* (Davies 2000) suggest that size discrepancy in parasite vs. host eggs does not constrain cuckoos from parasitizing hosts as large as thrushes – azure-winged magpie eggs (26·0 × 21·2 mm; Hosono 1983) are sized between redwing and blackbird eggs. However, we note that some model cuckoo eggs in our experimental nests were not very visible in blackbird nests, and blackbirds probably could not properly rotate and heat such eggs, which were positioned in the bottom of nests. This factor may contribute to lower benefits for cuckoos from parasitizing thrushes, but it does not totally prevent successful parasitism (see records of successfully hatched and fledged cuckoos from blackbird nests; Glue & Morgan 1972).

We weighed cuckoo chicks to the nearest 0·1 g. Sample sizes in these experiments are relatively small because of logistic constraints (low availability of cuckoo chicks, high predation) and ethical and conservation reasons (recently cuckoo populations show declining trends across Europe; BirdLife 2004). Cuckoo nestlings showed very low survival in thrush nests. Hence, the results were clear-cut and did not justify increasing samples at the cost of animal suffering (see Taborsky 2010).

To disentangle the effects of nest sizes and egg sizes on the eviction success, we tested for eviction of large (thrush) and small (Eurasian reed warbler *Acrocephalus scirpaceus*; hereafter: reed warbler) eggs from both large (thrush) and small (reed warbler) nests. In these experimental nests, cuckoo chicks faced eviction of two to five thrush or warbler eggs (depending on original host clutch size). To study the effects of cohabitation with host chicks, we transferred newly hatched cuckoo chicks into host nests with three same-aged host chicks (each cuckoo into a different host nest). We matched chicks for age (days) because average incubation periods are similar and their ranges overlap considerably among cuckoos (mean = 12·4, range = 11–14; Hudec & Šťastný 2005), and both blackbirds (mean = 12·8, range = 11–17) and song thrushes (mean = 12·6, range = 10–16; Hudec 1983) in Central Europe where we performed the experiments.

We scored chick fate as 'predated', 'survived' or 'deserted'. Predated chicks either disappeared from nests (that showed typical signs of being disturbed by a predator) or only the remains of fresh corpses were found in the nest. Deserted chicks were found dead in the nest cups without any injuries, but parents were present near the nest – showing that chick death was not caused by death of host parents instead suggesting that hosts decided not to feed the chick further but remained in the territory (see also Langmore, Hunt & Kilner 2003). Death because of unsuitable diet was excluded because cuckoo chicks were shown to be able to digest and survive on diet that is typically fed by thrushes to their chicks (predominantly earthworms and molluscs: Grim 2006a; rarely fruits: Martín-Gálvez *et al.* 2005).

As a control for possible effects of the cross-fostering itself, we transferred cuckoo chicks among (i) reed warbler nests, (ii) great reed warbler *Acrocephalus arundinaceus* nests and (iii) between reed and great reed warbler nests. No nestlings suffered from low growth or survival because of cross-fostering (Kleven *et al.* 1999; Grim & Honza 2001b).

STATISTICAL ANALYSES

In the exploratory part of this study, we did not analyse data statistically (see above). In the experimental part of the study, we were primarily interested in the effects of sympatry and allopatry and type of experimental dummy and egg on host behaviour. We also included factors that were shown to affect host discrimination behaviour in some host species in previous studies (as recommended by Grafen & Hails 2002). We analysed our experimental data using either generalized linear mixed models (aggression to dummies, egg rejection) or general linear mixed models (GLM) (latency to egg rejection in days).

The full models contained the following explanatory variables: (i) random effects of 'year' (nominal) and 'locality' (nominal), (ii) fixed effects of 'geography' (nominal: sympatry vs. allopatry with the cuckoo), 'dummy' type (nominal: cuckoo vs. crow) or 'egg model' type (nominal: blue vs. spotted) and the interaction of geography with dummy or model type, respectively and (iii) covariates of final 'clutch size' (continuous), 'laying date' of the first egg in the clutch (continuous) and 'nest stage' (nominal: egg laying, 1–3 days of incubation, 4–9 days of incubation, 10 days of incubation to hatching, nestlings – the last two categories only for dummy experiments). 'Year' was entered as a random (i.e. not fixed) effect because we had no specific year-based temporal predictions.

The response variables were host reaction either to experimental eggs (nominal: accepted vs. rejected) or to dummies (nominal: aggression vs. no aggression) and latencies to egg rejection (continuous: in days). We followed backward elimination of nonsignificant terms, starting with the interaction term, then covariates and we kept two major fixed effects of interest (geography, dummy/egg type) in the models until the last step regardless of their significance (Grafen & Hails 2002). Additionally, in another series of analyses, we removed all covariates and confirmed that the interaction was nonsignificant even when covariates were not present in the models.

The final clutch size was included as a surrogate measure of host quality. In 'egg' models, we did not test for a possible effect of number of host eggs at the time of addition of the experimental egg because this variable inevitably positively covaried with nest stage (which was already included in the models; see the issue of multicollinearity: Graham 2003). The 'laying date' in the breeding season was centred for each host species separately by mean within each year to exclude a possible confounding effect of between-year variation in our seasonal sampling effort. Test statistics and *P*-values reported in Results for nonsignificant terms are from backward elimination procedure just before the particular term (being the least significant) was removed from the model.

We analysed data separately for each of the study host species. Nominal responses to dummies and eggs were analysed using GLIMMIX macro of SAS (generalized linear mixed model with binomial error and logit link; Bolker *et al.* 2009). Continual response of latency to egg rejection was analysed using GLM.

In all our models, the random effects of year and locality were very small (likelihood ratio tests; Bolker *et al.* 2009), i.e. there was no significant spatio-temporal variation in the data. When removed, the resulting simpler models with the same structure of fixed effects had a dramatically better fit (much lower $\mathrm{AIC_c}$) and very similar parameter estimates. Hence, we decided to present results of the models without random effects (Bolker *et al.* 2009).

In all, we successfully finished 543 dummy experiments (including data from Grim & Honza 2001a; Røskaft *et al.* 2002), 421 egg rejection experiments (including data from Moksnes *et al.* 1991; Grim & Honza 2001a) and 247 experiments and observations at nests with chicks (including some data from Grim 2006a; Grim *et al.* 2009a,b). The vast majority of data are new: 80·1% of dummy, 74·8% of egg and 83·8% of chick data points have not been published before. Importantly, all data on host responses to eggs and dummies from six Czech and Hungarian populations are new, and none of 193 nests where eviction success was studied (the most important part of the present study) were included in any previously published work. Sample sizes differ among analyses because some data points were missing (e.g. the final clutch size was unknown for nests where experimental egg was ejected during laying stage, and the nest was depredated before clutch completion). We fitted all models in SAS 9.2 (SAS Institute 2008). All statistical tests are two-tailed (Lombardi & Hurlbert 2009), and values are given as mean ± SE.

Results

DO LIFE-HISTORY TRAITS OF THRUSHES AND REGULAR HOSTS DIFFER?

Regression of number of cuckoo eggs in European collections (Moksnes & Røskaft 1995) against minimum breeding population estimates (in millions pairs) of all six European *Turdus* thrushes explained 78% of variation ($F_{1,4} = 14{\cdot}3$, $P = 0{\cdot}019$; slope = 0·48 ± 0·13). This pattern suggests that cuckoos parasitize thrushes only by mistake (random sampling effect).

Thrushes did not deviate from regular cuckoo hosts in the majority of the investigated general life-history characteristics (Fig. S1a). Thrushes are well available to cuckoos in both space and time, but some of them show lower breeding success. Still, this factor cannot explain avoidance of thrushes by cuckoos: the most common cuckoo host, the reed warbler, experiences a breeding success (42·7%) similar to some thrush species.

Values of specific parasitism-related traits of thrushes were either within the range of those traits in common hosts or deviated in the direction opposite to the hypothesis that thrushes are abandoned cuckoo hosts (intra-clutch variation; Fig. S1b). Thrushes tended to show lower aggression towards adult cuckoos and rejected alien eggs more slowly than common hosts (Fig. S1b).

Overall, there are some striking differences between thrushes and common hosts (Fig. S1a):

1. Average body size of thrushes is five times larger than that of common hosts. The smallest thrush – the redwing – is more than twice the size of the largest commonly used European host (the great reed warbler). However, body size *per se* has no direct causal negative influence on cuckoo parasitism and, thus, cannot obviously explain avoidance of thrushes by cuckoos (see Materials and methods for a discussion of the azure-winged magpie as a cuckoo host).
2. Because of a general positive correlation between body size and egg size, thrushes lay large eggs that consequently already produce large nestlings at hatching.
3. Thrushes feed their nestlings with less insects and spiders (which are almost exclusively brought to nestlings by common fosterers) and more earthworms (which are almost absent in the diet of current common hosts).
4. A review of cuckoo chicks reported in previous studies showed that cuckoos may fail to evict host clutch or brood from nests of almost any host (T. Grim & P.

Table 1. Responses (mean ± SE) of the four thrushes towards dummies and model eggs in sympatry and allopatry with cuckoos. Effect sizes for aggression and rejection rates are back-transformed values from the final models. For statistics and sample sizes (degrees of freedom), see Table S2. For details on analyses, see Materials and methods

Host response	Factor	Blackbird	Song thrush	Redwing	Fieldfare
Dummy (% aggression)	Cuckoo	49·2 ± 6·4	14·3 ± 4·4	8·2 ± 3·9	0·0 ± 0·0
	Crow	33·3 ± 4·7	20·8 ± 5·6	78·4 ± 4·8	83·2 ± 3·5
Dummy (% aggression)	Sympatry	38·9 ± 6·0	15·1 ± 3·9	–	–
	Allopatry	42·7 ± 5·3	23·3 ± 7·7	33·5 ± 7·4	72·9 ± 3·9
Egg model (% rejection)	Blue	65·7 ± 4·8	54·2 ± 10·2	44·4 ± 11·7	26·3 ± 10·1
	Spotted	50·0 ± 8·8	82·0 ± 5·4	30·5 ± 4·1	14·0 ± 4·9
Egg model (% rejection)	Sympatry	61·8 ± 6·6	78·6 ± 7·3	19·1 ± 8·6	9·4 ± 5·1
	Allopatry	61·8 ± 5·6	61·4 ± 8·6	34·4 ± 4·2	24·3 ± 7·1
Latency to rejection (days; mean ± SE)	Blue	2·0 ± 0·2	3·0 ± 0·5	2·7 ± 0·5	5·9 ± 0·7
	Spotted	2·5 ± 0·4	2·3 ± 0·3	3·0 ± 0·3	3·9 ± 0·6
Latency to rejection (days; mean ± SE)	Sympatry	1·7 ± 0·3	2·7 ± 0·3	1·8 ± 0·9	4·1 ± 1·4
	Allopatry	2·5 ± 0·2	2·1 ± 0·4	3·0 ± 0·3	5·0 ± 0·5

Procházka, unpublished data). However, unsuccessful evictions happened much more frequently in thrushes than in common hosts (Fig. S1).

Taken together, these differences suggest that the major obstacle for cuckoos is present during the nestling period. The large size of host eggs could decrease the effectiveness of eviction behaviour leading to detrimental competition with host chicks. Alternatively, the diet of thrushes with high proportions of earthworms and lower proportions of insects could pose digestion problems for cuckoo chicks independently of presence of host chicks. We tested these hypotheses experimentally.

EXPERIMENTS – DUMMIES

Out of 543 dummy experiments, 60% were done during laying or early incubation (nest stage had no significant effect on host responses, Table S2). Aggression towards cuckoo dummies was generally weak, with fieldfares ignoring the cuckoo dummy completely (Table 1). Sympatry/allopatry had no effect on thrush responses to either crows or cuckoos (Table 1; no such data were available for fieldfares and redwings).

Fieldfares and redwings attacked the crow much more frequently than the cuckoo, whereas the responses of song thrushes and blackbirds were similar towards the two kinds of dummies (Table 1). Most importantly, aggression towards cuckoos was generally lower in thrushes than in common hosts (Fig. S1). Therefore, the intensity of nest defence cannot be responsible for the absence of cuckoo parasitism in thrushes.

EXPERIMENTS – EGGS

Out of 421 egg experiments, 84% were done during laying or early incubation (nest stage had no significant effect on host responses, Table S2). Song thrushes rejected significantly more meadow pipit type models than more mimetic redstart type eggs, while other thrushes tended to reject more the latter type (Table 1). Contrary to our predictions, rejection rates were not higher in sympatry with cuckoos (Table 1).

Effects of egg type and sympatry/allopatry on latency to rejection were generally small and nonsignificant (Tables 1 and S2). Importantly, latencies were almost always longer than 2 days thus excluding the possibility that natural cuckoo parasitism goes undetected because of extremely fast egg ejection by hosts.

EXPERIMENTS – CHICKS: EVICTION SUCCESS

Egg eviction experiments (n = 193) showed that cuckoos evicted all host eggs in natural nests of reed and great reed warblers (Table 2). They also succeeded in evicting all large song thrush eggs from reed warbler nests and even larger blackbird eggs from old used blackbird nests attached at the top of active great reed warbler nests (all tested host pairs were willing to accept this nest change; we did not test eviction success in active blackbird nests because cuckoo chicks survived poorly in such nests, see below). This indicates that egg size itself does not constrain eviction behaviour.

In contrast, cuckoo chicks were unable to evict not only large song thrush eggs, but also small reed warbler eggs from song thrush nests (Table 2). Cuckoo chicks successfully evicted some host eggs only from one nest that was relatively shallow (4·5 cm deep) and slightly tilted; the cuckoo chick accomplished the eviction of the whole host clutch only when 5 day old. Video-recordings revealed that chicks tried to evict experimental eggs, but the cuckoo's legs slipped on the hard and smooth lining of nest cups and effectively prevented the chicks from pushing host eggs higher than half-way to the nest rim. But it was nest size (not the smooth lining) that impeded eviction success because cuckoo chicks were also unable to evict any eggs/chicks from similar sized fieldfare nest cups that do not have smooth structure (like song thrush nests) but are lined with grasses. Unsuccessful evictions were not caused by large host egg size *per se* as cuckoo chicks (i) were also unable to evict small reed warbler eggs from the same song thrush nests, and (ii) they evicted song thrush eggs from reed warbler nests in all cases (Table 2).

Table 2. Eviction success of cuckoo chicks, i.e. the percentage of *nests* where the cuckoo chick succeeded in complete elimination of host eggs by eviction. Only at one nest (of the fieldfare) did the cuckoo chick partly succeed, evicting two out of three eggs

Nest	Treatment	Sample size (nests)	What was evicted?	Eviction success (%)	Locality
Reed warbler	Natural	99	Reed warbler eggs	100	Czech Republic
Reed warbler	Experimental	7	Song thrush eggs	100	Czech Republic
Great reed warbler	Natural	18	Great reed warbler eggs	100	Czech Republic
Great reed warbler	Natural	36	Great reed warbler eggs	100	Hungary
Blackbird	Experimental	10	Blackbird eggs	80	Hungary
Song thrush	Experimental	3	Song thrush chicks	33	Czech Republic
Song thrush[a]	Experimental	10	Song thrush eggs	10	Czech Republic
Song thrush	Experimental	4	Reed warbler eggs	0	Czech Republic
Fieldfare	Experimental	3	Fieldfare eggs	0	Norway
Fieldfare	Experimental	3	Fieldfare chicks	0	Norway

[a] Includes six natural active song thrush nests and four old thrush nests attached at the top of active reed warbler nests (nest owners always accepted the change immediately as evidenced by video-recordings).

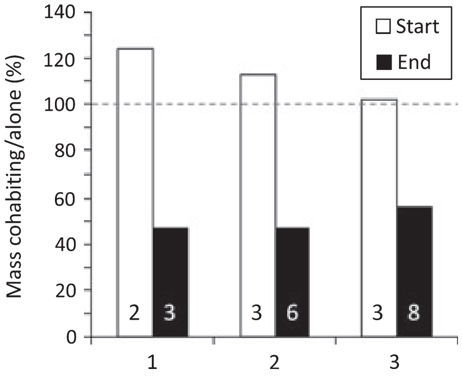


Fig. 1. Relative mass growth differences between cuckoo chicks in song thrush nests either cohabiting with host chicks or raised alone (in the latter treatment, we removed host eggs to eliminate possible confounding effects of costs of eviction; see Grim *et al.* 2009a). Shown are data for three successful (i.e. not depredated) experiments. Each cohabiting cuckoo chick was matched for age (at the start of experiment) and mass with one cuckoo chick raised alone (see Methods in Grim *et al.* 2009a). At the start of the experiment (i.e. when cuckoo chicks were cross-fostered from reed warbler nests, where they hatched, into song thrush nests; *open bars*), the cohabiting chicks had a slightly larger mass than lone chicks (as evidenced by mass ratio of 'cohabiting'/'alone' > 1). At the end of the experiment (i.e. when cohabiting cuckoo chicks died; *full bars*), the cohabiting cuckoo chicks had dramatically lower masses (by *c*. 50%) than their matched lone chicks (the last mass values for cohabiting chicks were measured when chicks were still alive and host parents were present at the nests as evidenced by video-recordings). Inset numbers show chick ages within each matched pair. The horizontal line shows the expectation of observed mass ratios under the null hypothesis of no costs of cohabitation with host chicks.

Cuckoo chicks evicted host song thrush chicks at only one nest (Table 2), but the cuckoo accomplished the task when 7 days old – much later than under normal conditions and just before the eviction instinct naturally ceases (Grim *et al.* 2009a). Thus, it probably was the result of nestling competition and not eviction *per se* (see Moskát & Hauber 2010). Also, this apparently successful evictor suffered from poor growth (chick no. 3 in Fig. 1) and soon after evicting the last (3rd) host chick it died.

Observed differences in eviction success across hosts make sense in the context of nest cup architecture. Mean nest depths (cm) decreased in the order fieldfare (6·86 ± 0·13, $n = 36$), song thrush (6·70 ± 0·11, $n = 61$), blackbird (6·32 ± 0·07, $n = 144$) and redwing (5·65 ± 0·09, $n = 39$). The differences were significant except between the fieldfare and song thrush ($R^2 = 0{\cdot}16$, $F_{3,279} = 15{\cdot}76$, $P < 0{\cdot}0001$; Tukey–Kramer HSD: $P < 0{\cdot}05$). The index of nest cup steepness decreased in a similar order: song thrush (0·73 ± 0·01), fieldfare (0·66 ± 0·01), redwing (0·65 ± 0·01) and blackbird (0·63 ± 0·01). Song thrush nests cups were significantly steeper than those of the three other species which in turn did not differ from each other ($R^2 = 0{\cdot}15$, $F_{3,279} = 16{\cdot}55$, $P < 0{\cdot}0001$; Tukey–Kramer HSD: $P < 0{\cdot}005$).

In line with the significant differences in nest sizes and shapes among thrushes, cuckoo chicks were significantly less successful in evicting at least one host egg from deep and steep song thrush and fieldfare nests (2 out of 13 chicks) in comparison to shallower and less steep blackbirds nests (eight out of eight chicks; $\chi^2_1 = 17{\cdot}90$, $P < 0{\cdot}0001$). Overall, thrushes showed deeper (but not steeper) nest cups than common hosts (Fig. S1).

EXPERIMENTS – CHICKS: GROWTH AND SURVIVAL

Cuckoo chicks raised alone in the nests of song thrushes survived successfully to fledging (Table 3) and also grew at the highest rates observed among cuckoo hosts (Grim 2006a). This rejects diet composition as a possible explanation for absence of cuckoo parasitism in song thrushes. In striking contrast, cuckoo chicks that cohabited nests with song thrush nestlings fared extremely poorly – all decreased their growth rates to 50% in comparison to lone chicks (Fig. 1), and all died within a week after being cross-fostered to song thrush nests (Table 3).

Table 3. Survival of cuckoo chicks under natural and experimental conditions. We either removed host eggs (alone) or added cuckoo chicks into nests with freshly hatched host chicks (cohabiting). 'Survival age' is the number of days (mean and range) the cuckoo chicks survived until either fledging or death caused by parental desertion. In the *blackbird* nests in the Czech Republic, cuckoo chicks were either deserted (1) or predated (2), but the latter chicks grew very poorly and similarly to deserted chicks (thus, the predated chicks would most likely die anyway even in the absence of predation; see Grim 2006a). In the *song thrush* nests, lone cuckoos either survived to fledging (1) or were predated (2), but the latter chicks grew until predation similarly to fledged chicks (thus, the predated chicks did not suffer from host discrimination; see Grim 2006a)

Host	Treatment	Sample size (nests)	Survival age (days)	Survival rate (%)	Locality
Blackbird	Alone	4	1·75 (1–2)	0	Hungary
Blackbird (1)	Alone	2	4·0 (2–6)	0	Czech Republic[a]
Blackbird (2)	Alone	4	6·5 (3–13)	0	Czech Republic[a]
Song thrush	Cohabiting	3	5·7 (3–8)	0	Czech Republic
Song thrush (1)	Alone	3	18·3 (18–19)	100	Czech Republic[a]
Song thrush (2)	Alone	3	7·0 (2–11)	100	Czech Republic[a]
Fieldfare	Cohabiting	3	5·7 (1–12)	0	Norway
Redstart	Alone	16	19·3 (17–22)	100	Finland[b]
Redstart	Cohabiting	9	22·8 (11–26)	44	Finland[b]

[a] Data from Grim 2006a.
[b] Data from Grim *et al.* (2009a,b).

We found some interspecific variability in host responses to parasitic chicks. Both fieldfares and song thrushes did not show outright rejection of cuckoo chicks: fosterers fed both parasitic and own chicks, but cuckoos grew poorly in both song thrush (Fig. 1) and fieldfare (Fig. S2) nests and none survived (Table 3). In contrast, three out of four blackbird fosterers in Hungary did not feed the lone cuckoo chick at all and abandoned the nest, so cuckoos died. In another case, we found the cuckoo chick under the nest, but the female blackbird continued to brood her eggs just before hatching. Chicks survived only for 1 or 2 days (one and three chicks, respectively). Also in the Czech Republic, cuckoo chicks failed in nests of blackbirds even in the absence of the hosts own chicks: cuckoos grew very poorly, and out of six transferred chicks, none survived until fledging (also depredated nestlings grew very poorly before predation and similarly to nonpredated chicks; Grim 2006a). In contrast, lone blackbird chicks always ($n = 7$) survived well in blackbird nests until fledging (predated nests were excluded from analyses). These chicks included three cases where only one egg per clutch hatched (these chicks spent 11–13 days alone in their nests and successfully fledged) and another four cases when all chicks but one disappeared (fledged or died) extremely early (age: 9 days posthatch). The last chicks from the latter nests spent another 3–5 days alone in their nests. Thus, cuckoo chicks survival (0%, $n = 7$, excluding predated chicks) was significantly lower than that of lone own host blackbird chicks (100%, $n = 7$; Fisher exact test: $P = 0{\cdot}0006$).

Overall, cuckoo chicks in thrush nests suffered high mortality. These data come from song thrushes (Czech Republic), fieldfares (Norway) and two geographically distinct populations of blackbirds (Czech Republic, Hungary). We did not collect more data because of ethical considerations; moreover, despite modest sample sizes (overall $n = 22$), the results were clear-cut (see Taborsky 2010).

Discussion

The present study aimed to solve a long-standing ecological and evolutionary conundrum 'Why are thrushes, extremely common birds constructing highly conspicuous nests, avoided by the cuckoo?' In general, hosts can evade parasitism by cuckoos at three breeding stages – egg-laying, incubation and nestling stages (Davies 2000). Both comparative and experimental evidence concurred that the apparent absence of cuckoo parasitism in thrushes was not caused by host defences during the first two stages or by unsuitable host life-history traits. The negligible rates of observed cuckoo parasitism in thrushes were not explained by host aggression (excluding parasites from approaching host nests). Rapid ejection of foreign eggs was also excluded as an explanation, because experimentally parasitized thrushes did not reject eggs faster than current cuckoo hosts. Moreover, thrushes did not remove all foreign eggs, even highly nonmimetic ones, from their nests. In contrast, we demonstrated that a specialized 'thrush' cuckoo host race cannot establish itself because of problems experienced by the parasite at the chick stage. In some thrushes (song thrush, fieldfare), nest design hindered eviction success. Thus, cuckoo chicks were forced to compete with host hatchlings and suffered from decreased growth and high mortality. In other thrushes (blackbirds), hosts were unwilling to care even for lone cuckoo chicks.

IMPORTANCE OF THE CHICK STAGE

The great majority of studies on brood parasitism focused on host–parasite interactions at egg stages – aggression to adult parasites and host responses to eggs (see Grim 2007). Inevitably, host–parasite interactions at the chick stage remained neglected (reviewed in Grim 2006b). The present study highlights the importance of studying the chick stage because cuckoos seem to be impeded from colonizing thrushes as hosts exactly at the chick stage, but not at laying or incubation stages.

In contrast to some traditional explanations, neither large host body (Moksnes *et al.* 1991) nor egg (Kleven *et al.* 1999) sizes seemed to prevent cuckoo parasitism in thrushes. This is because cuckoo chick eviction attempts succeeded in nests of large hosts (blackbirds), but failed in nests of smaller hosts (song thrushes, fieldfares). Furthermore, and counterintuitively, host hatchling size is also not an important factor because (i) it is nest design that constrains eviction success, and (ii) cuckoo chicks are poor competitors irrespective of the size of fosterer chicks (Grim *et al.* 2009a). This raises a possibility that nest cup design in some thrushes evolved as an adaptation to prevent nest-mates eviction by cuckoo chicks. Although the special plaster-like lining of song thrush nests may contribute to hinder eviction success it is not necessary: cuckoo chicks were also unable to evict host eggs/young from fieldfare nests that are lined with grasses. Therefore, the nest size *per se* is sufficient to prevent cuckoo chicks from evicting nest contents. In fact, birds in 16 families/subfamilies (close to 5% of the world's birds) use mud in building their nests, and most of them are not victimized by evicting parasites (Rowley 1971). Special plaster-like lining in the song thrush may enhance nestling survival by rendering conditions inside the nest unsuitable for *insect* ectoparasites (Reichholf 2003).

Both song thrushes and fieldfares were willing to feed cuckoo chicks while blackbirds seemed to feed cuckoo chicks only at low rates (Czech Republic) or refused to feed them completely (Hungary). Additionally, Glue & Morgan (1972) reported 'nest abandonment' as a reason for cuckoo failure in blackbird nests in Britain. Lowered feeding rates of parasite chicks were documented in several hosts of other brood parasites (Lichtenstein 2001; Payne, Woods & Payne 2001). Importantly, blackbirds were willing to care for lone own chicks, sometimes for extensive periods from hatching till fledging. Thus, death of lone cuckoo chicks in blackbird nests seems not to be explained as a host strategy to desert any single-chick broods (Langmore *et al.* 2003). The evolutionary origin of low blackbird willingness to care for cuckoo chicks remains an exciting subject for future work (see also Grim 2006b).

A traditional explanation for absence of regular cuckoo parasitism in thrushes was 'unsuitable diet' (Moksnes *et al.* 1991). Cuckoo nestlings are never fed earthworms or food items of similar size by their most common hosts, reed warblers (Grim & Honza 2001a) and other regular hosts (Fig. S1). Interestingly, although this comparative evidence suggests that diet is an important factor explaining absence of cuckoo parasitism in thrushes, the experimental and observational data reject this hypothesis. Cuckoo chicks in song thrush nests were fed mainly with large earthworms and still achieved higher growth rates than in reed warbler nests (Grim 2006a). Cuckoo chicks may digest considerable amounts of plant diet (grapes; Martín-Gálvez *et al.* 2005), and Mikulica (1993) even observed cuckoo chicks fed with 'voles and bird nestlings in the nests of the red-backed shrike'. Still, more experimental studies are needed to test whether some particular host species or even populations specialize on diet that is indigestible for parasite chicks.

All comparative and experimental data combined strongly suggest that thrushes were not involved in long-term co-evolution with the cuckoo. This conclusion raises the question of what is the origin of egg discrimination in thrushes. That question is beyond the scope and aims of this study. In general, egg rejection could be because of conspecific parasitism, interspecific parasitism (or both) and/or nest sanitation (Honza *et al.* 2005). This provides an interesting subject for future studies. Whatever the evolutionary cause of egg rejection in thrushes, our conclusion remains the same – low or intermediate egg rejection rates and low rates of aggression to adult cuckoos cannot explain virtual absence of cuckoo parasitism in thrushes.

THRUSHES: SUITABLE OR UNSUITABLE CUCKOO HOSTS?

So far, there has been an inconsistency in classifying thrushes into 'suitable' (Davies & Brooke 1989) or 'unsuitable' (Moksnes *et al.* 1991) categories of hosts. Our data support the latter view. Nevertheless, there are anecdotal observations of cuckoo nestlings successfully fledging from nests of various *Turdus* species (Glue & Morgan 1972). Still, nonzero reproductive success of 'thrush' cuckoos cannot lead to the conclusion that thrushes are suitable hosts. The important variable is the difference between cuckoo reproductive success in the nest of a thrush and other available sympatric hosts. The extremely low breeding success of parasitic chicks in thrush nests indicates that these species are parasitized only by mistake or as a last resort when nests of main hosts are unavailable.

'Suitable hosts' and 'unsuitable hosts' are discrete categories. However, (un)suitability of hosts is a continuous variable: factors influencing the probability of successful recruitment from a host nest are continuous (host egg and nest size, food quality and quantity, etc.). This makes strict categorization of potential hosts difficult. However, selection by cuckoo females should lead to a preference for the most suitable hosts (Kleven *et al.* 1999), thus lowering parasitism rates in hosts of low or intermediate quality (De Mársico & Reboreda 2008). This could be the major evolutionary force behind the fact that some potentially suitable, but lower quality hosts are avoided by brood parasites (see also Jaenike 1990).

Røskaft *et al.* (2002) showed that a more detailed classification of host species (to five categories) can better explain the pattern of parasitism than the traditional suitable–unsuitable dichotomy. Interestingly, a category 'large nest and eggs' (thrushes) shows almost identical level of aggression against dummy cuckoos as the category 'seed eaters' and 'hole nesters' – birds that clearly cannot serve as cuckoo hosts. Thus, thrushes probably experienced similar selection pressures from cuckoos as the two latter categories.

In general, different thrush species prevented cuckoo parasitism at different stages. For example, song thrushes showed relatively low aggression and low rejection of alien eggs, but nest architecture (size) forced cuckoos to share the parental care with host young (which was fatal for young parasites). In contrast, blackbirds were more aggressive, rejected more alien eggs, but their nests were too shallow to prevent the cuckoo from evicting host progeny. Thus, in the case of successful eviction of their eggs/young by the cuckoo chicks, egg acceptors may adopt another line of defence: low willingness to care for lone alien chicks (alternatively, low willingness to feed the parasite chick may result from selection forces unrelated to brood parasitism, see Grim 2006b, but with the same consequences for the parasite; thus, evolutionary origin of such host behaviours does not have any bearing on the conclusions of the present study).

Fieldfare and blackbird clutches hatch asynchronously (Perrins 1998). These hosts start to incubate before clutch completion, thus parasitic eggs not laid very early in the host laying period could have low chances of hatching before host eggs. Molnár (1939) reported cases where the cuckoo chick hatched a few hours *after* the first great reed warbler nestlings; these cuckoo chicks were unable to evict their nestmates. Host nestlings started to grow faster than the cuckoo chicks in these nests, and all cuckoo chicks in these mixed broods died within 5 days posthatch. Recent studies showed that even competition with small passerine nestlings can have deleterious effects on cuckoo growth and survival (Soler 2002; Martín-Gálvez *et al.* 2005; Hauber & Moskát 2008; Grim *et al.* 2009b). Therefore, hatching asynchrony could decrease suitability of potential hosts irrespective of their body size.

These considerations suggest that comparing average traits of whole groups of species (common vs. rare/avoided hosts) and application of comparative methods (Soler *et al.* 1999) may mask real *species-specific* (vs. group-specific) differences in factors that affect the success of cuckoo parasitism.

Of course, it is always possible that cuckoos frequently parasitized thrushes a long time ago and that the anti-parasite responses we detected in thrushes represent evolutionary relics of adaptations against cuckoos that are no longer adaptive. Unfortunately, such a scenario is impossible to test. Moreover, it cannot explain *current* absence of parasitism. This is because relatively (in comparison to some current cuckoo hosts) weak anti-parasite defences would not prevent cuckoos from starting to parasitize thrushes again (assuming that thrushes were formerly used and later abandoned hosts).

Conclusions

Absence of a specialized 'thrush' cuckoo host race(s) cannot be explained by strong anti-parasite host defences at laying and incubation stages or by unusual host life-history traits. In contrast, it seems to be best explained by host–parasite interactions at the nestling stage. Importantly, although thrushes present superficially similar taxa, factors preventing successful cuckoo parasitism were species-specific. In song thrushes and fieldfares, nest size, rather than large egg size (as hypothesized previously; Kleven *et al*. 1999), turned out to be the primary impediment to egg eviction, forcing parasites to share parental care with host progeny. Owing to the low competitive ability of cuckoo chicks, parasites experienced an early death. In contrast, neither nest design nor competitive ability constrained cuckoo chicks' survival in blackbird nests – cuckoos successfully evicted host eggs but were soon deserted suggesting blackbirds possess traits that might serve as anti-parasite defences at the chick stage. In addition to these major factors, some others may additively decrease *Turdus* suitability as hosts, e.g. lower breeding success in some thrushes and/or larger eggs that incur larger energetic costs of eviction (Grim *et al*. 2009a). These results coupled with previous findings (e.g. there are no specialized cuckoo gentes parasitizing particular *Turdus* spp.) indicate that thrushes are poor quality hosts, were not regularly parasitized by cuckoos in the past and have not evolved specific adaptations against interspecific brood parasitism.

The aim of the present study was to answer a long-standing puzzle: 'Why do we hardly find any cuckoo eggs or chicks in nests of one of the most common and by far the most conspicuous forest passerines?' Still, our study highlights an important lesson for the study of host selection and resource use in general. To explain the rarity of parasitism in particular hosts, it was insufficient to consider single host traits in isolation and ignore other candidate traits as was done by virtually all previous studies. Furthermore, a comprehensive approach that tested host responses to all parasite developmental stages (eggs, nestlings, adults) proved to be more fruitful than the traditional single-stage (typically egg) approach. We predict that future studies of this fascinating phenomenon will reveal effects of various factors that additively and/or interactively (cf. Weidinger 2002) decrease overall reproductive success of parasites in the nests of particular hosts to levels that do not allow for long-term survival of parasite populations specialized on such hosts. Finally, future ecological studies of resource use might benefit from combining comparative and experimental approaches as exemplified by the present study.

Acknowledgements

T. Csörgö, A. Dvorská, Z. Karcza, P. Procházka and Z. Strachoňová helped with the fieldwork. We are grateful to A. Antonov, A. P. Møller, M. Reichard, V. Remeš and E. Tkadlec and three anonymous reviewers for helpful comments and to D. Campbell for correcting the language. Financial support was received from following institutions and grants: TG (MSM6198959212, GACR 206/03/D234, HFSP RGY69/07), MH (IAA600930605), ER and AM (grant from Nansen Foundation), BGS (grant from the Research Council of Norway, no. 151641/432). This study was approved by ethical committees of authors' home institutions and complied with the current laws of the respective countries.

References

BirdLife International (2004) *Birds in Europe*. BirdLife International, Cambridge, UK.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.

Briskie, J.V., Sealy, S.G. & Hobson, K.A. (1990) Differential parasitism of least flycatchers and yellow warblers by the brown-headed cowbird. *Behavioral Ecology and Sociobiology*, **27**, 403–410.

Briskie, J.V., Sealy, S.G. & Hobson, K.A. (1992) Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. *Evolution*, **46**, 334–340.

Davies, N.B. (2000) *Cuckoos, Cowbirds and Other Cheats*. T & AD Poyser, London, UK.

Davies, N.B. & Brooke, M.de.L. (1989) An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. *Journal of Animal Ecology*, **58**, 207–224.

De Mársico, M.C. & Reboreda, J.C. (2008) Differential reproductive success favours strong host preference in a highly specialized brood parasite. *Proceedings of the Royal Society B*, **275**, 2499–2506.

Glue, D. & Morgan, R. (1972) Cuckoo hosts in British habitats. *Bird Study*, **19**, 187–192.

Grafen, A. & Hails, R. (2002) *Modern Statistics for the Life Sciences*. Oxford University Press, Oxford, UK.

Graham, M.H. (2003) Confronting multicollinearity in ecological multiple regression. *Ecology*, **84**, 2809–2815.

Grim, T. (2005) Host recognition of brood parasites: implications for methodology in studies of enemy recognition. *Auk*, **122**, 530–543.

Grim, T. (2006a) Cuckoo growth performance in parasitized and unused hosts: not only host size matters. *Behavioral Ecology and Sociobiology*, **60**, 716–723.

Grim, T. (2006b) The evolution of nestling discrimination by hosts of parasitic birds: why is rejection so rare? *Evolutionary Ecology Research*, **8**, 785–802.

Grim, T. (2007) Equal rights for chick brood parasites. *Annales Zoologici Fennici*, **44**, 1–7.

Grim, T. & Honza, M. (2001a) Differences in behaviour of closely related thrushes (*Turdus philomelos* and *T. merula*) to experimental parasitism by the common cuckoo *Cuculus canorus*. *Biologia*, **56**, 549–556.

Grim, T. & Honza, M. (2001b) Does supernormal stimulus influence parental behaviour of the cuckoo's host? *Behavioral Ecology and Sociobiology*, **49**, 322–329.

Grim, T., Rutila, J., Cassey, P. & Hauber, M.E. (2009a) The cost of virulence: an experimental study of egg eviction by brood parasitic chicks. *Behavioral Ecology*, **20**, 1138–1146.

Grim, T., Rutila, J., Cassey, P. & Hauber, M.E. (2009b) Experimentally constrained virulence is costly for common cuckoo chicks. *Ethology*, **115**, 14–22.

Hauber, M.E. & Moskát, C. (2008) Shared parental care is costly for nestlings of common cuckoos and their great reed warbler hosts. *Behavioral Ecology*, **19**, 79–86.

Honza, M., Kuiper, S.M. & Cherry, M.I. (2005) Behaviour of African turdid hosts towards experimental parasitism with artificial red-chested cuckoo *Cuculus solitarius* eggs. *Journal of Avian Biology*, **36**, 517–522.

Honza, M., Procházka, P., Stokke, B.G., Moksnes, A., Røskaft, E., Čapek, M. & Mrlík, V. (2004) Are blackcaps current winners in the evolutionary struggle against the common cuckoo? *Journal of Ethology*, **22**, 175–180.

Hosono, T. (1983) A study of life-history of blue magpie. *Journal of the Yamashina Institute for Ornithology*, **15**, 63–71.

Hudec, K. (ed.) (1983) *Fauna ČSSR. Ptáci – Aves*. Vol. **3**, Part 1. Academia, Praha.

Hudec, K. & Šťastný, K. (2005) *Fauna ČR. Ptáci – Aves*. Vol. **2**, Part 2. Academia, Praha.

Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.

Jaenike, J. (1990) Host specialization in phytophagous insects. *Annual Review of Ecology and Systematics*, **21**, 243–273.

Kleven, O., Moksnes, A., Røskaft, E. & Honza, M. (1999) Host species affects the growth rate of cuckoo (*Cuculus canorus*) chicks. *Behavioral Ecology and Sociobiology*, **47**, 41–46.

Langmore, N.E., Hunt, S. & Kilner, R.M. (2003) Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature*, **122**, 157–160.

Lerkelund, H.E., Moksnes, A., Røskaft, E. & Ringsby, T.H. (1993) An experimental test of optimal clutch size of the fieldfare; with a discussion on why brood parasites remove eggs when they parasitize a host species. *Ornis Scandinavica*, **24**, 95–102.

Lichtenstein, G. (2001) Low success of shiny cowbird chicks parasitizing rufous-bellied thrushes: chick-chick competition or parental discrimination? *Animal Behaviour*, **61**, 401–413.

Lombardi, C.M. & Hurlbert, S.H. (2009) Misprescription and misuse of one-tailed tests. *Austral Ecology*, **34**, 447–468.

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.

Martín-Gálvez, D., Soler, M., Soler, J.J., Martín-Vivaldi, M. & Palomino, J.J. (2005) Food acquisition by common cuckoo chicks in rufous bush robin nests and the advantage of eviction behaviour. *Animal Behaviour*, **70**, 1313–1321.

Mermoz, M.E. & Fernandez, G.J. (1999) Low frequency of shiny cowbird parasitism on scarlet headed blackbirds: anti-parasite adaptations or nonspecific life-history traits? *Journal of Avian Biology*, **30**, 15–22.

Mikulica, O. (1993) The cuckoo. *Živa*, **41**, 84. (In Czech).

Moksnes, A. & Røskaft, E. (1995) Egg-morphs and host preference in the common cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. *Journal of Zoology*, **236**, 625–648.

Moksnes, A., Røskaft, E., Braa, A.T., Korsnes, L., Lampe, H.M. & Pedersen, H.C. (1991) Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour*, **116**, 64–89.

Molnár, B. (1939) *About the Cuckoo: Observations and Experiments on the Eviction Instinct of the Cuckoo Chick*. Szarvas, Hungary. (In Hungarian).

Moskát, C. & Hauber, M.E. (2010) Chick loss from mixed broods reflects severe nestmate competition between an evictor brood parasite and its hosts. *Behavioural Processes*, **83**, 311–314.

Moskát, C., Karcza, Z. & Csörgö, T. (2003) Egg rejection in European blackbirds (*Turdus merula*): the effect of mimicry. *Ornis Fennica*, **80**, 86–91.

Norman, D. (1994) *The Fieldfare*. Hamlyn, London, UK.

Partecke, J. & Gwinner, E. (2007) Increased sedentariness in European blackbirds following urbanization: a consequence of local adaptation? *Ecology*, **88**, 882–890.

Payne, R.B., Woods, J.L. & Payne, L.L. (2001) Parental care in estrildid finches: experimental tests of a model of *Vidua* brood parasitism. *Animal Behaviour*, **62**, 473–483.

Peer, B.D. & Bollinger, E.K. (1997) Explanations for the infrequent cowbird parasitism on common grackles. *Condor*, **99**, 151–161.

Perrins, C. (ed.) (1998) *The Complete Birds of the Western Palearctic on CD-ROM*. Oxford University Press, Oxford.

Procházka, P. & Honza, M. (2003) Do common whitethroats (*Sylvia communis*) discriminate against alien eggs? *Journal of Ornithology*, **144**, 354–363.

Reichholf, J.H. (2003) Warum macht die Singdrossel *Turdus philomelos* einen glatten Nestnapf? *Ornithologischer Anzeiger*, **42**, 235–242.

Røskaft, E., Moksnes, A., Stokke, B.G., Bičík, V. & Moskát, C. (2002) Aggression to dummy cuckoos by potential European cuckoo hosts. *Behaviour*, **139**, 613–628.

Rowley, I. (1971) The use of mud in nest-building – a review of the incidence and taxonomic importance. *Ostrich*, Suppl. 8, 139–148.

Rutila, J., Latja, R. & Koskela, K. (2002) The common cuckoo *Cuculus canorus* and its cavity nesting host, the redstart *Phoenicurus phoenicurus*: a peculiar cuckoo-host system? *Journal of Avian Biology*, **33**, 413–419.

Ruxton, G.D., Sherratt, T.N. & Speed, M.P. (2004) *Avoiding Attack. The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford University Press, Oxford, UK.

SAS Institute Inc. (2008) *SAS/STAT® 9.2 User's Guide*. SAS Institute Inc, Cary, NC, USA.

Sealy, S.G. & Bazin, R.C. (1995) Low-frequency of observed cowbird parasitism on eastern kingbirds: host rejection, effective nest defence, or parasite avoidance? *Behavioral Ecology*, **6**, 140–145.

Soler, M. (2002) Breeding strategy and begging intensity: influences on food delivery by parents and host selection by parasitic cuckoos. *The Evolution of Begging* (eds J. Wright & M.L. Leonard), pp. 413–427. Kluwer, Dordrecht, the Netherlands.

Soler, J.J., Møller, A.P. & Soler, M. (1999) A comparative study of host selection in the European cuckoo. *Oecologia*, **118**, 265–276.

Stokke, B.G., Rudolfsen, G., Moksnes, A. & Røskaft, E. (2004) Rejection of conspecific eggs in chaffinches: the effect of age and clutch characteristics. *Ethology*, **110**, 459–470.

Stokke, B.G., Hafstad, I., Rudolfsen, G., Moksnes, A., Møller, A.P., Røskaft, E. & Soler, M. (2008) Predictors of resistance to brood parasitism within and among reed warbler populations. *Behavioral Ecology*, **19**, 612–620.

Taborsky, M. (2010) Sample size in the study of behaviour. *Ethology*, **116**, 185–202.

Tuero, D.T., Fiorini, V.D. & Reboreda, J.C. (2007) Effects of Shiny Cowbird *Molothrus bonariensis* parasitism on different components of House Wren *Troglodytes aedon* reproductive success. *Ibis*, **149**, 521–529.

Weidinger, K. (2002) Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *Journal of Animal Ecology*, **71**, 424–437.

Received 11 August 2010; accepted 7 December 2010
Handling Editor: Sheena Cotter

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Location of the study sites.

Fig. S1. Life-history traits of thrushes and common hosts.

Fig. S2. Cuckoo chick growth in the nest of the fieldfare.

Table S1. Predictions for differences in life-history traits between common hosts and thrushes.

Table S2. Statistical results of analyses of host anti-parasite responses.

Supplementary on-line material

Constraints on host choice: why do parasitic birds rarely exploit some common potential hosts?

Tomáš Grim, Peter Samaš, Csaba Moskát, Oddmund Kleven, Marcel Honza, Arne Moksnes, Eivin Røskaft and Bård G. Stokke

Journal of Animal Ecology, doi: 10.1111/j.1365-2656.2010.01798.x

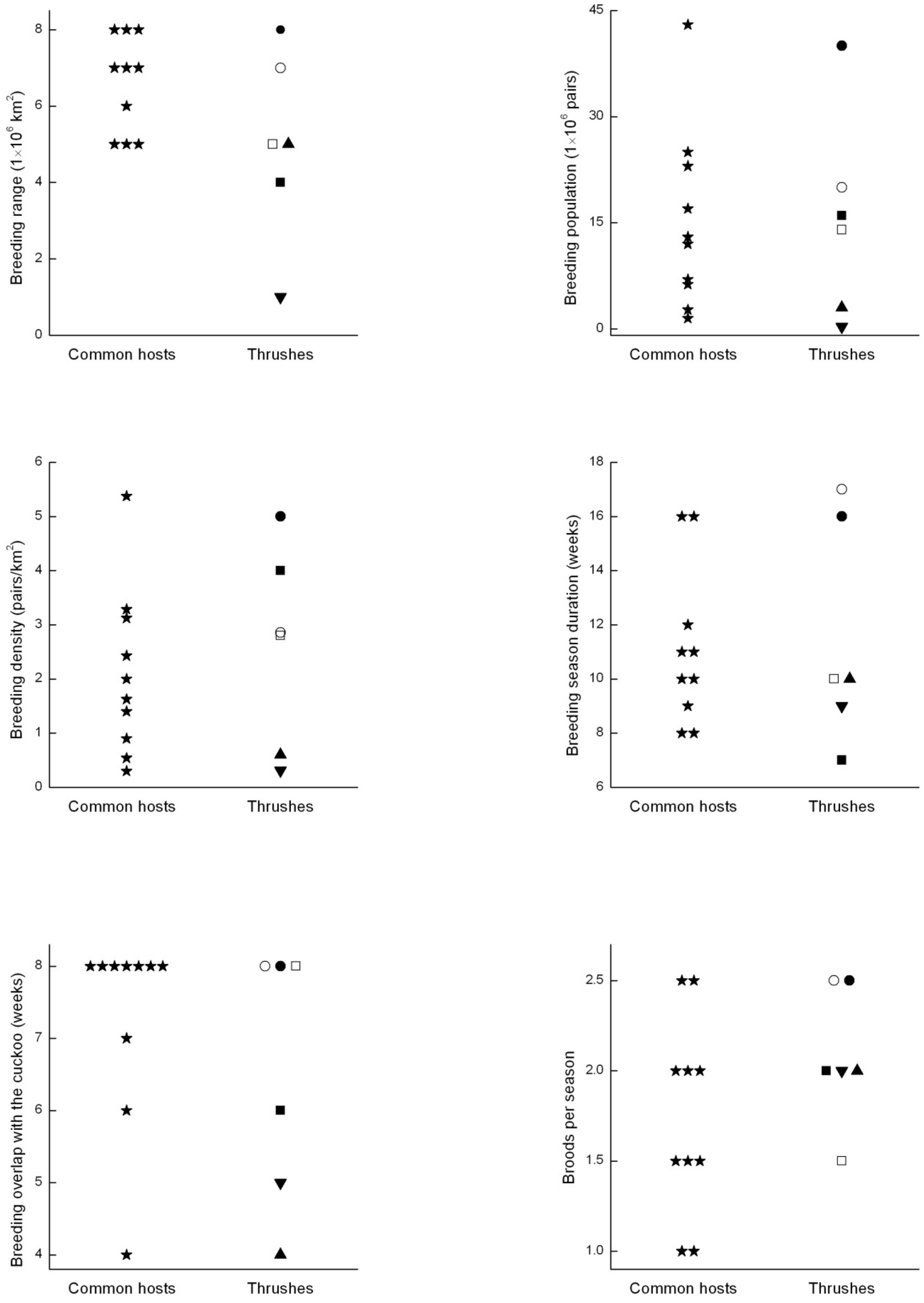
Appendix S1 Location of studied thrush populations living in sympatry or allopatry with cuckoos.

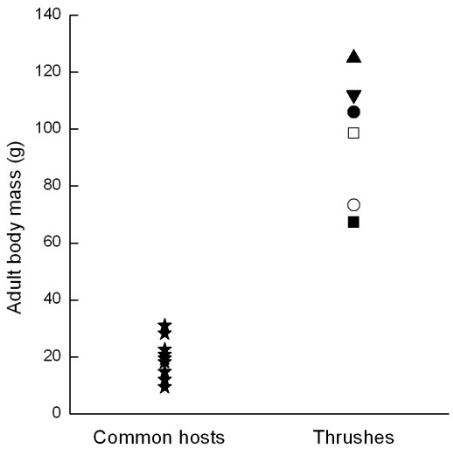
Study area	Country	Status	Latitude N	Longitude E
Buda hills	Hungary	sympatry	47° 01´	19° 00´
Budapest	Hungary	allopatry	47° 30´	19° 05´
Lužice	Czech Republic	sympatry	48° 51´	17° 04´
Brno	Czech Republic	allopatry	49° 12´	16° 38´
V. Knínice	Czech Republic	sympatry	49° 14´	16° 25´
Grygov	Czech Republic	sympatry	49° 32´	17° 19´
Olomouc	Czech Republic	allopatry	49° 35´	17° 15´
Rørkær	Denmark	sympatry	55° 25´	09° 14´
Lund	Sweden	allopatry	55° 42´	13° 10´
Oslo	Norway	allopatry	59° 55´	10° 45´
Tydal	Norway	sympatry	63° 04´	11° 34´
Stjørdal	Norway	allopatry	63° 27´	10° 57´

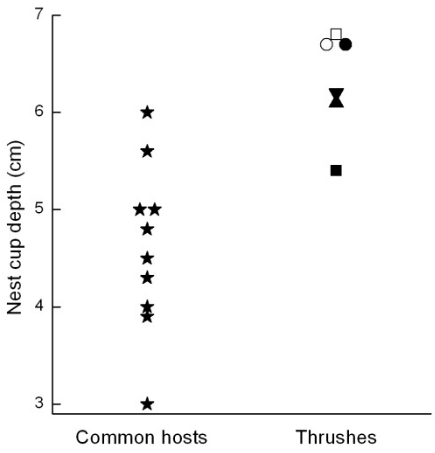
Figure S1. Variation in life-history traits between thrushes and common hosts: (a) general life-history traits, (b) specific parasitism-related traits (see Table S1 for explanation). Common hosts (★) include 10 most common hosts reported by Moksnes & Røskaft (1995). Thrushes include all 6 European members of genus *Turdus*: blackbird (●), song thrush (○), redwing (■), fieldfare (◘), mistle thrush (▲), ring ouzel (▼). We extracted data from literature (Perrins 1998; Soler, Møller & Soler 1999; N. B. Davies, pers. comm.; M. Martín-Vivaldi, pers. comm.). In some cases information on the particular trait was not available (e.g., latency to egg rejection in the dunnock *Prunella modularis* which is a pure acceptor of alien eggs).

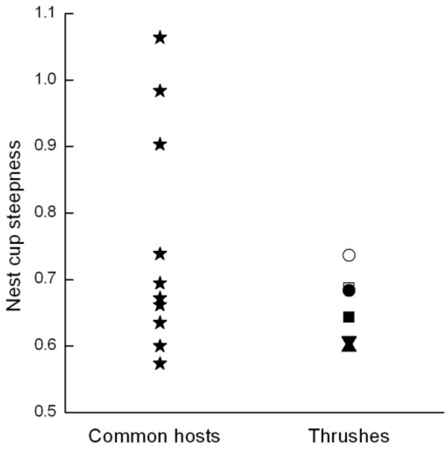
Figure S2. Cuckoo chick growth in the nest of the fieldfare. The cuckoo hatched one day before the host chick but was quickly overgrown by the host nestling. The latter fledged at a typical age of 13 days post-hatch whereas the cuckoo suffered from poor growth and died at the age of 16 days at extremely low mass.

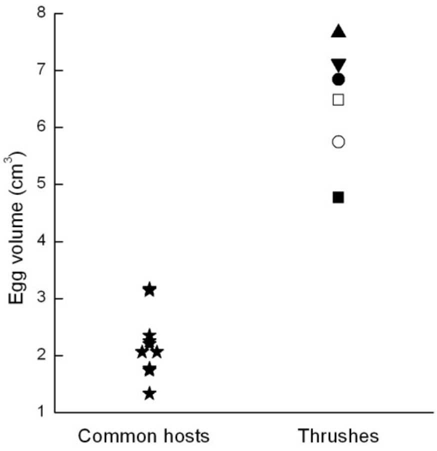
Figure S1a

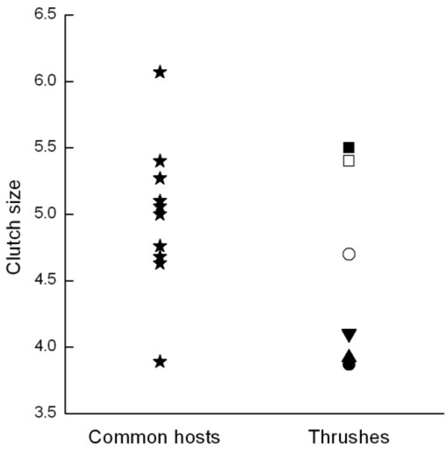

Breeding range (1×10^6 km^2)
0
2
4
6
8
Common hosts
Thrushes
Breeding population (1×10^6 pairs)
0
15
30
45
Common hosts
Thrushes
Breeding density (pairs/km^2)
0
1
2
3
4
5
6
Common hosts
Thrushes
Breeding season duration (weeks)
6
8
10
12
14
16
18
Common hosts
Thrushes
Breeding overlap with the cuckoo (weeks)
4
5
6
7
8
Common hosts
Thrushes
Broods per season
1.0
1.5
2.0
2.5
Common hosts
Thrushes

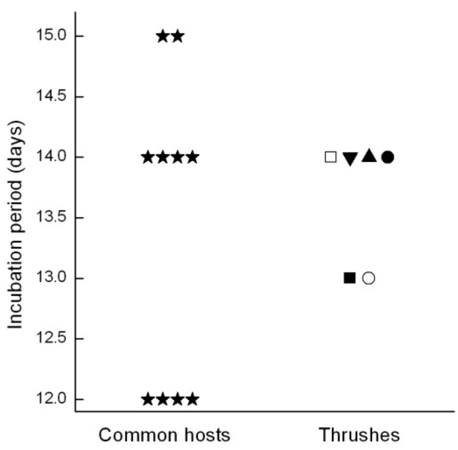

Adult body mass (g)
0
20
40
60
80
100
120
140
Common hosts
Thrushes

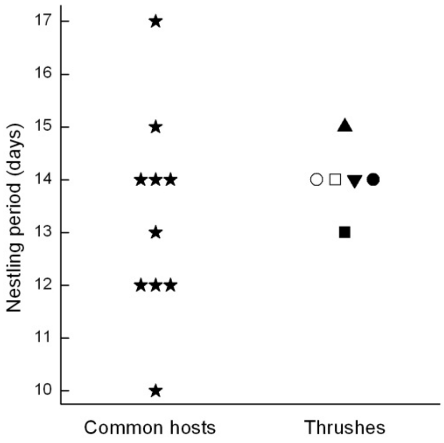

Nest cup depth (cm)
3
4
5
6
7
Common hosts
Thrushes

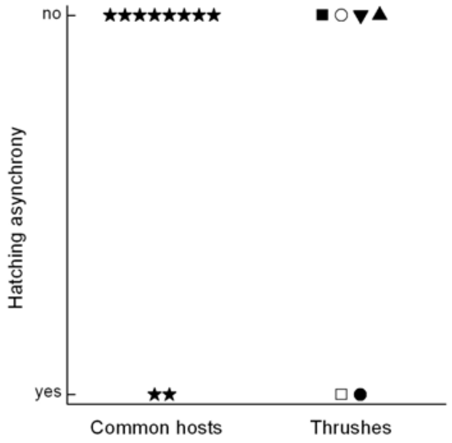

Nest cup steepness
0.5
0.6
0.7
0.8
0.9
1.0
1.1
Common hosts
Thrushes

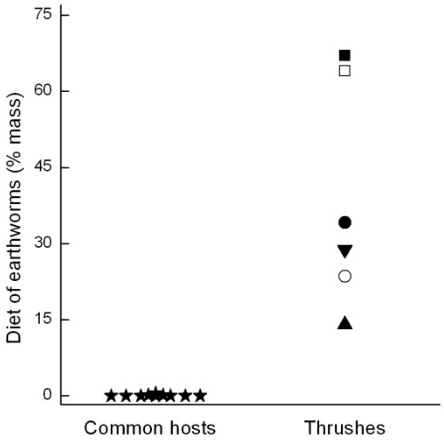

Egg volume (cm^3)
1
2
3
4
5
6
7
8
Common hosts
Thrushes

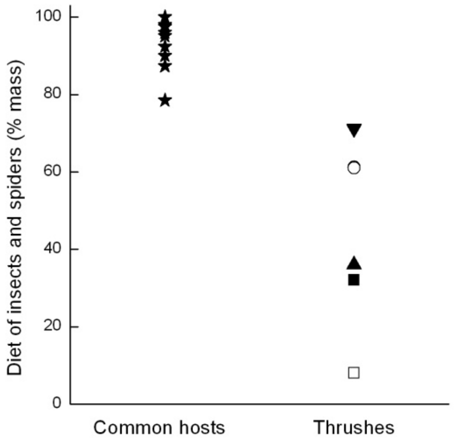

Clutch size
3.5
4.0
4.5
5.0
5.5
6.0
6.5
Common hosts
Thrushes


Incubation period (days)
12.0
12.5
13.0
13.5
14.0
14.5
15.0
Common hosts
Thrushes


Nestling period (days)
17
16
15
14
13
12
11
10
Common hosts
Thrushes


Hatching asynchrony
no
yes
Common hosts
Thrushes


Diet of earthworms (% mass)
75
60
45
30
15
0
Common hosts
Thrushes


Diet of insects and spiders (% mass)
100
80
60
40
20
0
Common hosts
Thrushes

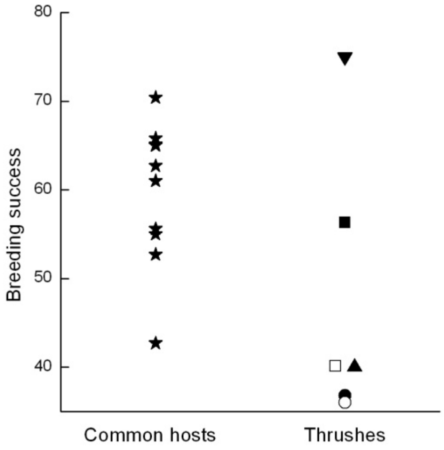
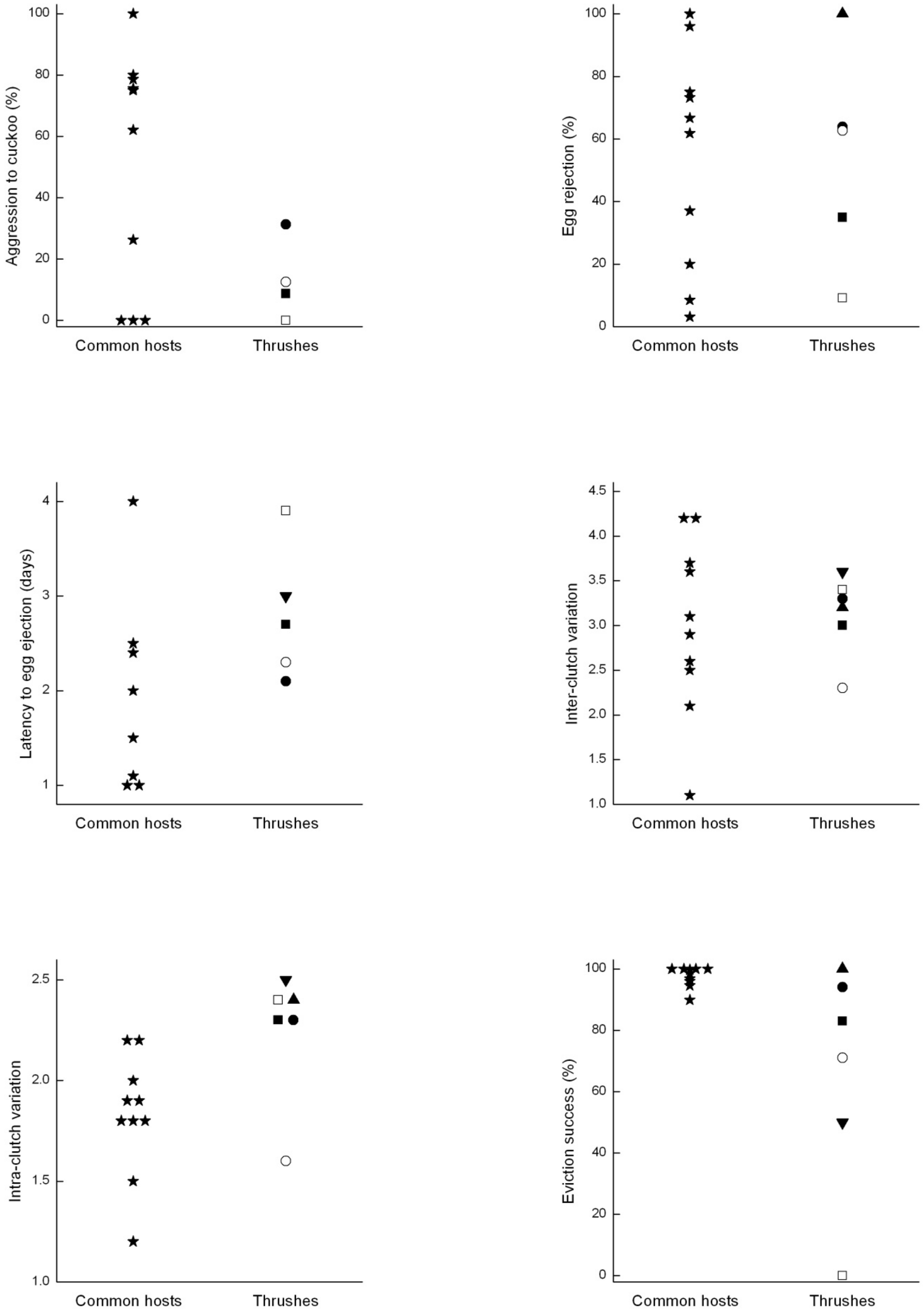

Breeding success
80
70
60
50
40
Common hosts
Thrushes

Figure S1b


Aggression to cuckoo (%)
100
80
60
40
20
0
Common hosts
Thrushes
Egg rejection (%)
100
80
60
40
20
0
Common hosts
Thrushes
Latency to egg ejection (days)
4
3
2
1
Common hosts
Thrushes
Inter-clutch variation
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
Common hosts
Thrushes
Intra-clutch variation
2.5
2.0
1.5
1.0
Common hosts
Thrushes
Eviction success (%)
100
80
60
40
20
0
Common hosts
Thrushes

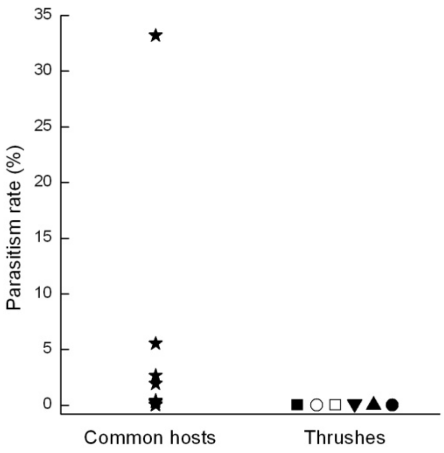

Parasitism rate (%)
35
30
25
20
15
10
5
0
Common hosts
Thrushes

Figure S2

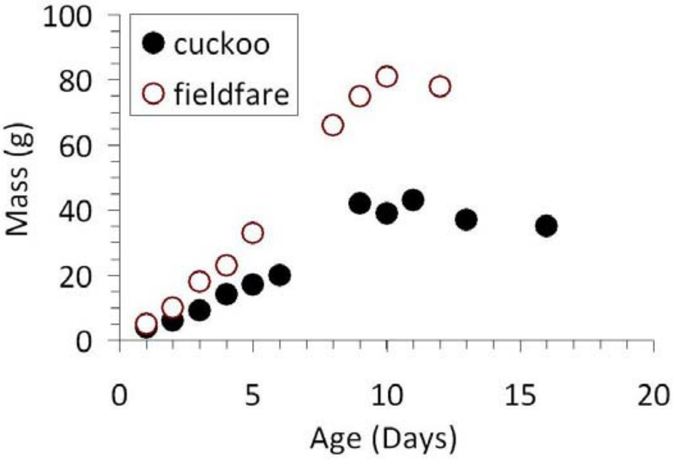


Table S1 Predictions for differences in candidate life-history characteristics between thrushes and regular cuckoo hosts. "Predicted differences" under the hypothesis that the particular factor explains the absence of cuckoo parasitism in thrushes. "–" = predicted lower value of the trait in thrushes than in common hosts, "+" = the opposite. "**General life-history traits**" may cause primary unsuitability of hosts for exploitation by parasites (such traits prevent host-parasite co-evolution). "**Specific parasitism-related traits**" may cause secondary unsuitability and represent host defences previously evolved due to brood parasitism (such traits do not enable parasites to colonize such hosts again). For rationales behind each hypothesis see sources in "References" column.

Trait	Predicted difference	References
General life-history traits		
Breeding range	–	Soler, Møller & Soler (1999)
Breeding population	–	Soler, Møller & Soler (1999)
Breeding density	–	Soler, Martín-Vivaldi & Møller (2009)
Duration of the breeding season	–	Soler, Møller & Soler (1999)
Overlap of breeding with the cuckoo	–	Honza, Kuiper & Cherry (2005)
Broods per season	–	Soler, Møller & Soler (1999)
Adult body mass	+	Soler, Møller & Soler (1999)
Nest cup depth	+	Grim *et al.* (2009a)
Nest cup steepness (depth/diameter ratio)	+	Grim *et al.* (2009a)
Egg volume	+	Moksnes *et al.* (1991)
Clutch size	+	Soler, Møller & Soler (1999)
Incubation period duration	–	Soler, Møller & Soler (1999)
Nestling period duration	–	Soler, Møller & Soler (1999)
Hatching asynchrony (presence)	+	Soler (2002)
Diet – insects + spiders	–	Grim & Honza (2001)
Diet – earthworms	+	Grim (2006)
Breeding success	–	Avilés et al. (2006)
Specific parasitism-related traits		
Aggression to cuckoo	+	Røskaft *et al.* (2002)
Egg rejection	+	Honza *et al.* (2004)
Latency to egg ejection	–	Honza *et al.* (2004)
Responses in sympatry vs. allopatry	S > A	Stokke *et al.* (2008)
Inter-clutch variation	+	Øien, Moksnes & Røskaft (1995)
Intra-clutch variation	–	Øien, Moksnes & Røskaft (1995)
Eviction success	–	Grim *et al.* (2009a,b)

Table S2 Responses by thrushes to simulated brood parasitism. Host responses include aggression to stuffed dummies of the common cuckoo and the hooded crow, rejection of parasitic model eggs (blue and spotted) and latencies to egg rejection in sympatry and allopatry with the cuckoo. For effect sizes see Table 1. For statistical and experimental procedure details see Methods. *d.d.f.* = denominator degrees of freedom. Nominator degrees of freedom = 1 in all cases except "nest stage" that had 4 *d.f.* in aggression analyses and 2 *d.f.* in egg rejection and latency analyses).

Predictor	Blackbird			Song thrush			Redwing			Fieldfare		
	d.d.f.	*F*	*P*	*d.d.f.*	*F*	*P*	*d.d.f.*	*F*	*P*	*d.d.f.*	*F*	*P*
Aggression												
Geography	160	0.22	0.64	114	1.04	0.31	120	2.09	0.15	138	0.00	1.00
Dummy	161	3.97	0.05	113	0.52	0.47	121	39.07	<0.0001	139	0.00	0.97
G*D	136	0.70	0.41	79	0.92	0.34	.	.	.	.	.	.
Clutch	137	0.11	0.74	94	2.09	0.15	105	2.47	0.12	118	0.12	0.73
Nest stage	156	1.43	0.23	90	2.20	0.08	102	0.79	0.50	115	0.05	0.98
Laying date	148	0.12	0.73	80	0.00	0.98	101	0.09	0.77	137	0.95	0.33
Egg rejection												
Geography	128	0.01	0.93	71	2.18	0.14	144	1.87	0.17	67	2.50	0.12
Egg model	129	2.47	0.12	72	6.00	0.02	143	0.93	0.34	66	0.08	0.77
G*E	121	3.15	0.08	67	0.00	0.95	.	.	.	.	.	.
Clutch	123	0.50	0.48	69	0.15	0.70	137	0.01	0.94	62	0.56	0.46
Nest stage	127	2.47	0.12	70	0.18	0.67	141	0.35	0.55	65	1.85	0.18
Laying date	122	0.27	0.61	68	0.04	0.85	.	.	.	64	0.56	0.46
Latency to egg rejection												
Geography	91	6.43	0.01	54	1.49	0.23	52	1.78	0.19	13	0.37	0.55
Egg model	90	1.41	0.24	53	1.41	0.24	51	0.46	0.50	14	4.64	0.049
G*E	84	0.72	0.40	49	1.36	0.25	.	.	.	.	.	.
Clutch	86	0.99	0.32	51	0.05	0.83	45	0.04	0.84	14	6.91	0.02
Nest stage	85	0.58	0.45	50	0.01	0.94	50	0.34	0.56	12	0.16	0.70
Laying date	89	0.18	0.68	52	1.97	0.17	49	0.19	0.67	14	11.84	0.004

References

Avilés, J., Stokke, B. G. & Parejo, D. (2006) Relationship between nest predation suffered by hosts and brown-headed cowbird parasitism: a comparative study. *Evolutionary Ecology*, **20**, 97–111.

Grim, T. (2006) Cuckoo growth performance in parasitized and unused hosts: not only host size matters. *Behavioral Ecology and Sociobiology*, **60**, 716–723.

Grim, T, & Honza, M. (2001) Does supernormal stimulus influence parental behaviour of the cuckoo's host? *Behavioral Ecology and Sociobiology*, **49**, 322–329.

Grim, T., Rutila, J., Cassey, P. & Hauber, M.E. (2009a) The cost of virulence: an experimental study of egg eviction by brood parasitic chicks. *Behavioral Ecology*, **20**, 1138–1146.

Grim, T., Rutila, J., Cassey, P. & Hauber, M.E. (2009b) Experimentally constrained virulence is costly for common cuckoo chicks. *Ethology*, **115**, 14–22.

Honza, M., Procházka, P., Stokke, B.G., Moksnes, A., Røskaft, E., Čapek, M. & Mrlík, V. (2004) Are blackcaps current winners in the evolutionary struggle against the common cuckoo? *Journal of Ethology*, **22**, 175–180.

Honza, M., Kuiper, S.M. & Cherry, M.I. (2005) Behaviour of African turdid hosts towards experimental parasitism with artificial red-chested cuckoo *Cuculus solitarius* eggs. *Journal of Avian Biology*, **36**, 517–522.

Moksnes, A. & Røskaft, E. (1995) Egg-morphs and host preference in the common cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. *Journal of Zoology*, **236**, 625–648.

Moksnes, A., Røskaft, E., Braa, A.T., Korsnes, L., Lampe, H.M. & Pedersen, H.C. (1991) Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour*, **116**, 64–89.

Øien, I.J., Moksnes, A. & Røskaft, E. (1995) Evolution of variation in egg color and marking pattern in European passerines: adaptations in a revolutionary arms race with the cuckoo, *Cuculus canorus*. *Behavioral Ecology*, **6**, 166–174.

Perrins, C. (ed.) (1998) *The Complete Birds of the Western Palearctic on CD-ROM*. Oxford University Press, Oxford.

Røskaft, E., Moksnes, A., Stokke, B.G., Bičík, V. & Moskát, C. (2002) Aggression to dummy cuckoos by potential European cuckoo hosts. *Behaviour*, **139**, 613–628.

Soler, J.J., Møller, A.P. & Soler, M. (1999) A comparative study of host selection in the European cuckoo. *Oecologia*, **118**, 265–276.

Soler, J.J., Martín-Vivaldi, M. & Møller A.P. (2009) Geographic distribution of suitable hosts explains the evolution of specialized gentes in the European cuckoo *Cuculus canorus*. *BMC Evolutionary Biology*, **9**, 88.

Soler, M. (2002) Breeding strategy and begging intensity: influences on food delivery by parents and host selection by parasitic cuckoos. *The Evolution of Begging*. (eds J. Wright & M.L. Leonard), pp. 413–427. Kluwer, Dordrecht, The Netherlands.

Stokke, B.G., Hafstad, I., Rudolfsen, G., Moksnes, A., Møller, A.P., Røskaft, E. & Soler, M. (2008) Predictors of resistance to brood parasitism within and among reed warbler populations. *Behavioral Ecology*, **19**, 612–620.