Ethology

Experimentally Constrained Virulence is Costly for Common Cuckoo Chicks

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Abstract

Chicks of some avian brood parasites show high virulence by eliminating all host progeny in the nest whereas others develop in the presence of host nestmates. Common cuckoo (*Cuculus canorus*) chicks are typically highly virulent parasites as they attempt to evict all host eggs and chicks soon after hatching. However, several features of nest design, including steep walls and/or cavity nests, may effectively prevent cuckoo hatchlings from evicting nestmates. A previous observational study showed low success of cuckoo chicks in evicting progeny of a cavity nester host, the redstart (*Phoenicurus phoenicurus*) but cuckoo chicks showed low survival both when reared alone or in mixed broods with host nestmates. Whether poor cuckoo performance was caused by eviction costs and/or by the effect of presence of host chicks *per se* remains unclear. We experimentally cancelled any potential eviction costs by removing host eggs immediately after the cuckoo hatched and creating mixed broods 5 days later when the eviction instinct of the cuckoo already ceased. Cuckoos that were forced to compete with host nestlings experienced lower provisioning rates, poorer growth, and lower fledging success than control lone cuckoos. Cuckoos in mixed broods that survived until fledging fledged later, and at lower masses, than those in the sole cuckoo group. Thus, the cuckoo gens specializing on redstarts is similar to other cuckoo gentes, whose chicks are more successful in evicting host nestmates, and it does not benefit from the presence of host brood. Cohabitation with host nestlings then should be viewed as a maladaptive by-product of host cavity nest design.

Introduction

One of the most impressive sights in the natural world is a newly hatched common cuckoo (*Cuculus canorus*, hereafter: cuckoo) nestling pushing host eggs or chicks from the foster parents' nest (Davies 2000). Still blind and naked, the relatively tiny cuckoo hatchling is able to accomplish such a formidable task even when the mass of a host egg or a nestling is similar to the size of cuckoo nestling itself (Honza et al. 2007). Moreover, some hosts nests are relatively deep, making the eviction task more difficult (Honza et al. 2007). Not surprisingly, such eviction behaviour is believed to be very costly. For example, before it succeeds in evicting the host progeny, a cuckoo chick grows more slowly in the deep nests of a relatively large host, the great reed warbler (*Acrocephalus arundinaceus*), than in the shallower nests of the smaller host, the reed warbler (*Acrocephalus scirpaceus*), but once it accomplishes the eviction act, the parasite chick grows much faster in the nest of that larger host (Kleven et al. 1999). The initial slow growth of cuckoos in great reed warbler nests may be caused by higher energetic costs of eviction in deeper nests. The eviction behaviour process may be prolonged up to several days (Hauber & Moskát 2008), and evicting parasite chicks can also risk self-eviction (Molnár 1944). Some cuckoos may even focus on evicting host progeny so much that they appear to ignore host parents, do not beg, and consequently die of starvation (Soler 2002).

The maintenance of virulent eviction behaviour in the cuckoo despite such costs implies that eviction behaviour should also have some benefits. Some hosts of brood parasites discriminate against alien chicks (Grim 2006a) and by evicting host progeny the parasite may eliminate a set of comparison-stimuli upon which hosts could have relied in their discrimination (Davies & Brooke 1989). A general lack of chick discrimination studies on brood parasites (Grim 2007a) still prevents the evaluation of this hypothesis. However, experimental work with mixed-species broods in non-parasitic species confirms lasting effects on the social dominance (Hansen & Slagsvold 2004), vocal displays (Johannessen et al. 2006), and species recognition abilities of cross-fostered individuals (Slagsvold 2004). Because of the ubiquity of nestling competition in birds, the obvious benefit seems to be the monopolisation of parental care by the evicting parasite (Davies 2000; Forbes 2007).

Evicting host nestmates may also be costly. In addition to prolonged effort and self-eviction (see above), comparative (Kilner 2003; Kilner et al. 2004) and experimental (Kilner et al. 2004) data show that chicks of brown-headed cowbirds (*Molothrus ater*), a non-evicting parasite, survive and grow better in the presence of some host chicks than when raised alone. The presence of host chicks stimulates parents to increase the feeding rates in larger, mixed host-parasite broods, but cowbirds usurp more than their fair-share of food that fosterers bring to the nest and receive more feedings than when raised alone (Kilner et al. 2004).

Thus, both high virulence (i.e. the propensity to kill host offspring) and benignity (i.e. tolerance of host progeny) in brood parasite young have associated costs and benefits (Kilner 2005; Grim 2006b; Servedio & Hauber 2006). To understand the evolutionary patterns among both parasite and host species of the extent of virulence thus requires the use of experimental paradigms where the fitness of parasite young raised alone vs. those being accompanied by host young is compared (Kilner et al. 2004; Martín-Gálvez et al. 2005; Hauber & Moskát 2008).

Kilner (2005, 2006) hypothesized that chicks of some evictor brood parasites, including the cuckoo, may experience subsequent costs when the host young die. Contrary to this prediction, in an experimental study where common cuckoo chicks were cohabiting nests with host rufous bush robin (*Cercotrichas galactotes*) chicks the parasite nestlings received considerably less food than when raised alone (Martín-Gálvez et al. 2005). Similarly, Hauber & Moskát (2008) showed experimentally in nests of the great reed warbler that cuckoo chicks did not benefit from increased growth or higher food delivery rates in the presence of two host nestmates. In the latter study, the number of host chicks presented alongside cuckoo chick was 2, i.e. just like the optimal host brood size predicted by Kilner (2003) for cowbird chicks. Nevertheless, (1) Kilner et al. (2004) predictions were based on comparative patterns of cowbird (not cuckoo) growth data and (2) unlike the cowbird's tolerance of some nestmates across several host taxa (Hauber 2003b; Kilner 2003), cuckoo eviction behaviour appears to be an all or none strategy, i.e. attempting to evict until all objects in the nest are removed. In contrast, cowbirds have several strategies to reduce host brood sizes fully, partially, or not at all (e.g. egg removal by laying female, earlier hatching by cowbird chick, vigorous competition with host nestmates, and the eviction of host chicks: Dearborn 1996, 1998; Lichtenstein & Sealy 1998; Hauber 2003a,b,c).

In virtually all regular hosts of the cuckoo, which are typically open-nesters, the parasite nestling as a rule successfully evicts host progeny (Davies 2000). One striking exception is the most frequent host of the cuckoo in Northern Europe, the cavity-nesting redstart (*Phoenicurus phoenicurus*) (Aviles et al. 2005). Rutila et al. (2002) observed that almost half of cuckoo chicks were unable to evict host eggs or nestlings in their study population in Finland (Fig. 1). Reports in Finland on mixed broods of cuckoo and redstart chicks include both natural cavities and artificial nest boxes (J. Rutila, pers. obs.). However, even though overall cuckoos in mixed broods tended to fledge less frequently (44%, n = 16) than those raised alone (58%, n = 19), this difference was not statistically significant (p = 0.51, Fisher's exact test, data from Rutila et al. 2002).

Rutila et al. (2002) did not study host provisioning behaviour, nor did they manipulate host brood size to compare cuckoo growth and survival experimentally. Therefore, we studied the same redstart-specific

Fig. 1: Common cuckoo chick cohabiting a nest box with host redstart progeny in Southern Finland. The eviction effort of the cuckoo chick was only partially successful as only two out of the original six host eggs were evicted. Such eggs – and also evicted host chicks – are typically ignored by parents, i.e. parents do not try to move them back into the nest cup and they do not feed their own evicted chicks even when those are begging. Both this cuckoo and the remaining four host chicks successfully fledged. Photo credit: Juha Haikola.

cuckoo gens (host race) and redstarts experimentally and recorded both host provisioning and cuckoo fitness in more detail. We experimentally created broods with (1) lone cuckoos and (2) mixed broods with sole cuckoos accompanied by five host chicks for a total brood size of six so as to represent the modal brood size in our study population. We were interested in the frequently 'eviction-unsuccessful' redstart-cuckoo gens so that we can contrast our results with prior experimental work on cuckoo gentes whose chicks are typically successful at eliminating host nestmates (Martín-Gálvez et al. 2005; Hauber & Moskát 2008). Therefore, in parallel to previous authors who studied effects of cohabitation with host chicks on parasite growth and provisioning in non-evictor brown-headed cowbirds (Kilner et al. 2004) and evictor common cuckoos (Martín-Gálvez et al. 2005; Hauber & Moskát 2008), we too recorded these variables but extended prior research so as to encompass the parasite chick's entire nestling period. Thus, we were also able to document survival to fledging, fledging age, and fledging mass of cuckoo chicks under the different treatments.

Hauber & Moskát (2008) argued that for those parasite species whose young routinely evict host egg and young, but occasionally fail to do so (e.g. common cuckoo), the nest design constraint (Grim 2006b) is likely to explain cohabitation between parasite and host chicks. Under this 'physical constraint' hypothesis we predicted poorer growth performance (Grim 2006c) and fledging success for cuckoos that were forced to cohabit the nest with redstart chicks in comparison with those raised alone. We also predicted higher feeding rates to sole raised cuckoos than to those in mixed broods.

Methods

Study Site and Field Procedures

The fieldwork was carried out in Ruokolahti (61°24′N, 28°37′E) in south-eastern Finland. Our study sites are cultivated pine forests of different ages. We provided 400 nest boxes specially designed for redstarts, see Rutila et al. (2002) for details. Data on parental care and cuckoo performance were collected from May to July 2007.

Two cuckoo treatment groups were created: (1) 'alone' (n = 10) and (2) 'mixed' (n = 9). First, when the cuckoo hatched, we removed all host eggs from the nest. Thus, we experimentally removed any potential eviction costs. Under natural conditions, eviction instinct disappears within 4 days post-hatch (Davies 2000). Therefore, we introduced additional five redstart chicks (six is the modal brood size in the redstart) to 'mixed' nests at day 5 after hatching. Thus, our 'mixed' and 'alone' nests differed only in the presence/absence of host nestlings during the linear phase of growth of the cuckoo (Grim 2006c).

Although the sample sizes are not large, previous studies using similar sample sizes (Kilner et al. 2004; Hauber & Moskát 2008) detected significant differences between experimental treatments. In addition, in retrospect our data show significant statistical results, which, from an animal ethics consideration, do not warrant further experimentation with the same treatments.

The chicks' masses were measured daily whenever possible. We recorded chick mass with a portable electronic balance to the nearest 0.1 g. In addition, we collected parental provisioning data twice at each nest. We videotaped parental care and feeding decisions from roof-mounted cameras (Mini-DV format, 60-min recordings) atop our nest boxes at the nests when chicks were young (5–7 days old) and old (10–13 days old) (hatching date was defined as 0). Average age of chicks was virtually identical in mixed (6.1 ± 0.11 days, n = 9) and alone cuckoo (5.9 ± 0.18 days, n = 10) treatment in the 'young' chicks category (Mann–Whitney U-test; $U_{9,10} = 0.92$, $p = 0.36$). Also in the 'old' chicks category the average ages were highly similar in the mixed (11.7 ± 0.29 d, n = 7) and alone cuckoo (11.4 ± 0.24 d, n = 9) treatment ($U_{7,9}$ = 0.47, p = 0.64). Therefore, we could reasonably use 'young' and 'old' age as a discrete categorical variable in some analyses. The sample size for 'old mixed' nests is smaller because of chick mortality and the sample is also smaller for 'old alone' nests due to technical reasons. We could not reliably determine sizes of prey items (Grim & Honza 2001), prey taxa (Grim 2006d) or feeding loads (Martín-Gálvez et al. 2005; Hauber & Moskát 2008) delivered to parasite and host chicks because the cameras were placed above feeding parents.

Sexual dimorphism of the redstart hosts allowed determination of the sex of the providing parent for each feeding event. In the analyses of male feedings to cuckoos males in two recording sessions, each at a different nest, were excluded because they did not visit the nests during the video-recordings.

Statistical Analyses

Despite not having banded host parents, each nest box in our sample was synchronously active and distant enough to be considered a different redstart territory, thus representing independent data points for our analyses.

In the main analysis we fitted GLMM (general linear mixed model; procedure MIXED in SAS) with the identity of a nest as random factor, feeding frequency as a response and treatment (alone, mixed), nestling age and their interaction as fixed effects. To fulfil the assumption of normality, we Box-Cox transformed feeding frequencies and chick ages. Because of the relatively small samples we conservatively analysed the data with non-parametric tests (Mann–Whitney U-test, Fisher's exact test). Proportion of feedings to the cuckoo chick in mixed broods and number of feeds to host chicks did not deviate from normality and were not transformed (Shapiro–Wilk W tests, p = 0.38 and 0.27 respectively).

In the main analysis of the growth data we also used GLMM (see Grim 2006c). In a more detailed comparison of growth during the linear phase of growth (see Grim et al. 2003) we calculated the exact length of period from the first to second video-recording within a particular nest in hours and then compared average growth increments per hour between the chicks in the two treatment groups.

For calculations we used transformed data, figures and tables show original raw data. Values are given as mean ± SE. All analyses were done in SAS (SAS Institute Inc 2000) and JMP software (SAS Institute Inc 1995).

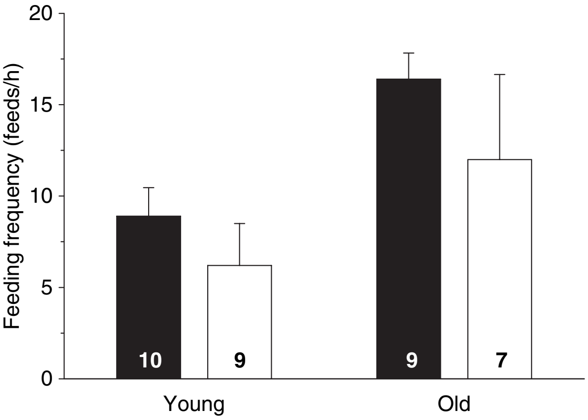

Fig. 2: Feeding frequency (mean + SE) by redstart hosts to common cuckoo chicks when alone (black bars) or accompanied by host young (white bars). Sample sizes are given within bars. Data are for 'young' and 'old' chick ages (for details see Methods.)

Results

Nestling Provisioning

Feeding frequencies to cuckoo nestlings increased with age (GLMM: $F_{1,15.8}$ = 16.39, p = 0.001). As predicted, cuckoos in mixed broods were fed less often than those raised alone ($F_{1,16.0}$ = 5.03, p = 0.039). The interaction between the treatment and age was non-significant ($F_{1,14.1}$ = 0.09, p = 0.77) and was removed from the final reduced model (Fig. 2).

In the mixed broods, we calculated the allocated parental food provisions to the cuckoo chick as the proportion of feedings received by the parasite out of total number of feedings per nest. This proportional feeding of the cuckoo (Box-Cox transformed) showed a decrease with increasing feeding frequencies to host own chicks (GLMM; $F_{1,10.2}$ = 6.12, p = 0.032; Fig. 3). However, old cuckoo chicks in mixed broods were able to monopolise a higher percentage of feeds (38.5 ± 6.71%) than young cuckoos (17.7 ± 5.76%) (GLMM: $F_{1,5.6}$ = 11.30, p = 0.017). Thus, the proportion of feedings monopolized by the cuckoo increased from random expectations (16.7%, i.e. the cuckoo was one chick out of brood size of six) at a young age to higher values at the older age.

Within the 'mixed' treatment we tested whether the cuckoo received a random portion of feedings which was calculated as: feeds to the whole nest/total no. of chicks in the nest (which was 6, i.e. 5 redstarts + 1 cuckoo). Observed feeding frequencies to young cuckoo chicks (6.2 ± 2.31 feeds/hour) did

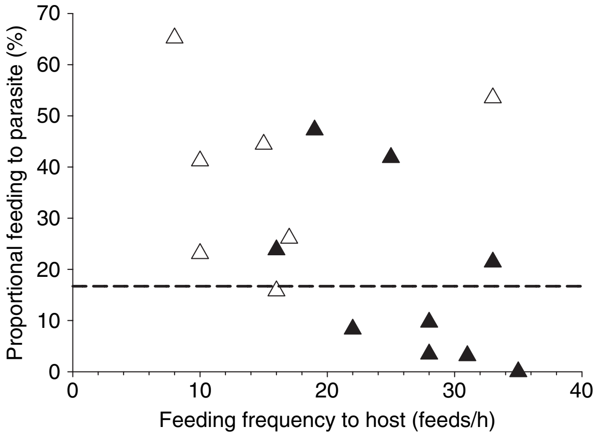

Fig. 3: Proportion of feedings to the cuckoo (% of total feeds delivered per nest per hour) in relation to the provisioning of redstart hosts' own chicks in mixed broods. Both data for young (black triangles) and old (white triangles) ages of chicks are shown. The dashed line represents the random expectation of feedings to each chick in a brood of 6 nestlings (16.7%).

not differ from the random portion of feedings (5.4 ± 0.38 feeds/hour) (Wilcoxon matched pair test; Z = 0.38, n = 9, p = 0.71). In contrast, observed feeding frequencies to older cuckoo chicks (12.0 ± 4.65 feeds/hour) were significantly higher than predicted by random distribution of provisioning within the nest (5.0 ± 0.27 feeds/hour) (Z = 3.22, n = 7, p = 0.0013). Overall the cuckoo chicks had much higher mass than the average redstart chick both at the younger age (29.4 ± 1.49 g vs. 11.4 ± 0.60 g; $U_{9,9} = 3.53$, p = 0.0004) and the older age (42.7 ± 5.63 g vs. 16.5 ± 0.34 g; $U_{7,7} = 3.07$, p = 0.002).

Within nest paired comparison of female versus male behaviour showed that females delivered more of their feedings (29.3 ± 5.80%) to the cuckoo than their respective partners (21.2 ± 5.03%; Wilcoxon matched-pair test, Z = 2.37, n = 19, p = 0.018). From the perspective of the cuckoo the parasite chicks received on average 64.5 ± 4.39% of feedings from females irrespective of treatment (GLMM: effect of treatment: $F_{1,15.4} = 0.71$, p = 0.41). Host females increased the proportion of food they delivered to the cuckoo with increasing cuckoo chick age (GLMM: $F_{1,6.6} = 13.66$, p = 0.0085). Similarly, males fed increasingly higher proportions of food to the cuckoo with its increasing age (GLMM: $F_{1,5.8} = 13.53$, p = 0.01).

Growth Rates

Cuckoo chicks in the two treatment groups had similar masses after hatching (Table 1). Although the mass of all cuckoo chicks significantly increased with age (Fig. 4), the experimentally induced presence of host chicks strongly reduced the rate of parasite chick growth (treatment vs. age interaction: $F_{1/212} = 450.46$, p < 0.0001). From approximately 1 wk of age (Fig. 4) cuckoos in mixed broods showed dramatically slower growth than lone cuckoos.

Cuckoo chicks assigned to 'mixed' treatment grew very similarly to those raised in the 'alone' treatment during the first 5 d when both groups of cuckoo chicks were sole occupants of host nests (see Methods). Specifically, until day 7 there were no differences between 'alone' and 'mixed' groups of chicks (each day analysed separately; Mann–Whitney U-tests: all p > 0.14, except of day 2 when cuckoos from mixed treatment were slightly heavier than those raised alone, p = 0.03). This confirms that the differences between treatments that were detected at later stages of cuckoo development (Fig. 4) were not caused by other confounding factors or a non-random assignment of chicks to the two respective

Table 1: Breeding parameters (mean ± SE) of cuckoo chicks raised alone ('Alone') and those cohabiting the nest with the host redstart brood ('Mixed')

Breeding parameter	Alone	Mixed	Sample size	test-statistic	p
Mass after hatching (g)	3.7 ± 0.22	3.8 ± 0.12	9, 8	1.01	0.31
Fledging success (%)	100.0	44.4	10, 9	–	0.011
Fledging age (days)	19.8 ± 0.59	22.8 ± 1.18	10, 4	2.00	0.046
Fledging mass (g)	104.2 ± 4.24	77.1 ± 2.56	10, 4	2.47	0.013
Age fledging mass (days)	17.8 ± 0.83	21.8 ± 1.18	10, 4	2.07	0.039
Died at age (days)	–	17.0 ± 3.42	5	–	–

'Mass after hatching' was measured when chicks were 1 d old. 'Fledging age' was estimated as a mid-point 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 fledging mass' is the chick age when it was weighed for the last time. Differences in fledging success were tested with Fisher's exact test; all other differences were tested with Mann–Whitney U-test.

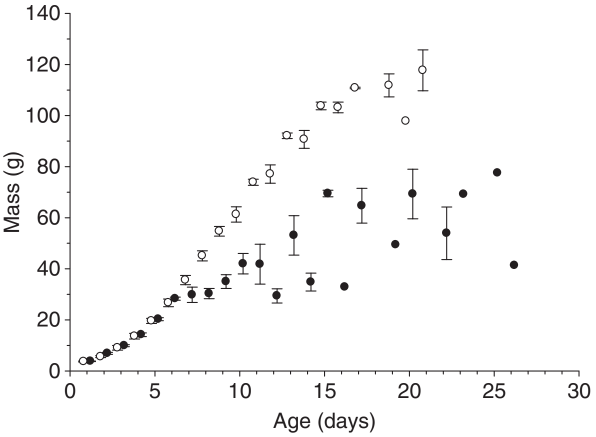

Fig. 4: Growth of cuckoo chicks in redstart nests where host chicks were absent (white circles, 'alone' treatment) or present (black circles, 'mixed' treatment). In the 'mixed' treatment cuckoo chicks were sole inhabitants of their nests until day 5 post-hatch when the host chicks were introduced (see Methods for details). Values are means ± SE.

treatment groups. After the addition of redstart chicks to 'mixed' nests (from day 8 till day 12) cuckoos in mixed broods weighed significantly less than those raised alone (daily comparisons; Mann–Whitney U-tests: all $p < 0.02$). Sample sizes for older chicks were too small (due to mortality in the mixed group), thus no meaningful statistical comparisons were possible.

Survival of Cuckoo Nestlings

All cuckoo chicks raised alone successfully fledged (100%), whereas those in mixed broods suffered high mortality (54%) (Table 1). There was significant variation in growth rates among cuckoo chicks (Fig. 5; Kruskal–Wallis test: $\chi^2 = 13.86$, df = 2, p = 0.001). Specifically, cuckoos that finally fledged from mixed broods showed much lower increments in mass (g/hr) during the linear phase of growth than those that were sole occupants of host nests (Table 1; Fig. 5). Cuckoo chicks in mixed broods that later died showed extremely small growth increments (Fig. 5). Cuckoo chicks forced to compete with host chicks fledged approximately 3 d later than cuckoo chicks raised alone (Table 1). Although the fledging mass of cuckoos from mixed broods was measured 3 d later than that of lone cuckoos (Table 1), cuckoos in the 'mixed' treatment still fledged with much lower masses than cuckoos raised alone (Table 1). The presence of host chicks decreased the mass of the fledging cuckoo chick by approximately 30% (Table 1).

In a striking contrast we observed host chick mortality at only one nest (out of nine). At that nest, two chicks were evicted by the cuckoo and neglected by parents and soon died. Thus, the host mortality was only 4.4% (2 out of 45 total redstart nestlings cohabiting nests with the cuckoo chicks).

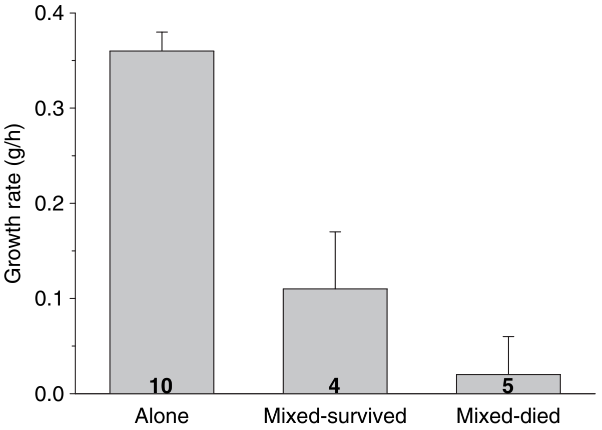

Fig. 5: Growth performance (mean + SE) of cuckoo chicks measured as increments in mass (g). Sample sizes are given within bars. Data are from linear phase of growth between 'young' and 'old' age (for details see Methods).

Growth rates (g/hr) during the linear phase of growth were positively associated with future survival of the cuckoo chicks (nominal logistic regression with fledged/died response: $R^2 = 0.48$, $\chi^2 = 10.49$, df = 1, p = 0.0012). Also, combined parental feeding frequencies to cuckoos at a younger age well predicted parasite chicks' fate of fledging successfully or not. The chance of successful fledging increased with increasing feeding frequencies both when all nests (n = 19) were included in the analysis ($R^2 = 0.70$, $\chi^2 = 15.38$, df = 1, $p < 0.0001$) and when only 'mixed' broods (n = 9) were analysed ($R^2 = 1.00$, $\chi^2 = 12.37$, df = 1, p = 0.0004).

Discussion

In contrast to results of prior observational work (Rutila et al. 2002), we experimentally determined that being raised together with host redstart chicks was very costly to common cuckoo chicks. Specifically, cuckoo chicks in mixed broods were fed less, grew slower, fledged later, showed lower fledging masses, and experienced higher mortality prior to fledging than parasite chicks that were the sole occupants of host nests. Thus, the eviction of host young by common cuckoos parasitizing redstarts in Finland is clearly adaptive for the young parasite. We did not, however, test whether an intermediate number of host nestmates would be non-costly or even beneficial in terms of potentially lost extra provisioning induced by the presence of some host chicks (Kilner et al. 2004). Still, the experimental number of host chicks in mixed broods in our study (five per nest) is close to the typical number of host chicks that are raised in naturally mixed broods (four per nest; Rutila et al. 2002).

Previous observational study of the same host and parasite population (Rutila et al. 2002) found high mortality among cuckoo chicks that were raised alone. One possibility for the lack of consistent differences in survival rates of cuckoos in naturally mixed vs. naturally alone broods is that parasite hatchlings in both nest types would have engaged in attempting to evict (unsuccessfully or successfully) host eggs and nestmates, thus paying an early cost of eviction behaviour (Kleven et al. 1999). Thus, there could have been growth and survival costs of 'a ghost of eviction past' affecting performance of cuckoo chicks even after they became sole occupants of host nests and these may have outweighed the subsequent benefits of not having to compete for foster parental provisioning in parasite only broods. In our study, we experimentally removed any possible effects of the eviction behaviour itself, representing a likely explanation for nil mortality rates among our cuckoo chicks raised alone. Future work with redstarts and other hosts of cuckoos should, nevertheless, address specifically the magnitude of such costs of eviction relative to the benefits of sole nest occupancy for cuckoo chicks across a diversity of host egg dimensions and nest architectures (Grim 2006b).

In contrast to a 'costly virulence' scenario (Kilner 2005) cuckoo chicks in our study even received relatively lower *relative* proportions of food with increasing feeding frequencies to the hosts' own chicks (Fig. 3). This was the case despite increasing *absolute* feeding frequencies to cuckoo chicks (Fig. 2). Thus, there seems to be a trade-off between feeding own and alien chicks for redstart parents. Although cuckoos in mixed broods received increasingly more than random proportions of provisioning, they still grew very poorly. This is most likely explained by larger body size, and thus presumably higher diet demands, in the cuckoo in comparison to increasingly relatively smaller redstart chicks (see Results).

The comparison of survival rates from hatching until fledging (100 vs. 44% for cuckoos in alone vs. mixed treatments) would certainly underestimate the negative effects of competition with host nestlings for the cuckoo fledgling. This is because successfully fledged cuckoos from mixed broods fledged both later and at much lower masses than those that did not experience the competition with redstart chicks (Table 1). Fledging mass and date strongly affect survival chances of fledgling birds (e.g. Weatherhead & Dufour 2000), including hosts of brood parasites (Payne & Payne 1998; Hoover & Reetz 2006). Therefore, it is also likely that cuckoos from mixed broods experienced higher mortality not only before but also after fledging. Previous study from the same study site detected another cost of non-eviction – some cuckoo chicks were deserted by redstart fosterers that followed their fledged chicks and let the cuckoo starve to death in the nest (Rutila et al. 2002). The long fledging period may further put the parasite chick at disadvantage when parents show time-limited durations of parental care provided to nestlings (Grim et al. 2003; Grim 2007b).

Very poor growth performance and survival of cuckoos in mixed broods are remarkable also because the cuckoo chicks were on average 2 or 3 times bigger (as for their body mass) than an average host chick, and body size provides an important advantage in within-brood competition (e.g. Lichtenstein & Sealy 1998). Such poor success of parasite chicks could in principle be explained by host chick discrimination (Grim 2006a). Our results are inconsistent with a hypothesis of innate chick discrimination – cuckoos in all broods (both lone and mixed) grew identically and well when they were alone in the nest during first 5 d post-hatch. The poor success of cuckoos in mixed broods during cohabitation of nests with host chicks is also not consistent with learned chick discrimination – host redstarts *first* experienced parasite chicks in all nests and they faced their own chick only 5 d later. The patterns of growth and survival are, however, consistent with the hypothesis (Schuetz 2005) that parasite chicks were simply imperfectly adapted to the host parent-offspring communication system. Bird responses to some focal stimuli (e.g. chick traits eliciting provisioning) may be high when there is no other stimulus for comparison. Alternatively, bird responsiveness to the very same focal stimulus may decline in the presence of other stronger and/or more typical stimulus as shown experimentally by Lyon et al. (1994). Such a scenario seems to provide a plausible explanation for our observations that the same cuckoo chick individuals performed well when alone in the nest but fared considerably worse when host chicks were added to the nests despite the fact that the identity of both nest environment and host parents remained identical (i.e. within subject design).

Brown-headed cowbird chicks frequently cause high mortality among host nestlings (Hauber

2003b). In a striking contrast, host redstart chicks survived well in the presence of a parasite nestling (the survival rate was 95.6%). Comparative analyses showed that parasitism by cowbirds selected for the evolution of faster growth rates in cowbird hosts (Remeš 2006). Here, we detected no obvious effect of the cuckoo presence on the fledging mass of redstart chicks.

In summary, for the evicting common cuckoo nestling there are no costs associated with the loss of assistance in soliciting fosterer care. The presence of host chicks in the nest is costly for the cuckoo chick in terms of provisioning, growth and survival. Under natural conditions, the nest structure is probably responsible for the inability of the parasite chick to succeed in evicting host offspring. Thus, nest design may be an inadvertent defence mechanism for hosts against interspecific brood parasitism (Grim 2006c).

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