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The cost of virulence: an experimental study of egg eviction by brood parasitic chicks

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Hatchlings of some virulent brood parasitic birds have evolved to eliminate host offspring. We experimentally studied the dynamics and potential costs of the egg eviction behavior of hatchlings of the common cuckoo *Cuculus canorus* in broods of common redstarts *Phoenicurus phoenicurus,* a cavity nesting host. Eliminating the labor of egg tossing per se improved the cuckoo chick's growth during the eviction period by ~20–30%. Evictor cuckoo chicks recovered from the cost of egg tossing to fledge at similar masses compared with solitary chicks, although they did so at older ages. Foster parents fed evictor chicks less often compared with nonevictors. Feeding frequencies by hosts to evictors correlated negatively with eviction effort as evicting chicks often appeared to ignore fosterers offering food. Nest cup steepness was negatively related to eviction success and positively to age at first eviction. We propose that eviction behavior by cuckoo hatchlings is favored by selection because the costs of eviction are much lower than the costs of cohabitation with host chicks. *Key words:* arms race, coevolution, host–parasite interactions. *[Behav Ecol 20:1138–1146 (2009)]*

> *"It is wonderful to see the extraordinary exertions of the young Cuckoo, when it is two or three days old, if a bird be put into the nest with it that is too weighty for it to lift out. In this state it seems ever restless and uneasy"* (Jenner 1788, p. 226)

Eliminating host progeny, which may become costly competitors for parental provisions (Hauber and Moskát 2008; Grim et al. 2009), is one of many adaptations to have evolved in virulent obligate brood parasites (Kilner 2005). Among the best studied examples is the eviction behavior of the common cuckoo chick (*Cuculus canorus,* hereafter: cuckoo). The cuckoo hatchling tossing the eggs or nestlings of the host over the nest rim is "perfectly naked, without a vestige of a feather… its eyes are not yet opened, and its neck seem[s] too weak to support the weight of its head" (Blackburn 1872, p. 383). Thus, the cuckoo chick eliminates its nest mates even before it has a chance to observe them.

Not surprisingly, the process of evicting the eggs and chicks of hosts, which are sometimes heavier than the cuckoo chick itself (Honza et al. 2007), from a relatively deep host nest is an achievement so incredible that it was strongly disbelieved by laypeople and scientists from the time of Aristotle. The very first detailed eyewitness description of the eviction behavior was published over 220 years ago by Jenner (1788). Today, photographic and film evidence allows everyone to observe egg tossing by cuckoo chicks (Attenborough 1998, p. 247). Yet, even so many years after Jenner's pioneering observations, the cuckoo's eviction instinct still remains "subject hitherto not sufficiently investigated" (Jenner 1788, p. 220). Recently, Honza et al. (2007) reported detailed observational data on cuckoo chicks' eviction behaviors in the nests of 2 common hosts, the great reed warbler (*Acrocephalus arundinaceus*) and the reed warbler (*Acrocephalus scirpaceus*). This study found that cuckoos in great reed warbler nests evicted faster than in reed warbler nests. Virtually all other knowledge of the eviction instinct of the cuckoo is based on anecdotal observations (e.g., Molnár 1944; Wyllie 1981), whereas more detailed experiments are reported from 2 evictor Australian *Chalcites* cuckoos (Payne RB and Payne LL 1998).

Previously, Gill (1998) and Kleven et al. (1999) hypothesized that their data on differing growth rates of evictor parasite chicks were related, in part, to differences in the growth costs of the cuckoo chicks' eviction effort between different host species. More generally, Kilner (2005, 2006) hypothesized that growth rates and virulence of brood parasite chicks represent a trade-off between costly competition with host nest mates and increased parental provisioning for larger broods (Kilner 2003; Kilner et al. 2004). To date, empirical data regarding the fitness-relevant mechanics and dynamics of the eviction behavior of the cuckoo remain sparse, including the quantification of the costs and benefits of the cuckoo chicks' virulent evictor behavior. Information on the latter aspects of eviction is especially critical because cohabitation with host nest mates by evictor brood parasitic cuckoos is predicted to be costly, as opposed to nest mate tolerant *Molothrus* cowbird parasites which benefit from cohabitation with host chicks (Kilner 2003; Kilner et al. 2004). Specifically, experimental manipulations documented lower feeding and growth rates, delayed fledging, and lower fledging success of experimentally cohabiting *Cuculus* cuckoo chicks, compared with "solitary" cuckoo chicks (Martín-Gálvez et al. 2005; Grim 2006b; Hauber and Moskát 2008; Grim et al. 2009).

In contrast to the benefits of cuckoos' growing up alone, it is unknown whether cuckoo chicks' virulence is costly and what the potential mechanisms behind these costs of eviction may be. Kleven et al. (1999) proposed that larger nests and/or larger host eggs might increase energetic costs of eviction and, consequently, decrease parasite growth rates. Similarly, the success and cost of eviction might also vary across different designs of host nest architecture (Grim 2006b). Finally, Soler (2002) described the case of a cuckoo chick focusing on nest mate eviction in which the parasite ignored fosterers' attempts to feed it and finally died. Thus, there also seems to be

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a trade-off between eviction and other nestling activities, including begging and feeding. To date, no study has tested quantitatively this "costly eviction hypothesis." Here we approached the issue of the eviction behavior to test the trade-off hypothesis for the evolution of virulence in brood parasites developed by Kilner (2005, 2006). According to this hypothesis, costs of eviction must be smaller than costs of cohabitation with host nestlings for the eviction behavior to evolve.

We performed a study in Finland in nests of the common redstart (*Phoenicurus phoenicurus*; hereafter: redstart), which is the only cavity nester known to be frequently parasitized by the cuckoo. One of the remarkable features of the redstart–cuckoo system is that, in contrast to all other regular host species, cuckoo chicks are frequently unable to evict all host offspring and are forced to share the nest with at least some of them (Rutila et al. 2002). Thus, there is much natural variation in the cuckoo's success to eliminate host progeny which, in turn, might translate into varying benefits and costs of eviction (Aviles et al. 2005). In our previous experimental study on this host–parasite system, we demonstrated that competition with redstart chicks per se had dramatic negative effects on cuckoo growth, survival, and fledging time and mass (Grim et al. 2009). Here we addressed the complementary question of whether egg eviction behavior by cuckoo chicks is costly. We tested the effects of egg tossing on cuckoo chicks' growth and survival, while removing confounding effects of competition with host hatchlings. We also quantified eviction effort and success, nest cup design, and fosterer care (i.e., feeding rates and brooding) to assess potential mechanisms of costly virulence by evictor cuckoo chicks.

METHODS

Study site and general field procedures

We conducted fieldwork in Ruokolahti (61°24′N, 28° 37′E) in southeastern Finland from May to July 2007 and 2008. The study sites were cultivated pine forests. We utilized 400 nest-boxes specially designed for redstarts, for details, see Rutila et al. (2002). Our nest-boxes were similar (inner size: width = 12 cm, depth = 12 cm, height = 25 cm) to natural cavities typically used by redstards (10–12.5 × 10–12.5 × 20–30 cm (Aviles et al. 2005), and the nest cup had wide rims where the evicted egg can be deposited (for a representative photo, see Figure 1 in Grim et al. 2009). Thus, the nest-box design could not confound our estimations of eviction costs by constraining the eviction success of cuckoo chicks. We checked nest-boxes several times during the laying and incubation stages to establish clutch completion dates (assuming a single egg laid per day) and once or twice daily during expected hatching time, as well as during the first 7 days posthatch (see below). Older nests were checked whenever feasible (typically every other day).

Although we did not study genetic aspects of cuckoo chick relatedness to assign them to particular cuckoo mothers, we are confident that most cuckoo chicks were the offspring of different female parasites, thus reducing the chance of pseudoreplication. This was because 1) our study area consists of many spatially widely isolated sites, supplied with nest-boxes over an area of 350 km^2; 2) we introduced some cuckoo eggs from other distant areas (Grim et al. 2009); and 3) densities of cuckoo females were very high at each locality (Rutila et al. 2002).

Experimental procedures

Host eggs frequently hatch during the prolonged eviction attempts of the cuckoo hatchlings in redstart nests (Rutila et al. 2002). Competition with host redstart chicks is known to have strong negative effects on cuckoo growth, fledging, and survival (Grim et al. 2009). To avoid confounding effects of nest mate competition on the measurement of eviction costs per se, we removed hosts eggs immediately after the cuckoo hatched in all nests.

Figure 1
A common cuckoo chick attempts to evict experimental model cuckoo eggs in the nest of the common redstart in South Karelia, Finland. The nest lining contains feathers of the hazel grouse (*Bonasa bonasia*). Photo: T. Grim and V. Ward.

We then randomly assigned 30 cuckoo chicks to 2 treatment groups: 1) evictor group where cuckoo chicks could perform egg tossing behaviors ($n = 14$ nests) and 2) solitary group where each cuckoo chick was raised alone in an otherwise empty nest ($n = 16$ nests). In the evictor treatment, immediately after removing original host eggs, we added 5 artificial model cuckoo eggs into the nest cup. Cuckoo nestlings start to evict host progeny when about 2 days old (Honza et al. 2007, also see our Results) and so we are confident that solitary cuckoos did not experience any eviction costs.

Artificial eggs were painted to resemble the blue color of the redstart eggs (Rutila et al. 2002, see Figure 1) to prevent any rejection response by fosterers (Järvinen 1984). Artificial ($n = 25$) and natural cuckoo ($n = 33$) eggs from our study area had similar (mean ± standard error) mass (3.3 ± 0.03 vs. 3.4 ± 0.06 g: $t_{57} = 0.85$, $P = 0.40$), length (22.3 ± 0.07 vs. 22.2 ± 0.17 mm: $t_{57} = 0.72$, $P = 0.48$), and width (16.9 ± 0.07 vs. 16.8 ± 0.10 mm: $t_{57} = 1.11$, $P = 0.27$). We chose to add 5 model eggs to evictor nests for 2 reasons: 1) the typical clutch/brood size of the redstart is 6 eggs which is equivalent to 1 cuckoo chick plus 5 model eggs and 2) the total mass of models approximated the average total mass of eggs and/or hatchlings of the redstart that a cuckoo chick typically evicts (Rutila et al. 2002).

Each model egg was used only once at the first 9 experimental nests, at another 5 nests, we randomly selected 5 models from the pool of already used models. Thus, each cuckoo chick was presented with a unique combination of model eggs. Before reuse, we cleaned the model eggs to minimize the risk of pathogens and other cues transferred between nests.

The eviction instinct normally ceases at the age of 4 days posthatch (Wyllie 1981). However, we conservatively removed the models from the nest when the chick was 7 days old or at least 1 day after the last recorded eviction attempt by the cuckoo at all studied nests.

Video recording and measurements

Honza et al. (2007) reported that during daylight hours *Cuculus* cuckoos' eviction patterns were distributed randomly. In contrast, Payne RB and Payne LL (1998), who studied *Chalcites* cuckoos, detected most eviction attempts in the morning. Therefore, we recorded each chick at varying times of day (from 7 AM till 9 PM CET) throughout the nestling period to be able to detect possible daytime patterns of eviction.

We videotaped cuckoo chicks' and host parents' behaviors at both evictor and solitary nest-boxes using roof-mounted digital cameras (Mini-DV system, 1.5-h long recordings). We attempted to film experimental nests twice daily from day 0 (hatching day) till day 7. This was not always possible due to adverse weather conditions (e.g., heavy rain) and/or logistical reasons (e.g., when too many nests were synchronous in distant nest-boxes). Nevertheless, all experimental nests were recorded at least once on each day.

We quantified the dynamics of the eviction effort as a proportion of time the cuckoo chick spent in a typical eviction posture, as described by earlier authors (Jenner 1788; Blackburn 1872). Typically, cuckoo chicks' legs are spread wide and braced against the nest walls, wings are raised, and head is pointing downward (Figure 1). In all, we recorded 279 h of chick and host behaviors from hatching till fledging. We measured the length of each uninterrupted eviction attempt during the "push-up" phase (*sensu* Payne RB and Payne LL 1998) till the time when the model egg was pushed across the nest cup rim (successful eviction) or when the model fell back into nest cup or the cuckoo chick simply stopped to push the model (unsuccessful eviction). We predicted a negative relationship between chick mass growth and eviction effort ([sum of time the cuckoo spent in the eviction posture/total recording time] × 100).

Each day we recorded chick mass, measured by portable electronic balance to the nearest 0.1 g. Overall, we predicted a lower age-specific mass for evictor than solitary cuckoo chicks. We also characterized the design of host nests by measuring nest cup diameter (di) and nest depth (de; both to the nearest 0.5 cm). Each measurement was taken twice with 2 diameter measurements per nests taken perpendicularly to each other, and the average of the 2 data points was used in calculations. We calculated an index of nest cup steepness as the ratio of de/di. Thus, higher values of this index indicate steeper nest cups and lower values indicate nest cups with shallower slopes. We predicted a negative relationship between the index of nest cup steepness and cuckoo growth and eviction success. Honza et al. (2007) tested for correlations between nest volume and eviction behavior. We also calculated nest volume according to the same formula: $2/3 \times \pi \times (di/2)^2 \times de$. Finally, we classified nest material as a categorical variable "grass" versus "non-grass" in the lining of the nest cup. The latter category also contained "moss" (5 nests) and "feathers" (2 nests; Figure 1). We did not manipulate nest architecture but studied correlates of these nest design parameters within their natural variation.

Measurements of eviction behavior

Payne RB and Payne LL (1998) recognized 2 phases of eviction behavior. The "searching" phase referred to the nestling cuckoo moving actively around the nest cup to come into contact with host eggs or nestlings. The push-up phase referred to eviction per se, that is, the cuckoo shifted its body under the egg or nestling and moved it across the nest rim. In our study system, the cuckoo chicks were brooded by the female redstart most of the time during the first 5 days after hatching (Grim T, Rutila J, Cassey P, and Hauber ME, unpublished data). Therefore, we could not determine eviction attempts directly during periods of brooding. Instead, we looked for footage when the redstart female repeatedly rose above the nest cup, presumably in response to the cuckoo chick pushing against her body and the chick in the eviction position became visible. Another cue for determining the eviction activity was seeing the cuckoo's feet braced against the nest lining (frequently well visible even when the female redstart was brooding). Thus, we focused on the push-up phase of the eviction process. In contrast, the searching phase virtually did not occur (or was very short) because the cuckoo chick was in physical contact with the many artificial eggs representing the typical redstart clutch size due to the size of the nest cup.

Under natural conditions, when a cuckoo chick successfully evicts host progeny, it is impossible to determine when the eviction instinct finally dissipates (Honza et al. 2007). This is simply because there are no more cohabitants or other objects in the nest that could trigger eviction behavior of the parasite chick. Therefore, if the cuckoo succeeded at eviction, we recorded how many model eggs were evicted and then returned them into the nest cup. This enabled us to detect both the start and end of the eviction period by the cuckoo, while also both increasing the variability in eviction effort and approximating the natural situation of prolonged and unsuccessful evictions in the redstart gens of the cuckoo, whose chicks frequently end up cohabiting with host nest mates in natural parasitism (Rutila et al. 2002; Aviles et al. 2005).

Together, we used 4 lines of evidence to determine the start and end of the eviction activity: 1) direct observations of chick movements during regular nest checks, 2) direct capture of chick eviction activity on video recordings, 3) indirect evidence of model eggs tossed outside the nest cup, and 4) direct evidence elicited by the "finger" method of Payne RB and Payne LL (1998); the latter method is done by gently placing a finger on cuckoo chick's back to determine whether the cuckoo assumed the typical eviction posture with legs spread, wings raised, and head bracing against the background (Figure 1). We applied the finger method on evictor chicks only. Each evictor chick was tested on every nest check from hatching till the eviction behavior was not elicited by the finger on several consecutive nest visits. When video recording was taken at the nest, we applied the finger method only after the recording was finished so as not to affect the chick behavior during recording. The tested chicks typically responded to finger stimulation within seconds. If the chick did not respond immediately, we left the finger on its' back for approximately 30 s. If no response was recorded within that period, the chick was scored as "not actively evicting."

For one chick, we had no reliable cues to determine the timing of eviction activities (notably, this was the nest with the highest value of nest cup steepness index and no model eggs were evicted in that nest). Conservatively, we assigned this chick the average timing of eviction activity observed at the other nests (Table 1). The exclusion of this nest from the growth analyses had no effect on our conclusions.

The start of the eviction period was estimated as the midpoint hour between the last direct (personal) or indirect (video recorded) observation of the nest when there were no signs of eviction activity and the first observation when there were such signs. The end of the "eviction phase" was similarly estimated as the midpoint hour between the time of the last recorded eviction activity and the first time no eviction activity was either observed or elicited. The length of the eviction period was then calculated to the nearest hour.

Table 1

Characteristics of common cuckoo eviction behavior in the nests of the host redstart

Parameter	Sample size	Minimum	Maximum	Mean	Standard error
Age when eviction started (days)	13	0	2	1.5	0.18
Age when eviction ceased (days)	12	3	8	5.7	0.43
Length of eviction activity (days)	12	1.9	6.4	4.3	0.46
Age at first successful eviction (days)	10	1.5	3.5	2.6	0.18
Mass at first successful eviction (g)	10	7.2	15.8	9.9	0.83
Eggs evicted (%)	13	0	100	56.9	12.37

For estimation of eviction parameters, see Methods. Hatching day = day 0. The sample sizes differ because 4 (out of total 14) chicks were unable to evict any model eggs (1 of those chicks died before the typical end of the eviction phase). For 1 nest, we had no reliable cues to determine the timing of eviction activities.

Statistical analyses

There was extensive individual variability in the dynamics of cuckoo chicks' eviction behaviors. Different parasites varied in age and mass when their eviction behavior started as well as the lengths of their eviction phase (Table 1). Thus, owing to ontogenetic difference, it is not relevant to directly compare the evictor and solitary treatment groups, even when of the same age, because of the variability such that for any given age some evictor cuckoos might not yet be evicting (i.e., before their individual timing of the start of eviction activity), whereas others may have already completed their eviction period.

To control for these ontogenetic differences, as potential confounds for the cost of eviction, we used a paired analytical approach in our data analyses. Specifically, first we estimated the individual length of the eviction phase for each chick with model eggs. Second, each evictor chick was matched with a solitary chick according to 2 criteria: 1) chicks had identical or almost the same mass and age at the start and 2) the solitary chick had its mass measured at the same or almost the same ages throughout the nestling period as its matched experimental chick (for ranges of mass and age matching, see Results). Thus, within the matched pair, chicks had virtually identical ontogenetic start lines (for mass and age) and finish lines (for age in each developmental phase, see below). Our selection criteria incidentally also resulted in that solitary and evictor nests did not consistently differ in original host clutch size (6.6 ± 0.2 vs. 6.4 ± 0.3 total eggs; paired *t*-test: $t_{13} = 0.65$, $P = 0.53$), which is a surrogate measure of host quality that could in turn influence chick growth (Slagsvold and Lifjeld 1990).

We confirmed that our results were not contingent on the particular pattern of chick pairing: 1) using the identical time periods as those presented in the Results, we changed identity of matched pairs so that each chick was paired with a different chick (consequently with slightly less similar initial mass and age); we repeated this "rematching" protocol twice; and 2) we changed the time periods so that we used the previous or subsequent measurement for each nonevictor chick (thus, the lengths of comparative periods for solitary vs. evictor chicks were less similar that those shown in Results). Despite this relaxation of the quality of analyses, we found that in all cases our statistical conclusions remained identical. Thus, the results were confounded neither by particular chick assignment into matched pairs nor by the length of the estimated eviction periods for evictor chicks.

We then compared the differences between the chicks' growth rates. Growth rate was calculated as the increase in mass during the particular nestling developmental phase divided by the length of that phase (measured to the nearest hour between consecutive measurements). The advantage of this analytical design is that it controls both for initial conditions of the chicks within the matched pair and also for the developmental stage of a chick. Differences in the developmental phase might otherwise invalidate the comparison of growth rates between chicks that have different position on the growth curve (Hegyi and Török 2007).

We analyzed chick growth in several a priori defined developmental phases. Eviction phase; limits of the phase were determined for each matched pair by subtracting the start from the end of the evicting activity period. "Posteviction phase"; period of 5 days after the eviction activity ceased (approximately the early part of the linear phase of growth, days 5–10, see Grim 2006a, Grim et al. 2009). "Prefledging phase"; the late part of the linear phase of growth (days 10–15). "Fledging phase"; the asymptotic phase of growth (days 15–20).

The growth parameters for the matched pairs of chicks were analyzed using paired *t*-tests. Analyzing the data with nonparametric Wilcoxon matched rank tests gave qualitatively identical results. In the analyses of the resulting parameters at fledging between the treatment groups of solitary and evictor cuckoo chicks, we used unpaired comparisons (unpaired *t*-test for unequal variances) because there was no need to control for developmental stage and we could also use data from another 2 solitary cuckoo chicks to increase the sample size (these chicks had no available evictor chicks to be matched with).

Correlative relationships among feeding frequencies (number of feeds per hour), eviction effort (proportion of time spent evicting), brooding (proportion of time the chick was brooded by a host female), age (days), as well as the experimental treatments (evictor vs. solitary) were analyzed using general linear mixed models (GLMMs; PROC MIXED module in SAS; normal error distribution, parameters estimated by REML, denominator degrees of freedom calculated using Kenward–Roger method). GLMMs included nest (i.e., cuckoo chick) identity as a random factor. The covariance structure used variance components in all models. All models were checked for linearity of effects, normality of errors, and homogeneity of variances and were found to perform satisfactorily (Grafen and Hails 2002). To satisfy these assumptions, some variables were log transformed (as indicated in Results). Results are presented as mean ± standard error.

Although we performed multiple tests in the comparison of developmental periods, we did not apply a Bonferroni correction. This is because we agree with the arguments that Bonferroni corrections are largely inappropriate for ecological studies (Nakagawa 2004 and references therein). In addition, we did not test for any and all differences between treatments, rather we made specific temporal comparisons (before, during, and after eviction period) and tested directional predictions (lower mass in evictors than solitary chicks during eviction period). Still, we note that application of the sequential Bonferroni procedure would not change the interpretation of results of this study. Further, there is no pseudoreplication in this study because we statistically controlled for repeated measurements by including chick identity as a random effect in our GLMMs (in all cases, there was only one cuckoo chick per nest thus chick identity equals nest identity).

Finally, we note that 1) other studies of brood parasite growth based on smaller (Grim 2006a) or similar sample sizes (Kleven et al. 1999) were able to detect significant predicted differences, including studies on parasite species with smaller effect sizes (e.g., Kilner et al. 2004); 2) analyses of data in the present study clearly show that the samples are sufficient to detect differences in growth in "small" chicks (data from eviction period), thus lack of statistical differences in the growth of "large" chicks are unlikely to be explained as an artifact of small sample and/or effect sizes; and 3) we designed analyses so as to control for possible confounding traits (matched-pair comparative design), resulting in a novel approach to increase the power of comparisons, instead of simply increasing sample sizes in our animal manipulations.

RESULTS

Eviction success and temporal dynamics

The eviction behavior started typically when chicks were 1 or 2 days old but first successful evictions typically occurred a day later (Table 1). After a peak in eviction activities on day 4 (Figure 2), the eviction behavior dissipated up to day 8 (Table 1; Figure 2).

The eviction success of cuckoo chicks in redstart nests was highly variable. Of 14 experimental nests, 6 chicks evicted all model eggs, whereas 4 chicks did not succeed at evicting any eggs at all. At the 4 remaining nests, chicks evicted 1, 1, 2, and 3 models, respectively. One of the chicks died when 4 days old (although it showed eviction activity prior to that, it did not eventually succeed at evicting any eggs). Further, 3 chicks that evicted all model eggs initially, also evicted them repeatedly when we put the eggs back into the nest cup, whereas another 3 chicks that evicted all model eggs did not succeed again.

We detected 77 successful evictions, including 11 video-recorded evictions and 1 directly observed eviction (during a nest check). The average length of directly observed or video-recorded successful evictions was 108 ± 32 s (range: 15–405 s, $n = 12$). The remaining 55 evictions were not observed directly, but evicted eggs were found outside the nest cup in the nest-boxes; thus, the lengths of eviction attempts in those cases were unknown. In only 3 cases the evicted egg later fell back into the nest cup. Successful evictions occurred both when chicks were brooded (7 cases) or when the female was not present at the nest (5 cases, $\chi^2 = 0.17$, df = 1, $P = 0.68$). Females brooded the chicks up to day 11 post-hatch. At younger ages (up to day 5), chicks were brooded by female redstarts most (>50%) of the time (males never brooded). Chicks showed eviction attempts independently of whether being brooded (Figure 2; paired within-chick comparison, data for brooding vs. nonbrooding periods averaged for each chick to avoid pseudoreplication; paired t-test: $t_{13} = 0.97$, $P = 0.35$).

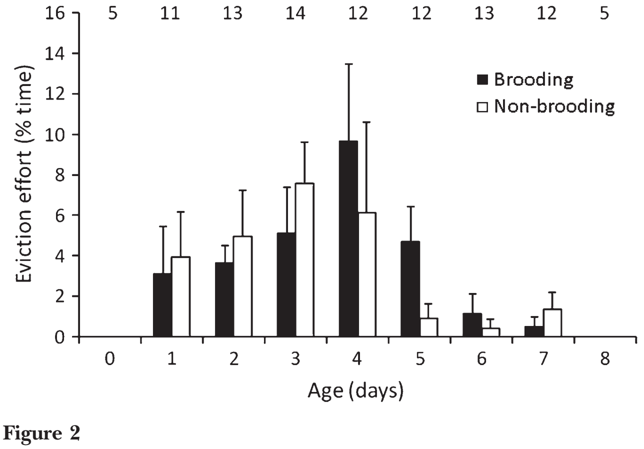

Figure 2
The temporal patterns of the eviction effort and its variation with the age of common cuckoo chicks in nests of common redstart hosts during brooding by foster parents (black bars) and nonbrooding (white bars) as recorded by videotapes. The results are given as mean + standard error. Sample sizes are given above the bars (number of chicks video recorded on the particular day, hatching = day 0).

The overwhelming majority of directly observed evictions occurred in the afternoon. Only 1 out of 12 directly observed successful evictions happened in the morning (at 9 AM), all others occurred after 4 PM. This was not a result of biased distribution of recording sessions: Our video recordings were conducted from 7 AM till 9 PM local time during the eviction period (days 0–8) and were distributed normally throughout the day (recording hour: median = 14:00, mean = 14:00 h ± 18 min). There was a nonsignificant tendency for a higher eviction activity in the afternoon (GLMM: log daytime hour: $F_{1,116.9} = 2.61$, $P = 0.11$; controlling for chick age including a quadratic term because the relationship between age and eviction effort was nonlinear, see Figure 2; effects of log (age^2): $F_{1,109.3} = 16.89$, $P < 0.0001$).

Costs of eviction behavior

Eviction behavior was temporarily costly for cuckoo chicks in terms of mass growth (Table 2). At the start of the eviction period, the mass and age of evictors was statistically identical to solitary chicks. In contrast, when the eviction phase ceased, the evictor cuckoos weighed significantly less than the solitary cuckoos of the same age (Table 2). The experimental elimination of potential eviction costs yielded an increase in age-specific chick mass in the solitary treatment by ~20–30% in comparison to the evictor treatment. However, the mass discrepancy between the 2 treatments gradually decreased in subsequent developmental phases (Figure 3), and evictors fledged at virtually the same mass as did nonevictors (Table 3). Overall, chicks in the evictor treatment fledged a day later compared with the solitary treatment (Table 3). Within the evictor treatment, chicks that evicted for more days showed greater fledging ages (Table 4). In contrast, eviction effort (averaged across the whole eviction period) showed a weak negative relationship with growth rates within the eviction period ($r_s = -0.44$, $n = 13$, $P = 0.13$).

Fosterer care

During the eviction phase, parental feeding frequencies (females and males combined for each nest), to provision solitary and evictor cuckoos, increased with chick age ($F_{1,93.3} = 72.60$, $P < 0.0001$) in a similar pattern as the age × treatment interaction was nonsignificant and we removed it from the final model ($F_{1,114.1} = 0.92$, $P = 0.34$). However, after controlling for age effects, the solitary cuckoos received significantly more feedings per hour (7.9 ± 0.9) than did the evictor cuckoos (5.1 ± 0.6; $F_{1,23} = 7.04$, $P = 0.014$).

Correlational data within the evictor treatment were consistent with a trade-off between eviction activity and feeding effort by fosterers (Figure 4). Specifically, increasing eviction effort was associated with decreasing feeding frequencies during the eviction phase, even when strong positive effects of the chick age were controlled for (log eviction effort: $F_{1,119.3} = 17.95$, $P < 0.0001$; log age: $F_{1,116.2} = 85.91$, $P < 0.0001$). Video recordings revealed cases whereby the cuckoo chicks ignored fosterers that actively attempted to feed them (e.g., cuckoo chicks either focused on evicting model eggs or lay exhausted in the nest after previous eviction attempts).

Table 2

Differences in mass growth (mean ± SE) between pairs of cuckoo chicks raised alone (eviction costs removed) and chicks that evicted model eggs (see also Methods and Table 1)

Phase	Solitary	Evictor	*t*	*P*
Mass at start (g)	6.0 ± 0.8	6.1 ± 0.7	0.67	0.52
Age at start (days)	1.4 ± 0.2	1.4 ± 0.2	0.00	1.00
Eviction ($n = 14$ pairs of matched cuckoo chicks)				
Length of the phase (days)	3.5 ± 0.3	3.4 ± 0.3	1.18	0.26
Mass at end (g)	22.9 ± 1.9	19.6 ± 2.0	4.14	0.001
Growth rate (g/day)	4.4 ± 0.3	3.9 ± 0.4	4.57	0.0005
Posteviction ($n = 13$ pairs of matched cuckoo chicks)				
Length of the phase (days)	4.1 ± 0.3	4.2 ± 0.3	0.84	0.42
Mass at end (g)	58.1 ± 1.9	52.3 ± 3.0	2.64	0.02
Growth rate (g/day)	8.4 ± 0.3	7.6 ± 0.5	1.47	0.17
Prefledging ($n = 12$ pairs of matched cuckoo chicks)				
Length of the phase (days)	5.2 ± 0.4	5.1 ± 0.4	0.40	0.70
Mass at end (g)	97.9 ± 3.5	88.2 ± 3.5	2.63	0.02
Growth rate (g/day)	6.9 ± 0.3	6.8 ± 0.3	0.27	0.79
Fledging ($n = 12$ pairs of matched cuckoo chicks)				
Length of the phase (days)	4.3 ± 0.2	4.6 ± 0.4	1.22	0.25
Mass at end (g)	109.8 ± 4.3	103.3 ± 3.1	1.61	0.13
Growth rate (g/day)	2.8 ± 0.4	3.1 ± 0.5	0.68	0.51

SE, standard error. Each evictor cuckoo was matched with a nonevictor cuckoo for initial mass and age at the start of the eviction period. Growth was analyzed in 4 phases (see Methods) Differences within matched pairs of chicks were tested with paired *t*-tests. Sample sizes differ between phases due to death or predation of 2 evictor chicks, respectively. Note that the large SE values are due to large variation in chick age (and consequently mass) within each group (solitary and evictor). This reflects large variation in the length of eviction periods among evictor chicks (Table 1).
In contrast, our comparisons were done not between entire treatment groups but within a priori matched pairs to control for this variation.

Notably, 1 cuckoo chick (age: 3.5 days) climbed over the nest rim while evicting 2 model eggs (both successfully evicted). The chick then spent 4 min outside the nest cup. The redstart female arrived at the nest when the chick was outside the nest cup, fed it, and started to brood the empty nest cup. Later the cuckoo climbed back into the nest cup traveling approximately 15 cm in total. In an open cup nesting host, such an eviction attempt would likely be fatal to the cuckoo (Molnár 1944).

Correlates of nest design

Nest cup steepness was a major determinant of egg eviction success (Table 4). Chicks in nests with steeper nest cups showed lower eviction success (Figure 5) and also only tended to succeed at evicting the first egg when they were older (Table 4) than chicks in shallower nests. In contrast, nest cup volume was not correlated with eviction success (Table 4).

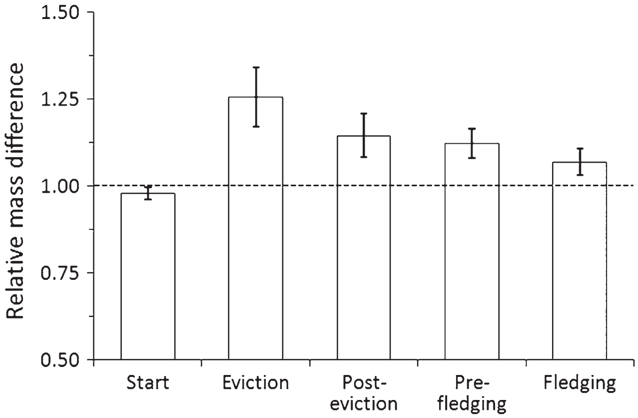

Figure 3
Relative mass differences between evictor and nonevictor common cuckoo chicks during the 4 studied phases (see Methods for definitions and Table 3 for sample sizes). Shown are means ± standard errors of relative growth differences (ratio of solitary chick's mass divided by the respective evictor chick's mass) within matched pairs of chicks (see Methods). The vertical line shows the expectation of growth under the null hypothesis of no costs of eviction.

We placed all successfully evicted eggs back in the nest cup at regular intervals throughout the eviction period. Thus, successful evictor chicks had a chance to evict more eggs than unsuccessful or partly successful evictors. To control for this effect, we recalculated correlations in Table 4 using percentage success (i.e., there was no difference between success of repeatedly successful evictors and those that evicted total of only 5 eggs). The resulting patterns of correlations (data not shown) remained qualitatively identical in all cases (see also Figure 5).

Eviction periods were not statistically different between nests lined with nongrass (median = 5.5 days) in comparison to grass materials (median = 3.1; Mann–Whitney $U_{6,6} = 2.56$,

Table 3

Fledging parameters of evictor and nonevictor cuckoos

Fledging parameter	Solitary	Evictor	*n*	*t*	*P*
Fledging success (%)	100	92	16, 13	—	0.45
Fledging age (days)	19.3 ± 0.4	20.4 ± 0.3	16, 12	2.48	0.02
Fledging mass (g)	105.4 ± 3.2	103.5 ± 3.5	15, 12	0.41	0.68
Age at fledging mass (days)	18.0 ± 0.4	19.7 ± 0.2	15, 12	3.40	0.003

Fledging age was estimated as a midpoint between the last nest check when the cuckoo chick was present and the first nest check when it was not in the nest, and there were no signs of predation. Fledging mass is the chick weight at the last weighing before fledging. Age at fledging mass is the chick age when it was weighed for the last time (including only chicks that were measured no more than 2 days before fledging). Differences in fledging success were tested with Fisher's exact test; all other differences were tested with unpaired *t*-tests for unequal variances.

Table 4

Correlates of nest design parameters, eviction activity, and eviction success (total number of artificial eggs tossed) of common cuckoo chicks raised in common redstart nests

Variable 1	Variable 2	n	r_s	P
Steepness	No. eggs evicted	13	−0.86	<0.001
	Age at first eviction	10	0.60	0.06
Nest cup volume	No. eggs evicted	13	−0.19	0.52
	Age at first eviction	10	0.22	0.54
Fledging age	Age when eviction started	11	0.31	0.35
	Length of eviction activity	11	0.71	0.01
Age at first eviction	No. eggs evicted	10	−0.70	0.02
Steepness	Length of eviction activity	12	−0.35	0.27
Length of eviction activity	No. eggs evicted	12	−0.09	0.79

When eviction success was measured by % eggs evicted the results were qualitatively identical (see Figure 5).

$P = 0.11$). However, when watching chicks in 2 nests lined with feathers of the hazel grouse (*Bonasa bonasia*; Figure 1) or the black grouse (*Tetrao tetrix*), respectively, we observed that they experienced difficulties in evicting model eggs because the feather lining slipped under their legs. One chick even became wrapped up in feathers during one directly observed eviction attempt and failed to evict any eggs during that particular attempt. In all, chicks in the 2 feather lined nests evicted only 2 and 3 of the 5 eggs, respectively.

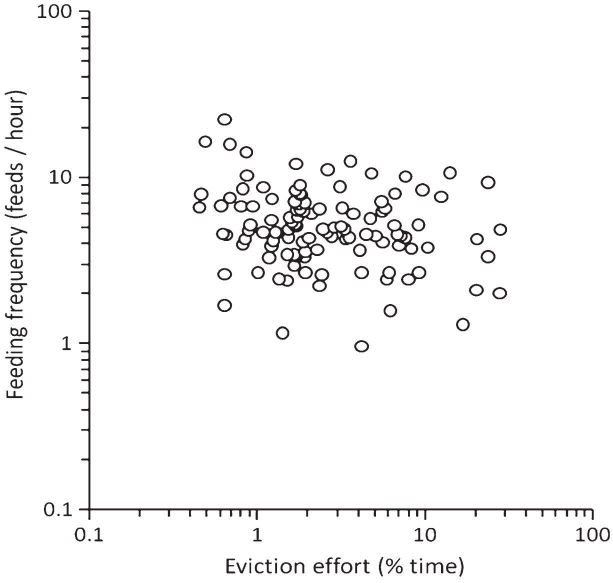

Figure 4
Trade-off between eviction effort by common cuckoo chicks and feeding frequencies by the fosterer common redstarts. Results from GLMM with the eviction effort as a predictor, the feeding frequency as a response, the chick age as a covariate (all log transformed), and the chick identity as a random effect (see Results).

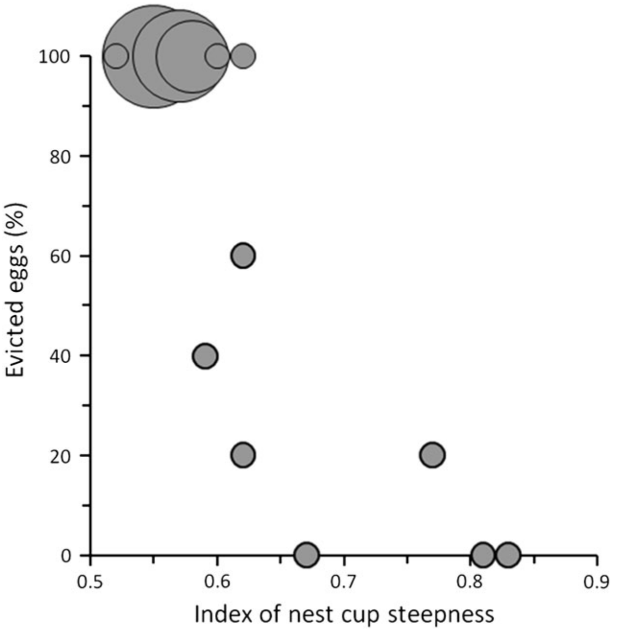

Figure 5
The relationship between eviction success (percentage of evicted model eggs) and nest cup steepness index (nest cup depth/nest cup width). For nests in which all eggs were evicted (100%), the sizes of data points are proportional to the cumulative number of eggs (5–21) evicted by each chick.

DISCUSSION

This study was aimed to experimentally characterize the temporal dynamics, success, and the costs of the fascinating eviction instinct of chicks of the brood parasitic common cuckoo. We found that eviction behavior was costly for parasite chicks; evictor cuckoos grew significantly slower than solitary, nonevictor cuckoos. This cost manifested in lower mass growth rates during the eviction phase (days 1–5 posthatch). We also detected a "ghost of eviction past" cost as evictor cuckoos grew more poorly for at least 5 days after they stopped in their eviction attempts. Nonetheless, these costs of eviction appear to be temporary and recoverable, as far as growth rates are concerned. Specifically, during later stages of development, the formerly evictor cuckoos showed similar growth rates and attained similar body masses as did the solitary chicks that had not paid the costs of eviction. Our study quantifies in detail the relative magnitude and suggests the potential mechanisms of the cost of egg eviction. Specifically, the variation in cuckoo's eviction success and total mass of evicted model eggs parallels published records of natural eviction success and total mass of redstart progeny evicted in our study area (Rutila et al. 2002).

Under normal conditions, some host eggs would typically hatch in redstart nests during the eviction phase (Rutila et al. 2002). Then, cuckoo chicks weakened by substantial eviction efforts could be at an even stronger disadvantage in nest mate competition (Hauber and Moskát 2008), which is permanently costly for cohabiting cuckoo chicks in redstart nests (Grim et al. 2009). Accordingly, the chicks in mixed broods in the latter study had large mass advantage over age-matched host redstart chicks; yet, still they were unable to compete with them successfully. Even in the absence of host nest mates in our study, evictor cuckoo chicks fledged at an older age than did solitary chicks in the nonevictor treatment. Eviction effort also positively correlated with age at fledging in the evictor treatment. Taken together, these patterns imply that in natural parasitism some ontogenetic costs associated with the virulence of chicks of the redstart gens of the cuckoo may persist beyond fledging and translate into reduced fitness of the cuckoo progeny.

What is the net selective advantage of eviction behavior?

Our previous work in the same study area quantified benefits of evicting host nest mates (Grim et al. 2009). Here we established the costs of the same behavior. Thus, we can quantify the pay off of eviction (by comparing Table 1 in Grim et al. 2009 and Table 3 in the current study). The net benefit of eviction was approximately a 2-fold increase in the successful chance of fledging ($\chi^2 = 6.37$, df $= 1$, $P = 0.01$), a shortening of the nestling period by ~2 days ($U_{12,4} = 2.56$, $P = 0.01$), and an increase in mass at fledging by around 35% ($U_{12,4} = 2.61$, $P = 0.009$). However, this quantification most likely underestimates the real net benefits of eviction. This is because raw benefits of eviction are probably underestimated by Grim et al. (2009) as cuckoo chicks in that study competed with host chicks only from the age of 6 days (i.e., they were experimentally freed from costs of cohabitation for the first 5 days posthatch).

The mechanistic basis of the costs of eviction

The cuckoo chick is often depicted as a superior competitor over host chicks (see supernormal stimulus hypothesis: Dawkins and Krebs 1979; Grim and Honza 2001; but see Davies and Brooke 1988). In this view, cuckoo chicks reap all the benefits by quickly and easily ridding the nest of host progeny. Our data from the redstart–cuckoo system suggest a different pattern. The cuckoo chick is clearly a poor competitor as it receives fewer feedings from fosterers during the egg tossing phase (this study) and fails to elicit sufficient provisioning in the presence of host chicks, even though these are several times smaller than the monstrous cuckoo nestling itself (Grim et al. 2009).

More generally, our data cast doubts on a prevalent view of brood parasitism as a strategy of foregoing several of the post-fertilization costs of reproduction by parents, including costly sibling competition in the brood (Hauber 2003). It appears that virulent brood parasites, including the cuckoo, exchanged the costs of parental investment and transferred them to their progeny, including the high energetic costs of eviction and reduced parental feeding rates (this study) and the risk of fatal self-eviction during egg tossing (Molnár 1944; Wyllie 1981).

We did not detect any consistent relationship between chick eviction effort and its success (Table 4). This might be because we did not record chick behavior at night. Honza et al. (2007) inferred that the great reed warbler cuckoos were involved in eviction more frequently during the night, whereas the reed warbler cuckoos evicted mostly during daylight hours. Further, eviction effort frequently dramatically changed within a period of several hours (when 2 consecutive recordings were done at the same nest within 1 day). This high temporal variability represents an important natural history trait of the cuckoo chick and implies that our estimates of the eviction effort from brief video recordings taken during daylight hour should be viewed as preliminary for the moment.

Honza et al. (2007) also found that cuckoos in great reed warbler nests evicted significantly quicker than cuckoos in reed warbler nests, during particular eviction events despite the pattern that the nests of the former host have much larger volume than those of the latter species. Our results suggest that nest size per se is not a major factor affecting the eviction behavior within host species, at least with respect to the limited variation of nest parameters of the studied redstarts. However, other aspects of nest design, specifically nest cup steepness, appear to be an important predictor of eviction success. This correlational result makes intuitive sense; eviction from a large nest might not be hard or unfeasible, if the nest cup is shallow, as was suggested by Kleven et al. (1999, p. 45) for cuckoo chicks in the large and shallow nests of the azure-winged magpies (*Cyanopica cyana*). In contrast, eviction from a small nest might still be a demanding or impossible task, if the nest is too deep in relation to its diameter; this scenario awaits future experimental work.

Temporal dynamics of egg tossing

Our results suggest new estimates of the age when cuckoo chicks start to evict (see also Honza et al. 2007). Age at first successful eviction was ~2 days in both these studies. Additionally, owing to our experimental methodology of replacing tossed eggs, we were also able to determine the time of cessation of the eviction period. Interestingly, we documented that eviction instinct subsides much later than 4 days posthatch as had been suggested by Wyllie (1981, p. 152) and the 4 or 5 days in great reed warbler or redstart nests used as the benchmark in our prior studies of chick competition (Hauber and Moskát 2008; Grim et al. 2009); some cuckoo chicks in redstart nests evicted up to day 8 posthatch.

Host behaviors and the timing of costly virulence by parasites

The cuckoo chick's eviction behavior is costly in terms of temporarily reduced growth (this study), delayed fledging (this study), and the risk of fatal self-eviction (Molnár 1944; Wyllie 1981). Also, eviction effort appears to be a trade-off against begging and fosterer provisioning (Soler 2002; this study).

So why does it fall to the blind and naked cuckoo chick to evict host eggs and nest mates? This is an important evolutionary conundrum because cuckoo mothers typically remove a host egg when laying their own parasitic egg (Wyllie 1981). However, Davies and Brooke (1988) demonstrated that if a host clutch is experimentally reduced to 1 or 2 eggs, the nest is almost always deserted. In addition, Moskát and Hauber (2007) reported the highest egg rejection rates of foreign eggs when a single host egg was naturally or experimentally exchanged for a natural or experimental parasite egg. The rejection of newly laid parasite eggs, when coupled with the elimination of all host eggs, might be a more general phenomenon that evolved even outside the context of obligate brood parasitism, that is, as a general response to partial clutch reduction (Kosciuch et al. 2006).

In contrast to single egg clutches, cuckoo hosts do not typically desert single chick broods of hosts or specialist parasites (Davies and Brooke 1988; Grim 2006c; also see Langmore et al. 2003). Although the desertion of a single chick can be induced experimentally (Grim 2007), this apparent rejection response is triggered not by the number of chicks at hatching but by the length of the time chick spends at the nest (see also Grim et al. 2003). The general willingness of the hosts to care for a single chick brood is a necessary prerequisite for the evolution and maintenance of the virulent eviction behavior by the cuckoo hatchlings. Even if eviction behavior is costly (see above), it can be favored by selection because the costs of noneviction and cohabitation with host chicks are even larger, as predicted by theory (Kilner 2005, 2006) and supported by experimental evidence (Hauber and Moskát 2008; Grim et al. 2009; see also Martín-Gálvez et al. 2005; Grim 2006b).

Overall, host behavior appears to both constrain and facilitate the timing of costly virulence of the hatchlings in the evictor brood parasites. It remains to be determined, however, whether the timing and the mechanism of virulence in other nest mate–eliminator brood parasite lineages are also costly (as seen in *Chalcites* cuckoos: Langmore et al. 2003; Kilner 2005, 2006) and influenced by host responses to the timing and extent of parasite virulence (Hauber 2003; Kilner 2005) and/or the physical constraints of the host nest milieu (Grim 2006b).

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REFERENCES

Attenborough D. 1998. The life of birds. Princeton (NJ): Princeton University Press.

Aviles JM, Rutila J, Møller AP. 2005. Should the redstart *Phoenicurus phoenicurus* accept or reject cuckoo *Cuculus canorus* eggs? Behav Ecol Sociobiol. 58:608–617.

Blackburn JH. 1872. Cuckoo and pipit. Nature. 5:383.

Davies NB, Brooke ML. 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. Anim Behav. 36:262–284.

Dawkins R, Krebs JR. 1979. Arms races between and within species. Proc R Soc Lond B Biol Sci. 205:489–511.

Gill BJ. 1998. Behavior and ecology of the shining cuckoo *Chrysococcyx lucidus*. In: Rothstein SI, Robinson SK, editors. Parasitic birds and their hosts. Studies in coevolution. New York: Oxford University Press. p. 143–151.

Grafen A, Hails R. 2002. Modern statistics for the life sciences. Oxford: Oxford University Press. p. 351.

Grim T. 2006a. Cuckoo growth performance in parasitized and unused hosts: not only host size matters. Behav Ecol Sociobiol. 60: 716–723.

Grim T. 2006b. Low virulence of brood parasitic chicks: adaptation or constraint? Ornithol Sci. 5:237–242.

Grim T. 2006c. The evolution of nestling discrimination by hosts of parasitic birds: why is rejection so rare? Evol Ecol Res. 8:785–802.

Grim T. 2007. Experimental evidence for chick discrimination without recognition in a brood parasite host. Proc R Soc Lond B Biol Sci. 274:373–381.

Grim T, Honza M. 2001. Does supernormal stimulus influence parental behaviour of the cuckoo's host? Behav Ecol Sociobiol. 49: 322–329.

Grim T, Kleven O, Mikulica O. 2003. Nestling discrimination without recognition: a possible defence mechanism for hosts towards cuckoo parasitism? Proc R Soc Lond B Biol Sci. 270:S73–S75.

Grim T, Rutila J, Cassey P, Hauber ME. 2009. Experimentally constrained virulence is costly for common cuckoo chicks. Ethology. 115:14–22.

Hauber ME. 2003. Hatching asynchrony, nestling competition, and the cost of interspecific brood parasitism. Behav Ecol. 14: 224–235.

Hauber ME, Moskát C. 2008. Shared parental care is costly for nestlings of common cuckoos and their great reed warbler hosts. Behav Ecol. 19:79–86.

Hegyi G, Török J. 2007. Developmental plasticity in a passerine bird: an experiment with collared flycatchers *Ficedula albicollis*. J Avian Biol. 38:327–334.

Honza M, Vošlajerová K, Moskát C. 2007. Eviction behaviour of the common cuckoo *Cuculus canorus* chicks. J Avian Biol. 38:385–389.

Järvinen A. 1984. Relationship between the common cuckoo *Cuculus canorus* and its host, the redstart *Phoenicurus phoenicurus*. Ornis Fenn. 61:84–88.

Jenner E. 1788. Observations on the natural history of the cuckoo. Philos Trans R Soc Lond Sci. 78:219–237.

Kilner RM. 2003. How selfish is a cowbird nestling? Anim Behav. 66:569–576.

Kilner RM. 2005. The evolution of virulence in brood parasites. Ornithol Sci. 4:55–64.

Kilner RM. 2006. Response to Grim: further costs of virulence for brood parasitic young. Ornithol Sci. 5:243–247.

Kilner RM, Madden JR, Hauber ME. 2004. Brood parasitic cowbird nestlings use host young to procure resources. Science. 305: 877–879.

Kleven O, Moksnes A, Røskaft E, Honza M. 1999. Host species affects the growth rate of cuckoo (*Cuculus canorus*) chicks. Behav Ecol Sociobiol. 47:41–46.

Langmore NE, Hunt S, Kilner RM. 2003. Escalation of a coevolutionary arms race through host rejection of brood parasitic young. Nature. 422:157–160.

Moskát C, Hauber ME. 2007. Conflict between egg recognition and egg rejection decisions in common cuckoo (*Cuculus canorus*) hosts. Anim Cogn. 10:377–386.

Kosciuch KL, Parker TH, Sandercock BK. 2006. Nest desertion by a cowbird host: an antiparasite behavior or a response to egg loss? Behav Ecol. 17:917–924.

Martín-Gálvez D, Soler M, Soler JJ, Martín-Vivaldi M, Palomino J. 2005. Food acquisition by common cuckoo chicks in rufous bush robin nests and the advantage of eviction behaviour. Anim Behav. 70: 1313–1321.

Molnár B. 1944. Cuckoo in the Hungarian plain. Aquila. 51:100–112.

Nakagawa S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. Behav Ecol. 15:1044–1045.

Payne RB, Payne LL. 1998. Nestling eviction and vocal begging behaviours in the Australian glossy cuckoos *Chrysococcyx basalis* and *Ch. lucidus*. In: Rothstein SI, Robinson JK, editors. Parasitic birds and their hosts: studies in coevolution. Oxford: Oxford University Press. p. 152–169.

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? J Avian Biol. 33:414–419.

Slagsvold T, Lifjeld JT. 1990. Influence of male and female quality on clutch size in tits (*Parus* spp.). Ecology. 71:1258–1266.

Soler M. 2002. Breeding strategy and begging intensity: influences on food delivery by parents and host selection by parasitic cuckoos. In: Wright J, Leonard ML, editors. The evolution of begging. Dordrecht (The Netherlands): Kluwer. p. 413–427.

Wyllie I. 1981. The cuckoo. London: Batsford.