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ORIGINAL ARTICLE

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Cuckoo growth performance in parasitized and unused hosts: not only host size matters

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Abstract The quality and quantity of food delivered to young are among the major determinants of fitness. A parental provisioning capacity is known to increase with body size. Therefore, brood parasitism provides an opportunity to test the effects of varying provisioning abilities of different-sized hosts on parasitic chick growth and fledging success. Knowledge of growth patterns of common cuckoo, *Cuculus canorus*, chicks in nests of common hosts is very poor. Moreover, no study to date has focused on any currently unused hosts (i.e., suitable cuckoo host species in which parasitism is currently rare or absent). Here, I compare the growth performance of cuckoo chicks in nests of a common host (the reed warbler, *Acrocephalus scirpaceus*) and two unparasitized hosts (the song thrush, *Turdus philomelos*, and the blackbird, *Turdus merula*). Parasitic chicks were sole occupants of the observed nests, thus eliminating the confounding effect of competition with host chicks. Experiments revealed striking differences in parasitic chick growth in the two closely related *Turdus* hosts. Cuckoo chicks cross-fostered to song thrush nests grew much quicker and attained much higher mass at fledging than those in nests of their common reed warbler host. Alternatively, parasitic chicks in blackbird nests grew poorly and did not survive until fledging. I discuss these observations with respect to host selection by parasitic cuckoos.

Keywords Brood parasitism · Host selection · Parental care · Growth · *Cuculus canorus*

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Introduction

Both the quality and amount of the food delivered by parents critically affects growth, future survival, and reproduction of young (Martin 1987; Starck and Ricklefs 1998). There is ample empirical evidence indicating that increased parental provisioning leads to a higher fledging mass and, consequently, higher survival (e.g., Davies 1986; Magrath 1991; Lindén et al. 1992). Furthermore, parental provisioning capacity is positively correlated with parent body size (Saether 1994).

Under natural conditions, nestlings cannot benefit by deciding to be fed by an alternative larger foster parent with greater provisioning ability. Therefore, heterospecific brood parasitism (Davies 2000) across different host species provides an opportunity to test the plasticity of nestling growth under various parental provisioning regimes and the possible effect on nestling survival (Kilner and Davies 1999; Kilpatrick 2002; Kilner 2003). We would expect, under equal conditions, to see higher parasitism rates of larger hosts with greater provisioning capacity (Wiley 1986; Kleven et al. 1999). This hypothesis assumes that a parasitic chick can evict its nestmates—potential competitors—and/or procure enough food in competition with host chicks (Kleven et al. 1999; Glassey and Forbes 2003).

The hypothesis that host size positively affects parasitic chick growth and fledging success was supported in the study of two sympatric cuckoo, *Cuculus canorus*, hosts (Kleven et al. 1999) and three hosts of the shiny cowbird, *Molothrus bonariensis* (Wiley 1986). In contrast, Soler and Soler (1991) found that host species size did not influence parasitic great spotted cuckoo, *Clamator glandarius*, growth, and Kilpatrick (2002) reported that brown-headed cowbird, *Molothrus ater*, nestling growth was not strongly linearly related to adult host mass. However, Kilner (2003) and Kilner et al. (2004) found a curvilinear relationship between host size and cowbird chick survival (cowbirds are most likely to fledge when reared alongside host young of intermediate size).

Despite the evidence presented by Kleven et al. (1999), the hypothesis is in striking contrast with the observed general pattern of natural parasitism rates in the common cuckoo: The most frequent cuckoo host is the miniature reed warbler, *Acrocephalus scirpaceus*, while large thrushes, *Turdus* spp., are almost never parasitized (Moksnes and Røskaft 1995) despite being an order of magnitude larger than warblers (12 g vs 70–100 g; Cramp 1988, 1992). Of course, various other factors can be important in host selection by parasitic birds—some hosts may, e.g., provide nestlings with food which is indigestible (e.g., seeds, fruits) to brood parasitic chicks (Glue and Morgan 1972), follow food allocation rules which disfavor parasitic chicks (Soler 2002), are too aggressive to female cuckoos near their nests (Grim 2005a), or reject almost all parasitic eggs (Moksnes and Røskaft 1992).

Nonetheless, it is puzzling that thrushes are not parasitized by cuckoos when they are considered to be suitable hosts, with their egg rejection rates and aggression levels within the range of commonly parasitized cuckoo hosts (Davies and Brooke 1989; Grim and Honza 2001a; Moskát et al. 2003). In contrast, Moksnes et al. (1990) considered thrushes to be unsuitable hosts because young cuckoos could not evict host eggs from fieldfare, *Turdus pilaris*, nests and survive. A cuckoo chick is, however, able to evict host eggs and chicks from song thrush, *Turdus-philomelos*, and blackbird, *Turdus merula*, nests (T. Grim, M. Honza, O. Kleven, A. Moksnes, C. Moskát, E. Røskaft, unpublished data). To my knowledge, there are no published data on chick growth and survival in nests of other unused hosts, including the European song thrush and blackbird, which, in comparison to fieldfares, are much more common potential hosts.

The growth of parasitic chicks has been studied in some host–parasite systems (see above), particularly in the brown-headed cowbird and its hosts (reviewed by Kilpatrick 2002). On the other hand, cuckoo chick growth has only been observed in the dunnock, *Prunella modularis*; the robin, *Erithacus rubecula* (Werth 1947); the white wagtail, *Motacilla alba* (Werth 1947; Numerov 2003, p 149); the redstart, *Phoenicurus phoenicurus* (Khayutin et al. 1982); the rufous bush chat, *Cercotrichas galactotes* (Alvarez 1994); the great reed warbler, *Acrocephalus arundinaceus*; and the reed warbler (Kleven et al. 1999) (see also Wyllie 1981).

All the hosts mentioned above are classified as current cuckoo hosts (Davies and Brooke 1989; Moksnes and Røskaft 1995), and no study thus far has considered the growth of cuckoo young in currently unused hosts. Such information is essential if we want to understand host selection and avoidance by parasitic birds (Rothstein and Robinson 1998; Strausberger 1998; Woolfenden et al. 2003). The aims of the current study were to compare the growth and survival of cuckoo chicks in nests of a common host, the reed warbler, and in the nests of two potential host species not currently parasitized by the cuckoo (the song thrush and the blackbird). This was to experimentally test across species the known correlative relationship between parent size and provisioning capacity (Saether 1994) and to improve our understanding of factors underlying host selection by brood parasitic birds.

Materials and methods

I studied cuckoo growth in nests of reed warblers from late May to mid July of each year from 1994 to 2005 at two fish pond systems in South Moravia, Czech Republic: Lednice (48° 48′ N, 16° 48′ E) and Luzice (48° 51′ N, 17° 04′ E), both about 60 km southeast of the city of Brno. For details on field procedures, see Grim and Honza (2001b). Cross-fostering experiments with song thrush and blackbird nests were done from 1998 to 2005 in several forest tracts adjacent to Luzice ponds. Adult masses of studied species averaged 12 g for the reed warbler (Cramp 1992), 70 g for the song thrush, and 100 g for the blackbird (Cramp 1988). In comparison, the adult cuckoo weighed 120 g on average (Wyllie 1981). The lengths of incubation period averaged 11 days for the reed warbler (Cramp 1992), 13 days for the song thrush, and 13 days for the blackbird (Cramp 1988). Cuckoo eggs hatch after 11–12 days of incubation (own observations). I analyzed cuckoo chicks' growth in 79 reed warbler nests, six song thrush nests, and six blackbird nests (O. Kleven, A. Moksnes, and E. Røskaft kindly provided their unpublished data on two cuckoo chicks transferred to blackbird nests; other chicks were opportunistically cross-fostered by me).

The sample size for "reed warbler" cuckoos is the largest published data set, but the sample sizes for thrush hosts are relatively low. This is due to the difficulty in finding well-synchronized nests of these alternative hosts, due mainly to relatively low breeding densities (especially the blackbird) and very high predation rates (for both thrushes; T. Grim, unpublished data; see also Grim and Honza 2001a). In some years, high predation on both warbler and thrush nests prevented any experiments. Moreover, parasitism rates generally declined throughout the study period, leading to a low availability of chicks for cross-fostering independently of predation. However, results were clear-cut and the sample sizes are sufficient to evaluate some hypotheses under investigation.

Both the song thrush and blackbird reject parasitic eggs in my study area (Grim and Honza 2001a). Therefore, I transferred cuckoo chicks after they had hatched in reed warbler nests to prevent eggs from being wasted due to the host rejection response. Nestling competition negatively influences nestling growth and survival (in nonparasitic broods: Martin 1987; in parasitic broods: Trine 1998; but see Kilner et al. 2004). In the present study this potentially confounding factor was eliminated by host eggs being evicted by the cuckoos themselves or being removed by the author after the eviction behavior ceased and the eggs did not hatch.

Kleven et al. (1999) tested for the possible confounding effect of genetic differences between cuckoo females and their progeny who were parasitizing the reed warbler and the great reed warbler. This was carried out by cross-fostering cuckoo chicks hatched in reed warbler nests to great reed warbler nests and vice versa. They found that the host species contributed significantly to the observed differences in cuckoo growth in the two respective hosts, suggesting that parental genetic effects were of minor importance (Kleven et al. 1999). In the present study I used only chicks hatched in the nests of the reed warbler, thus it is unlikely that the growth differences observed would result from parental genetic effects.

For each host I evaluated the length of the nestling cuckoo period (i.e., time from hatching to fledging in days) and several growth parameters (mass, tarsus length). Mass was measured with a portable electronic balance to the nearest 0.01 g and maximum tarsus length was measured with an electronic caliper to the nearest 0.01 mm (Sutherland et al. 2004). I measured nestlings every day when possible, and an effort was made to measure a particular nestling at the same time of day on each day. As some measurements were missing, sample sizes differ among tests. Further, predation decreased sample sizes from hatching through to fledging.

In calculations I used the raw data, results presented here are rounded up to 0.1 g to give biologically significant information. Part of the data set for "reed warbler" cuckoos was published by Grim et al. (2003); however, these data were analyzed in a different way and tested a different hypothesis. All data for "song thrush" and "blackbird" cuckoos are novel.

I used nonlinear regression (SAS Institute 2000) to fit the measures of body mass W to the logistic function

$$W(t) = A \Big/ \left(1 + e^{(-K^*(t - t_i))}\right)$$

where $W(t)$ is mass at age t, A is the asymptotic mass, K is a measure of growth rate, and t_i is the inflection point on the growth curve (Starck and Ricklefs 1998). I fitted logistic growth curves for each individual nestling. Table 1 provides average values for the three growth parameters (1) for all nestlings that survived at least 1 week and (2) for subset of successfully fledged nests. Further, I analyzed video recordings of cuckoo chicks (from 9 to 19 days of age) in two song thrush nests (11 and 8 h in total for the two nests) to get information on food delivered by hosts.

For a tentative interspecific test of a possible effect of host size on parasitic chick growth, I collated data on adult mass (averaged for the two sexes) from Cramp (1988, 1992) and data on chick growth from Werth (1947), Khayutin et al. (1982), Alvarez (1994), Kleven et al. (1999), and Numerov (2003).

To assess the possible effect of host species on chick growth I fitted a general linear mixed model (normal error distribution; parameter estimated by restricted maximum likelihood) using PROC MIXED in SAS (SAS Institute 2000). Nest was included as a random effect. Denominator *df* were computed using the Kenward–Roger method. I looked for a significant interaction between host species and chick age to test whether chicks grow differently in the different hosts nests. Because of the relatively smaller sample sizes for "song thrush" and "blackbird" cuckoo broods, I used nonparametric tests. Data are presented as means±SD. All tests are two-tailed. All analyses were done with SAS (SAS Institute 2000) and JMP software.

Table 1 Basic growth parameters for cuckoo chicks raised by reed warblers and song thrushes

Growth parameters	RW	ST	*P*
Whole data set			
A	64.3±13.5	97.4±2.6	0.0002
K	0.429±0.101	0.356±0.039	0.11
t_i	8.1±1.4	9.6±0.7	0.01
Fledged			
A	71.6±5.8	97.1±2.9	0.0016
K	0.372±0.085	0.357±0.045	0.80
t_i	9.0±0.9	9.6±0.8	0.22

A is the asymptotic mass, K is a measure of growth rate, and t_i is the inflection point on the growth curve (Starck and Ricklefs 1998). Results of separate analyses (Mann–Whitney tests) for all (n=65 and 5 for reed warblers and song thrushes, respectively) vs only successful (n=25 and 3 for reed warblers and song thrushes, respectively) nests are shown. Values are means±SD. For explanation, see "Materials and methods."

RW reed warblers, *ST* song thrushes

Results

Cuckoo chicks raised in nests of the reed warbler, song thrush, and blackbird did not differ in their mass after hatching (Kruskal–Wallis ANOVA: χ^2=0.25, df=2, P=0.88). At 3 days of age, both mass and tarsus length did not differ among the three hosts (Kruskal–Wallis ANOVAs, P>0.05), although both measures were lowest for "blackbird" cuckoos. Measured masses at fledging in nests of the reed warbler (70.8±4.6, n=25) and the song thrush (95.3±6.4, n=3) were very similar to asymptotic masses (logistic growth curve based on successful nests; Table 1), indicating that data are robust.

Naturally parasitized nests

I found no correlation between fledging age and mass at fledging for "reed warbler" cuckoos (r_s=0.22, n=25, P=0.29). The negative correlation between fledging age and tarsus length at fledging was significant despite a small sample size (r_s=−0.97, n=5, P=0.0048). All chicks fledged from reed warbler nests between 17 and 21 days old, with most fledging at 18 days of age.

Experimental nests

Cross-fostering experiments with song thrushes and blackbirds led to strikingly different results. In comparison to the commonly parasitized reed warbler, the cuckoo chicks in song thrush nests gained approximately one third more mass at comparable ages (Fig. 1). These differences appeared after day 3 and were most apparent at fledging when "song thrush" cuckoos were significantly (1.35 times) heavier than "reed warbler" cuckoos (Mann–Whitney test: $U_{25,3}$=2.75, P=0.006). Differences in tarsus length at fledging were less prominent but, again, significant (P=0.04). I did not find any differences in variance of logistic growth parameters (a, K, t) between "song thrush" and "reed warbler" cuckoos (O'Brien's tests: all P>0.25).

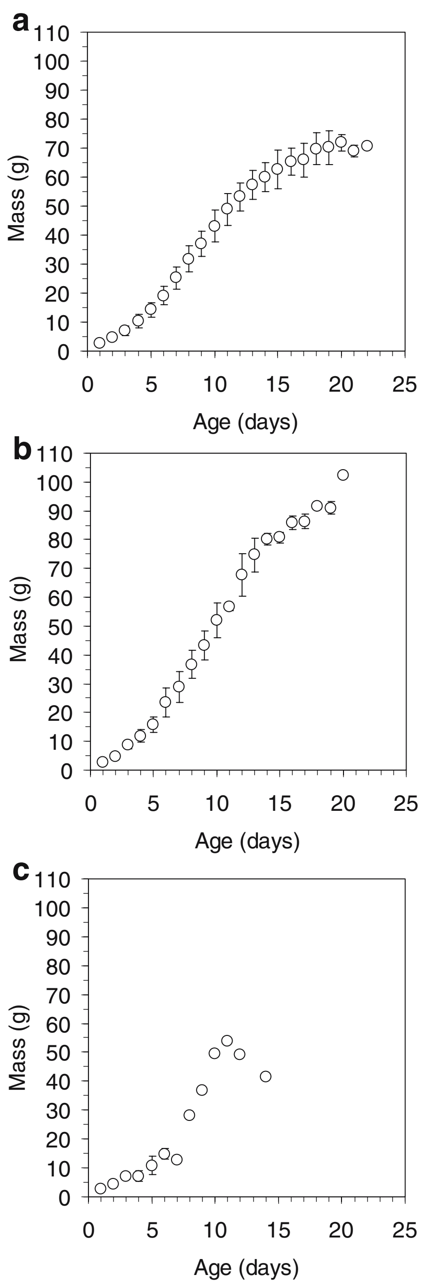

Fig. 1 Mass growth of cuckoo chicks in nests of reed warblers (**a**), song thrushes (**b**), and blackbirds (**c**). Day 1=day of hatching

Three out of six cross-fostered "song thrush" cuckoo chicks successfully fledged at the same age (18.3±0.6) as those in reed warbler nests (18.0±1.1; Mann–Whitney test: $U_{3,25}$=0.78, P=0.43). Of the other three, one was killed by a falling tree, one was predated upon, and one disappeared while the host clutch remained in the nest. The last nestling may have vanished due to partial predation or may have died and the corpse removed by the foster parents. All these chicks grew well until their disappearance.

Growth rate (K) was lower in "song thrush" cuckoos compared to "reed warbler" cuckoos. However, growth increments (mass increases in grams) were higher in "song thrush" cuckoos as indicated by their higher fledging mass (Table 1). Although "song thrush" cuckoo chicks attained higher mass before fledging, they did not fledge earlier (see above).

Although the sample size for blackbird experiments was also small (six transferred chicks), the results are again clear-cut. No significant differences were detected until the age of 3 days (the blackbird cuckoos' data were within the lower range observed at reed warbler and song thrush nests), but no cuckoo chick survived to 14 days of age. Figure 1c clearly shows very poor growth of cuckoo nestlings in blackbird nests; chicks survived for 2, 3, 4, 6, 6, and 13 days for the six nests. All six "blackbird" cuckoos weighed less at their maximum age than average "reed warbler" cuckoos at the same age (Wilcoxon matched-pairs test: Z=2.99, P=0.0028).

"Blackbird" cuckoo chicks had bloated bellies and suffered from diarrhea. Two of these chicks were found dead in the nests and four were predated upon, but this happened after their growth was stagnating or even declining. Because of this I could not calculate parameters of logistic growth curves for "blackbird" cuckoos. There was no indication of desertion, as the foster parents were observed near the nests.

A general linear mixed model confirmed a significant effect of host species on cuckoo chick growth (age vs species interaction: $F_{2,629}$=84.78, P<0.0001).

Diet composition

Video recordings at two song thrush nests with cross-fostered cuckoo chicks showed 55 feedings. At both nests the food composition was dominated by earthworms (62% of feedings in the pooled data set), including large specimens (up to 12 cm in length). Smaller diet items were insects (29%) and molluscs (9%). Cuckoo chicks routinely begged even after being fed with large food items (e.g., earthworms, caterpillars).

Interspecific comparison

The average fledging mass of cuckoos raised by eight host species studied by Werth (1947), Khayutin et al. (1982), Alvarez (1994), Kleven et al. (1999), Numerov (2003), and this study showed a slight, nonsignificant, increase with respective host species adult mass (r_s=0.21, P=0.61; Fig. 2). Exclusion of the data for dunnock (due to adverse weather conditions during growth of the studied cuckoo chick, see Werth 1947) or rufous bush chat (because of the smaller size of the studied cuckoo subspecies and unusually early fledging, see Alvarez 1994) showed that results are qualitatively the same. Fledging age nonsignificantly increased with chick size (r_s=0.61, P=0.11) and was not correlated with host body size (r_s=0.21, P=0.61; Fig. 3). Quadratic equations fit to these data (host adult mass vs cuckoo chick fledging mass and host adult mass vs cuckoo chick fledging age) were nonsignificant even after data transformation to normality.

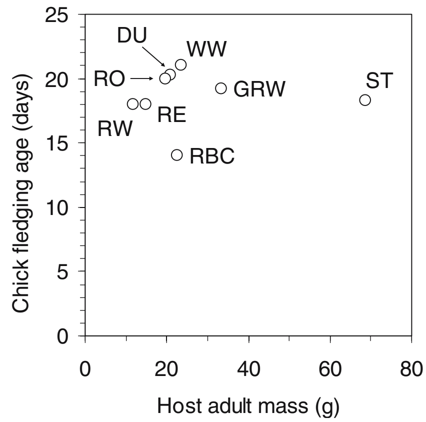

Fig. 3 Cuckoo chick fledging age plotted against host adult mass (sexes averaged). *DU* dunnock, *GRW* great reed warbler, *RBC* rufous bush chat, *RE* redstart, *RO* robin, *RW* reed warbler, *ST* song thrush, *WW* white wagtail

Discussion

This study showed striking differences in growth performance and survival of parasitic cuckoo chicks in nests of two closely related nonparasitized songbird species in comparison to a sympatric frequently parasitized host species. While "song thrush" cuckoo chicks grew faster and fledged heavier than "reed warbler" cuckoos, the "blackbird" cuckoo chicks showed relatively poor growth and none of them fledged successfully. The observed growth parameters and the successful fledging of three "song thrush" cuckoos clearly rejects the hypothesis that the song thrush is an unsuitable host in respect to diet quality or parental chick feeding rules (cf. Moksnes et al. 1990; Kleven et al. 1999). Cuckoo chicks in song thrush nests attained on average an even higher mass (95.3 g) than cuckoo chicks in the nests of the great reed warbler (88.3 g; Kleven et al. 1999). However, this difference is not significant (P=0.13), perhaps due to a low sample size. Chicks cared for by reed warblers grew in accordance with data published by others (see Table 2 in Kleven et al. 1999). The large variation in growth data from my study indicates that the fledging of cuckoo chicks is not triggered by some threshold mass, but rather may be caused by skeletal growth (see significant correlation between fledging age and tarsus length) or by tissue (e.g., feather) development (see also Starck and Ricklefs 1998).

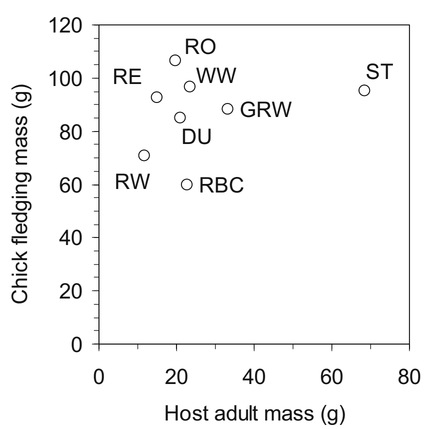

Fig. 2 Cuckoo chick fledging mass plotted against the host adult mass (sexes averaged). *DU* dunnock, *GRW* great reed warbler, *RBC* rufous bush chat, *RE* redstart, *RO* robin, *RW* reed warbler, *ST* song thrush, *WW* white wagtail

Why did "blackbird" cuckoos grow and survive so poorly?

The subnormal growth and survival of "blackbird" cuckoos could be caused by several factors.

1. High energetic costs of the eviction of large host eggs may play a role—blackbird eggs are heavier than song thrush eggs (7.0 vs 5.5 g, respectively; Cramp 1988). However, a cuckoo chick is able to evict blackbird eggs from a blackbird nest (M. Honza, C. Moskát, personal communication), and cuckoo chicks grew poorly even after I removed unevicted host eggs. Mass growth of "reed warbler" cuckoo chicks, which were unable to reject song thrush eggs from song thrush nests attached to reed warbler nests in another series of experiments, was similar to that of "reed warbler" cuckoos under normal conditions (T. Grim, unpublished data).
2. "Blackbird" cuckoos' growth may also be hampered by disease. However, I find it unlikely that all six "blackbird" cuckoo chicks would suffer from a disease while all six "song thrush" cuckoo chicks would remain healthy.
3. The hypothesis that foster parents refuse to feed chicks can be rejected, as nestling mass increased. However, one chick grew quite well until 11 days of age, but then its growth declined (Fig. 1c). This raises the possibility of discrimination without recognition when parents might detect alien chicks by their longer nestling periods than those of their own chicks (Grim et al. 2003; T. Grim, unpublished data; blackbird chicks are well able to fledge even when only 9 days old under normal conditions, Cramp 1988). However, all "blackbird" cuckoos grew subnormally even after spending

only a few days in blackbird nests, and five out of six did not survive for more than a week, which casts doubt on this explanation.

4. In some "blackbird" cuckoo chicks, their growth stagnated. This pattern is similar to that of a cuckoo chick hatched in a nest of the linnet, *Carduelis cannabina*, which grew normally 3 days posthatch, but later its mass stagnated at 8.5 g until it died at the age of 6 days (Alvarez 1994). This indicates a possible role of food composition, as the linnet feeds seeds to its chicks while all used cuckoo hosts are insectivorous. A priori, I expected that cuckoo chicks would not be able to survive in nests of both the song thrush and the blackbird because of the large proportion of noninsect prey delivered by these potential hosts to their nestlings (also A. Moksnes, E. Røskaft, personal communication). Song thrushes feed nestlings mainly with molluscs, while blackbirds with earthworms (Cramp 1988). In a striking contrast, both large molluscs and earthworms are never fed to nestlings by reed warblers and great reed warblers (Grim and Honza 1997; Grim 1999). However, video recording revealed that cuckoos in song thrush nests were frequently fed with large earthworms, and this caused no problems for the parasitic chicks; on the contrary, they grew even better than those fed on purely insect diets by reed warblers (unfortunately, no data on "blackbird" cuckoos diets were available). Interestingly, in another study, rufous bush chats fed relatively high amounts of plant diet (grapes, 16.9% in naturally parasitized nests) to parasitic cuckoo chicks without any obvious adverse effects on the chicks' growth (Martin-Galvez et al. 2005). This indicates that any a priori expectations on the effect of diet on cuckoo chick growth performance should be treated with caution and should be tested experimentally.
5. Alternatively, cuckoo chicks may be unable to communicate their hunger effectively, thus eliciting insufficient provisioning by the fosterers. This hypothesis cannot be currently evaluated due to a lack of data on parental provisioning rules in blackbirds.
6. The most intriguing explanation which fits the observed interspecific differences in growth considers host food allocation rules in respect to breeding strategy. Soler (2001, 2002) suggested that clutch-adjuster species (i.e., those in which usually all nestlings survive to fledging) preferentially feed smaller chicks, while brood reducer species (i.e., those in which usually some chicks starve) prefer to feed larger chicks, provoking the starvation of smaller chicks. If the parasitic chick is larger than host chicks, the parasite will benefit from parasitizing brood reducers. However, if the parasite is smaller than a host chick, then a clutch-adjuster host is a good choice. Blackbird and song thrush hatchlings weigh 6–8 g (Cramp 1988), which is two to three times more than the cuckoo hatchling (Honza et al. 2001). This size advantage of the host chicks is unlikely to be compensated for by cuckoo chicks through a slightly shorter (11–13 vs 12–14 days) incubation period, due to the very fast growth of thrush chicks and perhaps also improper incubation of parasitic eggs (cuckoo eggs are considerably smaller than thrush eggs; Cramp 1988; Honza et al. 2001). The blackbird, with its asynchronous hatching (Cramp 1988), is a brood reducer (Magrath 1992), while the song thrush shows synchronous hatching (Cramp 1988) and can be considered a clutch adjuster. Thus, Soler's (2002) hypothesis is apparently in accordance with cuckoo chicks surviving in nests of the song thrush but not in those of the blackbird. However, in my experimental nests, there were no host chicks left (see Materials and methods), thus leaving no role for intrabrood competition and parental favoritism. Nevertheless, previous coevolution between the cuckoo and its various hosts could have adapted cuckoo chicks for growth in song thrush nests. The quick elimination of cuckoo chicks in blackbird nests through brood reduction might prevent any coevolutionary adaptation of cuckoo chicks to blackbird parental provisioning rules and/or food composition.

Physiological constraints on growth

Cuckoo chick growth was very quick during the first 2 weeks after hatching, but after day 15 it leveled off (Fig. 1a,b). Interestingly, one "song thrush" cuckoo chick did not retard its growth as described above but increased its mass until fledging (see also Werth 1947). This observation and much faster growth of "song thrush" cuckoos in comparison to "reed warbler" cuckoos clearly contradicts previous suggestions that cuckoo chicks grow in reed warbler nests at the maximum rate enabled by physiological constraints (see, e.g., Brooke and Davies 1989; Alvarez 1994). However, the "physiological constraint on growth" hypothesis has been already falsified by growth data from cuckoos reared by great reed warblers (Kleven et al. 1999).

In an interesting experiment, Bussmann (1947) hand-reared a young cuckoo. This ad libitum-fed nestling reached 80.0 g on day 14 (day 13 in Bussmann's growth marking) and 100.0 g when 18 days old (fledging time). These data are very close to those obtained in the current study from "song thrush" cuckoos (80.0 g on day 14 and 95.0 g at fledging). This indicates that "song thrush" cuckoos indeed grow close to the upper limit of their physiological possibilities. This suggests that there is a limit on how cuckoo chicks can exploit host parental care. To gain more insight into this issue, it would be interesting to study chick-provisioning rules in large cuckoo hosts and test how these rules are exploited by parasitic chicks.

Interspecific comparison

The tentative interspecific comparison did not support the hypothesis that, by parasitizing larger hosts, the cuckoo chick benefits by a higher fledging mass and/or a shorter nestling period. Kilpatrick (2002) also found no significant effect of host size on the growth of parasitic brown-headed cowbird chicks, while Kilner (2003) and Kilner et al. (2004) found that cowbirds grow fastest in intermediate host sizes with 1–2 host nestmates. However, the sample size in my study is very small. It would be interesting to repeat this comparison after more data on cuckoo growth in various host species is available.

Conclusions

Results of this study indicate that host size may positively influence cuckoo chick growth (song thrush host), but other currently unidentified factors may also play a role (blackbird host). The fact that "song thrush" cuckoo chicks grew well and fledged at a very high mass raises a question as to why song thrushes are not regularly parasitized by cuckoos. At present, one can only reject hypotheses assuming that this host is too aggressive or rejects parasitic eggs at high rates (Grim and Honza 2001a). Alternatively, the poor survival of "blackbird" cuckoos raises questions concerning the origins of blackbird behaviors that are, so far, interpreted as antiparasitic responses (Davies and Brooke 1989; Grim and Honza 2001a; Moskát et al. 2003).

The biology of parasitic cuckoo chicks has so far received unwarrantedly little attention in general (Grim 2005b, 2006). This study indicates that cross-fostering of parasitic chicks to nests of currently nonparasitized hosts yields important insights into host selection and growth plasticity in brood parasitic birds (see also Soler 2002). This gives strong impetus for future research in this unexplored area.

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References

Alvarez F (1994) Rates of weight increase of cuckoo (*Cuculus canorus*) and host (*Cercotrichas galactotes*) chicks. Ardeola 41:63–65

Brooke ML, Davies NB (1989) Provisioning of nestling cuckoos *Cuculus canorus* by reed warbler *Acrocephalus scirpaceus* hosts. Ibis 131:250–256

Bussmann J (1947) Wachstum und Jugendzeit eines Kuckucks. Ornithol Beob 44:41–49

Cramp S (ed) (1988) The birds of the Western Palearctic. Tyrant flycatchers to thrushes, vol 5. Oxford University Press, Oxford

Cramp S (ed) (1992) The birds of the Western Palearctic. Warblers, vol 6. Oxford University Press, Oxford

Davies NB (1986) Reproductive success of dunnocks, *Prunella modularis*, in a variable mating system. 1. Factors influencing provisioning rate, nestling weight and fledgling success. J Anim Ecol 55:123–138

Davies NB (2000) Cuckoos, cowbirds and other cheats. T & AD Poyser, London

Davies NB, Brooke ML (1989) An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. J Anim Ecol 58:207–224

Glassey B, Forbes S (2003) Why brown-headed cowbirds do not influence red-winged blackbird parent behaviour. Anim Behav 65:1235–1246

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

Grim T (1999) Food of great reed warbler (*Acrocephalus arundinaceus*) young. Sylvia 35:93–99 (in Czech, with summary in English)

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

Grim T (2005b) Mimicry vs. similarity: which resemblances between brood parasites and their hosts are mimetic and which are not? Biol J Linn Soc 84:69–78

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

Grim T, Honza M (1997) Differences in parental care of reed warbler (*Acrocephalus scirpaceus*) to its own nestlings and parasitic cuckoo (*Cuculus canorus*) chicks. Folia Zool 46:135–142

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? 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 270:S73–S75

Honza M, Picman J, Grim T, Novak V, Capek M, Mrlik V (2001) How to hatch from an egg of great structural strength: a study of the common cuckoo. J Avian Biol 32:249–255

Khayutin SN, Dmitrieva LP, Tartygina NG, Aleksandrov LI (1982) The behaviour of a nestling of *Cuculus canorus* in the nest of *Phoenicurus phoenicurus*. Zool Z 61:1063–1077 (in Russian with English summary)

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

Kilner RM, Davies NB (1999) How selfish is a cuckoo chick? Anim Behav 58:797–808

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

Kilpatrick AM (2002) Variation in growth of brown-headed cowbird (*Molothrus ater*) nestlings and energetic impacts on their host parents. Can J Zool 80:145–153

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

Lindén M, Gustafsson L, Pärt T (1992) Selection on fledging mass in the collared flycatcher and the great tit. Ecology 73:336–343

Magrath RD (1991) Nestling weight and juvenile survival in the blackbird *Turdus merula*. J Anim Ecol 60:335–351

Magrath RD (1992) Roles of egg mass and incubation pattern in establishment of hatching hierarchies in the blackbird (*Turdus merula*). Auk 109:474–487

Martin TE (1987) Food as a limit on breeding birds: a life-history perspective. Annu Rev Ecol Syst 18:453–487
Martin-Galvez D, Soler M, Soler JJ, Martin-Vivaldi M, Palomino JJ (2005) Food acquisition by common cuckoo chicks in rufous bush robin nests and the advantage of eviction behaviour. Anim Behav 70:1313–1321
Moksnes A, Røskaft E (1992) Responses of some rare cuckoo hosts to mimetic cuckoo eggs and foreign conspecific eggs. Ornis Scand 23:17–23
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. J Zool 236:625–648
Moksnes A, Røskaft E, Braa AT, Korsnes L, Lampe HM, Pedersen HC (1990) Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. Behaviour 116:64–89
Moskát C, Karcza Z, Csörgö T (2003) Egg rejection in European blackbirds (*Turdus merula*): the effect of mimicry. Ornis Fenn 80:86–91
Numerov AD (2003) Interspecific and intraspecific brood parasitism in birds. Federal State Unitary Enterprise Publish & Polygraf Corporation, Voronezh (in Russian, with English summary)
Rothstein SI, Robinson SK (1998) Parasitic birds and their hosts. Oxford University Press, New York
Saether B-E (1994) Food provisioning in relation to reproductive strategy in altricial birds: a comparison of two hypotheses. Evolution 48:1397–1406
SAS Institute (2000) SAS online document, version 8. SAS, Cary
Soler M (2001) Begging behaviour of nestlings and food delivery by parents: the importance of breeding strategy. Acta Ethol 4:59–63
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 (eds) The evolution of begging. Kluwer, Dordrecht, pp 413–427
Soler M, Soler JJ (1991) Growth and development of great spotted cuckoos and their magpie hosts. Condor 93:46–54
Starck JM, Ricklefs RE (eds) (1998) Avian growth and development. Evolution within the altricial–precocial spectrum. Oxford University Press, New York
Strausberger BM (1998) Temporal patterns of host availability, brown-headed cowbird brood parasitism, and parasite egg mass. Oecologia 116:267–274
Sutherland WJ, Newton I, Green RE (2004) Bird ecology and conservation. A handbook of techniques. Oxford University Press, Oxford
Trine CL (1998) Wood thrush population sinks and implications for the scale of regional conservation strategies. Conserv Biol 12:576–585
Werth I (1947) The growth of a young cuckoo. Br Birds 40:331–334
Wiley JW (1986) Growth of shiny cowbird and host chicks. Wilson Bull 98:126–131
Woolfenden BE, Gibbs HL, Sealy SG, McMaster DG (2003) Host use and fecundity of individual female brown-headed cowbirds. Anim Behav 66:95–106
Wyllie I (1981) The cuckoo. Batsford, London