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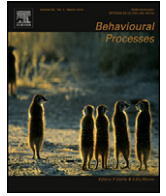
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### Highlights

**Competition with a host nestling for parental provisioning imposes recoverable costs on parasitic cuckoo chick's growth***Behavioural Processes xx (2012) xxx–xxx*

Nikoletta Geltsch, Márk E. Hauber, Michael G. Anderson, Miklós Bán, Csaba Moskát\*

► We studied great reed warblers' parental care toward brood parasitic cuckoo chicks. ► Cuckoos received less food and grew slower in broods with a host than when alone. ► After hosts fledged, cuckoos compensated for the costs of prior cohabitation.



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# Competition with a host nestling for parental provisioning imposes recoverable costs on parasitic cuckoo chick's growth

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## ABSTRACT

Chicks of the brood parasitic common cuckoo (*Cuculus canorus*) typically monopolize host parental care by evicting all eggs and nestmates from the nest. To assess the benefits of parasitic eviction behaviour throughout the full nestling period, we generated mixed broods of one cuckoo and one great reed warbler (*Acrocephalus arundinaceus*) to study how hosts divide care between own and parasitic young. We also recorded parental provisioning behaviour at nests of singleton host nestlings or singleton cuckoo chicks. Host parents fed the three types of broods with similar-sized food items. The mass of the cuckoo chicks was significantly reduced in mixed broods relative to singleton cuckoos. Yet, after the host chick fledged from mixed broods, at about 10–12 days, cuckoo chicks in mixed broods grew faster and appeared to have compensated for the growth costs of prior cohabitation by fledging at similar weights and ages compared to singleton cuckoo chicks. These results are contrary to suggestions that chick competition in mixed broods of cuckoos and hosts causes an irrecoverable cost for the developing brood parasite. Flexibility in cuckoo' growth dynamics may provide a general benefit to ecological uncertainty regarding the realized successes, failures, and costs of nestmate eviction strategies of brood parasites.

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## 1. Introduction

The common cuckoo (*Cuculus canorus*; hereafter 'cuckoo') is a well-known avian brood parasite, exploiting diverse host species in the Palearctic (Moksnes and Røskoft, 1995; Davies, 2000). Cuckoo chicks evict host progeny, both eggs and nestlings, typically within 3 days following hatching (Wyllie, 1981; Honza et al., 2007). This eviction behaviour results in the cuckoo becoming the only nest occupant, and the sole recipient of host parental care. Yet, in at least in one of the major European hosts of the cuckoo, the cavity-nesting common redstart (*Phoenicurus phoenicurus*), host eggs or nestlings frequently are frequently not evicted (Rutilla et al., 2002; Avilés et al., 2005), despite prolonged attempts by the cuckoo nestling to do so (Grim et al., 2009a). Consequently, cuckoo chicks are forced to share a nest with one or more redstart nestlings in about half of the naturally parasitized broods (Rutilla et al., 2002). In these broods, cuckoos do not seem to recover before fledging from the

early costs of reduced feeding, lower growth rates, delayed fledging, and frequent mortality in mixed broods with the redstarts compared to singleton broods of cuckoos (Grim et al., 2009a). In contrast, cuckoo chicks rarely survive together with host nestlings when nestmate eviction is unsuccessful from open cup-nesting hosts (Petrescu and Béres, 1997; Grim et al., 2011). Here, we investigated experimentally the foster parental responses and the nestling developmental patterns of host-parasite nestling cohabitation in an open-cup nesting host of the cuckoo.

In a previous study of the great reed warbler (*Acrocephalus arundinaceus*), experimentally induced mixed broods of one cuckoo chick and two host nestlings induced growth costs for both species during the early phase of cohabitation prior to the fledging of host chicks (Hauber and Moskát, 2008). The high level of nestling competition between cuckoos and their great reed warbler nestmates frequently led to the loss of some chicks from nests, and this impacted host nestlings more frequently, although it also occurred to cuckoo chicks on rare occasions (Moskát and Hauber, 2010). This host has a nestling period of 11–12 days, a much shorter time than that of the cuckoo chicks (18–21 days, Anderson et al., 2009). To date, however, the impact of early shared parental care on cuckoo nestlings during the period following the fledging by

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host nestlings has not yet been studied in this experimental context, and so there is no knowledge of whether cuckoo chicks can later compensate for the reported patterns of early growth cost of sharing a nest with host chicks (Hauber and Moskát, 2008). Compensatory growth during the stages of host parental provisioning for foreign chicks is a potentially critical component of physiological flexibility in the various avian brood parasitic strategies of both nestmate-evictor cuckoos (Anderson et al., 2009; Grim et al., 2009a,b) and nestmate-tolerant *Molothrus* cowbirds (Kilpatrick, 2002). For example, compensatory growth results in similar weights and ages at fledging, despite the temporary growth costs of evicting host eggs by the cuckoo chick from both cup-nesting great reed warbler broods (Anderson et al., 2009) and cavity-nesting common redstart broods (Grim et al., 2009b).

Here we report on field experiments to specifically assess the consequences of shared parental care. These include new manipulations of singleton host chick nests and collecting data beyond the period of predicted cohabitation between cuckoo and host nestlings (compared to the different treatments and periods reported in Hauber and Moskát, 2008). Critically, we collected and analyzed data from the full nestling period of singleton hosts, singleton cuckoos, and mixed broods of one host and one parasite chicks provisioned by great reed warbler parents. We studied an experimentally induced cuckoo chick to share the nest with a host nestling, which we considered the most plausible situation for successful joint fledging; this is because in larger clutches, containing more than one host nestling beside the cuckoo chick, the tight nest-cup space increases the chance for accidental falling of chicks from the nest (Moskát and Hauber, 2010). We hypothesized that sharing parental care with a host nestling is costly for cuckoo chicks and predicted reduced growth rates for cuckoo chicks raised in mixed broods compared to those growing up alone. However, we also predicted that cuckoos would compensate for their initial reduced growth rate in mixed broods, through a period of accelerated growth following the early fledging of the host nestling, as seen previously in the compensatory growth of cuckoo chicks following the cessation of costly egg eviction behaviours (Anderson et al., 2009; Grim et al., 2009b). To address potential proximate mechanisms of parental influence on reduced growth during cohabitation and compensatory growth after hosts fledge, we examined both the size of food items delivered by parents and per capita provisioning in mixed and singleton broods of cuckoos and/or great reed warblers.

## 2. Methods

Fieldwork was carried out about 40 km south of Budapest, Hungary, in the countryside adjacent to Apaj (47°07'N, 19°05'E), between mid-May and mid-July in 2008 and 2009. In our study area great reed warblers nest in reed (*Phragmites australis*) beds that grow in 2–4 m wide strips along both sides of small flood relief and irrigation channels. The modal clutch size of great reed warblers is 5 eggs and modal brood size is 4 chicks at this site (Moskát et al., 2008). A large proportion (41–68%) of the nests of these hosts are parasitized by cuckoos, which is an unusually high level of cuckoo parasitism (Moskát et al., 2008).

The cuckoo chick typically evicts all eggs and/or nestlings from the nests of the hosts within 3 days of hatching in a great reed warbler nest, and, consequently, it grows up alone (Honza et al., 2007; Anderson et al., 2009). To better understand host responses to foreign chicks relative to own chicks (Grim and Honza, 2001; Langmore et al., 2003, 2009), we followed up our prior cohabitation/mixed-brood experiments with cuckoos and great reed warbler chicks (Hauber and Moskát, 2008; Moskát and Hauber, 2010). Specifically, in our experiment we induced a 4–5 day old

cuckoo chick (when nestmate eviction behaviour has ceased) to cohabitate with a great reed warbler nestling of the same age (day of hatching = day 0), and we compared parental provisioning and chick growth rates with broods of singleton host or singleton parasite chicks.

We formed two types of treatment broods and one type of control brood: in the mixed-brood treatment one host young was moved into the nest with one cuckoo chick ( $n = 13$  nests), or the cuckoo chick was transferred from its nest to an unparasitized nest with one host nestling (2 nests). Regarding this asymmetry and the potential methodological confounds of these chick-transfer treatments, our previous study revealed no significant differences in any of the chick growth and parental feeding parameters measured between broods that initially had cuckoo or great reed warbler chicks only (Hauber and Moskát, 2008). We also documented previously that adult cuckoos parasitize great reed warblers without regard to the morphological or parental traits of the host parents (Avilés et al., 2009). Cuckoo and host nestlings raised in the same great reed warbler nest may displace each other and fall from the nest during the competition (Moskát and Hauber, 2010), therefore, a small artificial fence ridge, constructed of plastic mosquito netting, was placed around the rim of the nest to prevent chicks falling from nests, while still allowing parents to access and provision the chicks (as documented on our videotapes, see below). We established the mixed brood experiments when chicks were 4–5 days old, i.e. typically later than the eviction extinct of the cuckoo chicks has already terminated (ca. 3 days, Wyllie, 1981), therefore we assumed that the fence did not cause extra effort (and, therefore, a potential growth cost Anderson et al., 2009) for the cuckoo chick when trying to evict their nestmates. Consequently, the data from these mixed brood nests is considered methodologically comparable to our singleton chick broods (see below).

The second type of treatment brood consisted of non-parasitized nests from which all but one host chick was removed by the experimenters. In both treatments, the surplus host nestlings were transported to other active great reed warbler nests, with similarly aged host nestlings, where all survived and fledged successfully, provided that the nest was not depredated (altogether  $n = 19$  nests). An additional nest contained only one host nestling, naturally, and was also included in our analyses.

The third type of clutch consisted of naturally parasitized broods of a singleton parasite chick, in nests from which the cuckoo chick successfully evicted host eggs and nestlings ( $n = 13$  nests). We did not attach the raised netting to broods with the singleton host or the singleton parasite type of nests, and we acknowledge the necessary methodological limitation that these two nest types also differed from the mixed brood nests in that the former included naturally nonparasitized nests and the latter included naturally parasitized nests. However, we also note that the comparison of cuckoo chick growth rates across different nest architectures (c.f. Grim et al., 2011) would more likely generate differences rather than similarities in growth and fledging patterns through variation in eviction behaviour (Anderson et al., 2009), contrary to our predictions here. The novel treatments of mixed broods and singleton host broods in this study were carried out in 2008 and 2009, whereas for the singleton cuckoo type of broods we also used several nests with growth and videotaped data from our previous experiments in 2003–2006 (Hauber and Moskát, 2008). We detected no significant differences in interannual patterns response measures per treatment type (Mann–Whitney tests, all  $P > 0.08$ ) and so data for each nest type were combined across years.

To monitor nestling growth rates in the experimental and control broods, we weighed all chicks daily using Pesola spring balance with 0.25 g precision or 1.0 g precision, for cuckoos above 30 g. To assess parental provisioning patterns of nest visitation rates

**Table 1**  
Cuckoos' fledging weights and fledging age in mixed broods of one host and one parasite nestlings, and nests of singleton cuckoos (mean  $\pm$  SE).

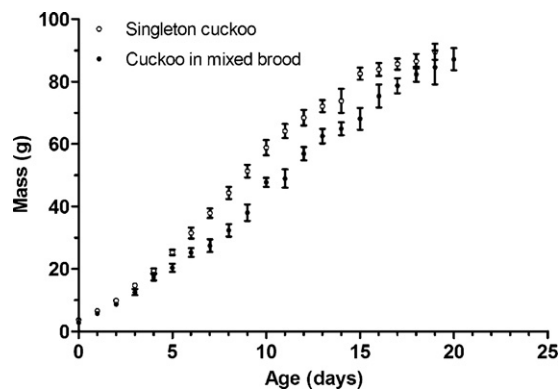
	Singleton cuckoos (control)	Cuckoos in mixed broods (experimental treatment)	n			t	P
				Singleton cuckoo	Mixed broods		
Weight at 4-days (g)	19.39 $\pm$ 0.762	17.32 $\pm$ 1.018	13	9	1.657	0.113	
Weight at 8-days (g)	44.30 $\pm$ 1.965	32.34 $\pm$ 1.9844	12	10	4.249	0.001	
Fledging weight (g)	88.17 $\pm$ 1.735	84.40 $\pm$ 2.649	10	10	1.192	0.249	
Fledging age (days)	18.70 $\pm$ 0.396	19.20 $\pm$ 0.593	10	10	-0.702	0.492	

and food amounts delivered to chicks in experimental and control broods, we videotaped nest attendance and feeding behaviours by (foster) parents at each nest type. To prevent premature fledging of host nestlings which normally occurs at 10–12 days of age, we did not videotape broods older than 9 days: we recorded parental visits twice, at 4–5 days, and 8–9 days of age. The sample sizes for each treatment ranged between 8 and 12 nests (mixed broods: 12 (4 days), 12 (8 days); singleton host: 10 (4 days), 9 (8 days); and singleton parasite: 8 (4 days), 11 (8 days). Although these sample sizes are not large, similar sample sizes led to statistically supported conclusions on parental provisioning patterns in previous studies on mixed broods of brood parasites and hosts (Kilner et al., 2004; Martín-Gálvez et al., 2005; Hauber and Moskát, 2008; Grim et al., 2009a).

We used two digital video cameras, Canon MV500i and MV550i, with Fuji 60 min DX cassettes for recording. Each camera was positioned 4–5 m from the nest on a tripod and was left for 15–20 min before recording started to allow habituation by the parents. We left the immediate vicinity of the camera to avoid human disturbance during videotaping but stayed nearby to avoid theft of the cameras by locals. Recording sessions typically lasted 60 min (range: 54–62 min, mean  $\pm$  SD: 61.68  $\pm$  0.15).

Videotapes were viewed after the end of the field season on a television screen to estimate prey sizes and parental feeding decisions to hosts or parasites. We could not discriminate female or male parents, owing to absence of sexual dimorphism or systematic colour banding in this population of hosts. The species identity of the nestlings in mixed broods was assigned by gape colour (cuckoo: red gape; great reed warbler: yellow gape). Using these video tapes and data, we calculated food delivery rates as the number of parental visits per unit time, recorded parental feeding patterns delivered per capita to either cuckoo or host chicks (mixed broods only), and quantified the size category of food items delivered to the chicks (as a quasi-continuous variable: 25%, 50%, 75%, etc. of 25% increments of bill volume; Hauber and Moskát, 2008).

We used general linear mixed models (GLMM) to evaluate the effects of feeding rate, prey size, and amount of food, either per brood or per capita relations. Nest identity and year of experiment were included as random factors in these models, species, and the age of chicks (4–5 days vs. 8–9 days) were treated as a fixed nominal factors (as 4 days or 8 days). We looked for an interaction term between age groups and treatments, but as none was found ( $P > 0.05$ ), we did not include interactions in the final models. Cuckoo growth rate was estimated by linear regression in the linear growth phase (between days 4 and 11, i.e. the start of experiments and fledging time for a host chick; Anderson et al., 2009). The slopes of the fitted linear regressions were compared with the slope factors (i.e. growth steepness parameter) from logistic curves. The slope factor describes the steepness of a curve, which is useful to characterize growth rate of nestlings (see e.g. Grim, 2006). We estimated the growth-curve's parameters with the R (R Development Core Team, 2009) drc package's drm (fitting dose-response models) model (Ritz and Streibig, 2005). We applied the general asymmetric five-parameter logistic model with three parameters, which is



**Fig. 1.** Weight of cuckoo chicks in relation to age and nest category: mixed broods of one host and one cuckoo nestling (treatment) or broods of a singleton cuckoo chick (control).

equivalent to the logistic function, which was also used by Grim (2006):

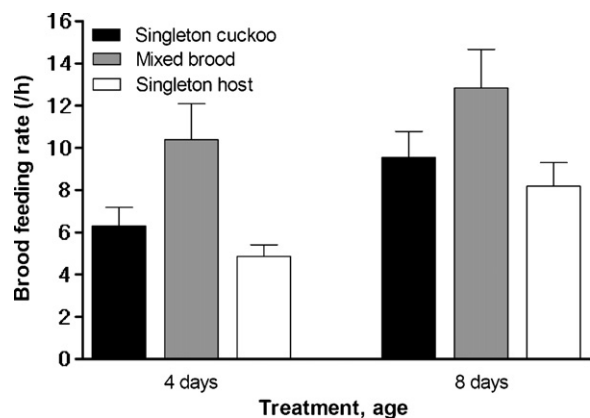
$$f(t) = \frac{d}{1 + e^{b(t-e)}}$$

where  $f(t)$  is mass at age  $t$ ,  $d$  is the asymptotic mass,  $b$  is a measure of growth rate, and  $e$  is the inflection point on the growth curve.

We used parametric tests for comparison of the parental feeding metrics (Kolmogorov–Smirnov test,  $P > 0.05$  for all variables), with the options equal variance (Levene test,  $P > 0.05$ ), or unequal variances (Levene test:  $P < 0.05$ ). For the comparison of growth curve parameters the Mann–Whitney  $U$ -test was applied. We used SPSS ver. 17 for the analyses of two tailed tests. We plotted means  $\pm$  standard errors (S.E.) of the raw data in the illustrations of each of the weight and provisioning measures for the different brood treatments and age groups.

### 3. Results

At the beginning of the experiments, at 4 days old, there were no statistical differences in the weights of cuckoo chicks between experimental mixed brood and singleton cuckoo (control) nests (Table 1). Later, at 8 days old, the differences in weight were highly significant, with cuckoo chicks in mixed broods weighing less than in control broods (Table 1). After the host nestling fledged at 10–12 days, the cuckoo chicks appeared to compensate for their lower weights in mixed broods, and fledged at similar weights and ages from mixed brood or control nests (Table 1 and Fig. 1). Accordingly, we detected significant differences between brood types in the shape of growth curves of the cuckoos. Specifically, during the linear phase of chick growth (ca. 4–11 days, between the onset of the experiment and fledging of host nestmates), the rate of weight gain was lower in the mixed broods than in the controls (range of steepness in linear regression for mixed broods: 0.808–0.986 and for controls: 0.961–0.997,  $U_{10,10} = 11.5$ ,  $P = 0.002$ ). Overall, the growth parameters of cuckoo chicks were also smaller in the mixed broods than in the control nests when the full nestling period was

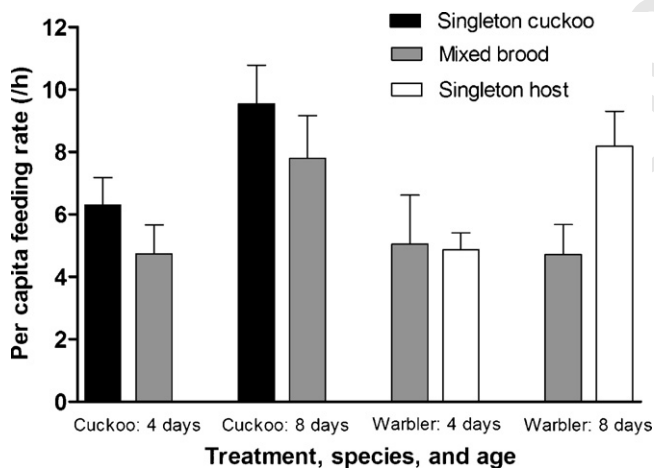


**Fig. 2.** Feeding rates of great reed warbler parents per brood, delivered to 4-day and 8-day old nestlings in three nest categories: singleton host nestling (treatment), mixed broods of one host and one cuckoo chicks (treatment), and singleton cuckoo chick (control). Feeding rate is expressed as feedings/clutch/hour.

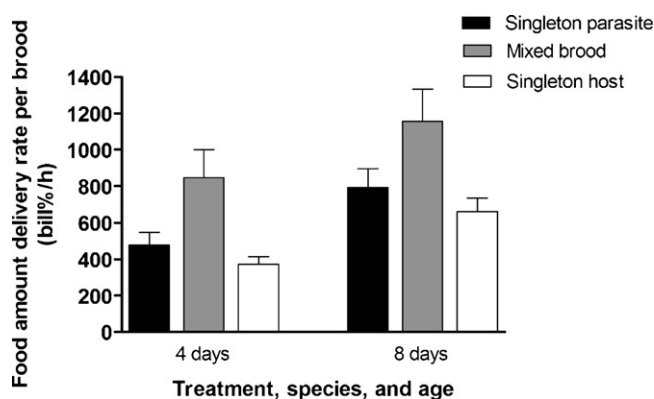
considered (range of absolute values of steepness of the growth curve for mixed brood experiments: 0.220–0.303; for controls: 0.224–0.373,  $U_{10,10} = 14.0$ ,  $P = 0.005$ ).

Regarding parental provisioning patterns, great reed warbler adults fed 8 day old chicks more often than the 4 day old chicks ( $F_{1,60.6} = 14.42$ ,  $P < 0.001$ ) (Fig. 2). Feeding rates were also higher in the mixed brood nests compared to the singleton host or singleton parasite nests ( $F_{2,44.7} = 5.94$ ,  $P = 0.005$ ); the overall feeding rate at the mixed broods of one cuckoo and one host nestling seemed to be the sum of the feeding rates at nests with a singleton cuckoo chick and at nests with a singleton host chick (Fig. 2). *Post hoc* comparisons revealed that feeding rates of mixed broods significantly differed from feeding rates of singleton host chicks ( $t_{44.0} = 3.32$ ,  $P = 0.002$ ) and also from singleton cuckoo chicks ( $t_{41.6} = 2.21$ ,  $P = 0.032$ ).

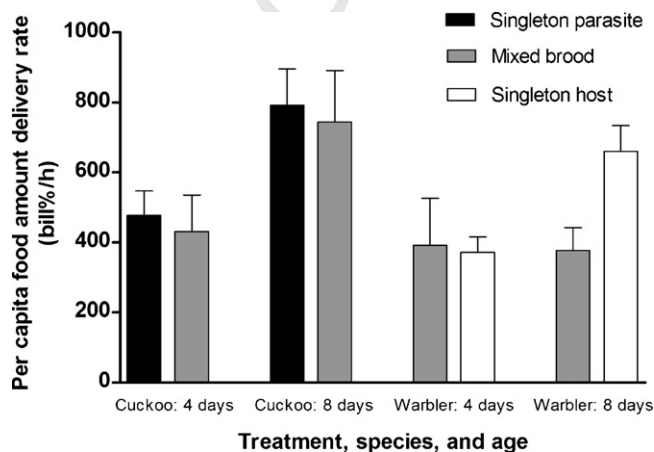
In the species-specific comparisons among either the host or parasite nestlings, per capita feeding rates did not differ between the control and experimental nests (4-day old cuckoos:  $t_{13} = 1.223$ ,  $P = 0.983$ ; 8-day old cuckoos:  $t_{20} = 0.949$ ,  $P = 0.354$ ; 4-day old great reed warblers: Mann-Whitney  $U = 31.00$ ,  $P = 0.740$ ), except for the 8-day old great reed warblers ( $t_{18} = 2.373$ ,  $P = 0.029$ ), where host nestlings were more frequently fed in the singleton nests than in the mixed broods (Fig. 3). Per capita feeding rates also increased with



**Fig. 3.** Per capita feeding rates of great reed warbler parents delivered to individual 4- and 8-day old cuckoo and host chicks in three nest categories: singleton host nestlings (treatment), mixed broods of one host and one cuckoo (treatment), and singleton cuckoo chicks (control). Feeding rate is expressed as feedings/chick/hour.



**Fig. 4.** Total amount of food per brood, delivered by great reed warbler parents for 4- and 8-day old to nests in three categories: singleton host nestling (treatment), mixed broods of one host and one cuckoo chicks (treatment), and singleton cuckoo chick (control). Amount of food was calculated as cumulative prey size delivered during all feedings/clutch/hour.



**Fig. 5.** Per capita total amount of food delivered by great reed warbler parents for 4- and 8-day old host and cuckoo chicks to nests in three categories: singleton host nestlings (treatment), mixed broods of one host and one cuckoo (treatment), and singleton cuckoo chicks (control). Amount of food was calculated as cumulative prey size delivered during all feedings/chick/hour.

nestling age (GLMM:  $F_{1,66.5} = 10.73$ ,  $P = 0.002$ ), but were statistically similar among treatments (GLMM:  $F_{2,25.3} = 3.04$ ,  $P = 0.066$ ).

Mean prey size per brood delivered to nests by great reed warbler parents increased with nestling age ( $F_{1,76} = 5.00$ ,  $P = 0.028$ ), and did not vary between treatments ( $F_{1,76} = 0.22$ ,  $P = 0.803$ ). The size of food items fed per capita did not change statistically with increasing nestling age (GLMM:  $F_{1,70} = 3.67$ ,  $P = 0.059$ ), and did not vary across nest treatments (GLMM:  $F_{2,70} = 0.02$ ,  $P = 0.981$ ). The total amount of food that nestlings were fed per brood increased with nestling age (GLMM:  $F_{1,67.8} = 12.64$ ,  $P = 0.001$ ) and across treatments (GLMM:  $F_{2,49.2} = 6.81$ ,  $P = 0.002$ ) (Fig. 4). On a per capita basis, the total amount of food delivered increased with nestling age (GLMM:  $F_{1,68.3} = 10.99$ ,  $P = 0.001$ ), but no difference was found across treatments (GLMM:  $F_{2,24.9} = 1.70$ ,  $P = 0.203$ ) (Fig. 5).

#### 4. Discussion

Our novel experimental results confirm that shared parental care for a cuckoo chick and a great reed warbler nestling was costly during the period of cohabitation for both the brood parasite and host nestling (Hauber and Moskat, 2008; Grim et al., 2009a), as indicated by reduced growth rates and lower per capita parental food delivery rates in mixed broods relative to singleton broods. Host

parents brought more food to the experimental mixed broods than to singleton broods of either the host or brood parasite: the size of food delivered, however, did not differ in prey sizes, relative to singleton broods of cuckoos or host chicks. These patterns of parental provisioning resulted in cuckoo nestlings receiving less food in mixed broods at both days 4 and 8 compared to when raised alone. By comparison, singleton host chicks in mixed broods received the same amount of food at 4 days, but less at 8 days compared to when developed alone. However, both cuckoo and host chicks, irrespective of treatment, fledged successfully. Most critically, weights and ages of cuckoo fledglings were similar between treatment and control nests. This implies that parasitic nestlings can recover from the growth cost of cohabitation by the time of fledging, although any long-term consequences of such compensatory growth, potentially resulting in differential migratory and recruitment success through (e.g. reduced immunocompetence or cognitive abilities; Morgan and Metcalfe, 2001) are yet to be investigated in brood parasitic birds. However, mixed broods of great reed warbler and cuckoo nestlings rarely occur naturally (Molnár, 1939), so selection on compensatory growth pressure from other kinds of developmental stress, including temporary food shortage or inclement weather, could be more important during parasitic chick development. Nevertheless, cohabitation of host nestlings with their brood parasites might have played a role in the evolution of eviction behaviour in ancient cuckoos. Contrary to evictor cuckoos documented here and elsewhere (Hauber and Moskát, 2008), the presence of host nestlings may induce the host parents to deliver more food per capita for the chick of the brown-headed cowbird (*Molothrus ater*) (Kilner, 2003). The evolutionary pathways of host-brood parasite co-evolution in nest-mate tolerant cowbirds and evictor cuckoos may be different, as cowbirds have not had the long co-evolutionary history with their hosts, whereas cuckoos have had (Davies, 2000).

Hauber and Moskát (2008) previously showed that there is a growth cost paid by the cuckoo chick when sharing the nest with host (in that case, two) great reed warbler young. In parallel, although the present study monitored cuckoo chick growth during cohabitation with just a singleton host nestmate, it still revealed a growth cost both in absolute weight and in the shape of the growth curves of cohabitating cuckoo chicks. However, the current study also collected data beyond the fledging age of host nestlings. We found that cuckoo nestlings can compensate for earlier reduced growth in the period after the host nestling fledged, when the brood parasite is the sole nest occupant.

Why is growth compensation in cuckoo chicks, that normally evict host offspring, important in mixed broods of hosts and brood parasites? Rutila et al. (2002) observed and Grim et al. (2009a) showed experimentally elevated mortality, and in surviving nestlings, reduced growth of cuckoos cohabiting with host nestlings. In the case of these cavity-dwelling cuckoo chicks, the parasitic young thus were not able to compensate depressed growth patterns in mixed broods of the redstart, causing lower fledging weights and older fledging ages (Grim et al., 2009a). However, in the Grim et al. (2009a) experiment, the number of host nestlings was higher (5 host chicks) than in either experiments with great reed warblers (Hauber and Moskát, 2008, this study), which were designed to simulate natural cases of mixed broods (Avilés et al., 2005), whereas our experimental design included one host and one cuckoo chick (i.e. numerically balanced to generate direct per capita competition between host and parasite chicks). Additionally, adult great reed warblers are larger than redstart parents (ca. 30 g and 15.5 g, respectively, Perrins, 1998), and can be regarded as higher quality hosts for the cuckoo, ensuring faster development and higher fledging weight for cuckoo chicks, than for example in the nests of the smaller reed warbler (*Acrocephalus scirpaceus*) hosts (Kleven et al., 1999; Butchart et al., 2003). A flexible strategy in compensatory growth of cuckoo nestlings, conditional on

ecological circumstances and opportunities, as seen here in mixed broods of great reed warbler nests, may therefore be a beneficial parasitic strategy for a host-generalist brood parasite, such as the cuckoo, where individual females specialize to parasitize on hosts based on habitat features, rather than species identity (Honza et al., 2002; Vogl et al., 2002). This is especially so when the otherwise evictor cuckoo is facing the rare cases of cohabitation with host nestmates in the large and deep nests of most of its typical host species (Grim et al., 2009b, 2011). From these nests host eggs and nestlings are temporarily costly to evict (Anderson et al., 2009), but the cohabitating host nestmates often fall out (Moskát and Hauber, 2010) and fledge earlier (Grim, 2006; this study).

In our experimental treatment of mixed broods, we found that cuckoos received more per capita parental care than host nestlings when they were in direct competition with each other, which is likely attributable to the cuckoo chicks presenting a superstimulus for parental provisions, either by exhibiting greater signals of need than host nestlings (Kilner et al., 1999; Davies et al., 1998; Grim and Honza, 2001) or physically outcompeting host nestlings with their greater size and more directed posture (Lichtenstein and Sealy, 1998; Hauber, 2003). We tentatively conclude that both of these non-exclusive proximate explanations are relevant for great reed warbler (foster) parental decisions. Consequently, 8-day old cuckoo nestlings were fed at the same rate as singleton cuckoos in control nests (in support of the signals of need explanation; Kilner et al., 1999), whereas host nestlings in mixed broods were fed at a reduced rate when compared nests with singleton host chicks (in support of the physical competition hypothesis: Hauber and Moskát, 2008) (Fig. 3).

Previous studies of mixed broods of cuckoos and their hosts revealed different aspects of chick competition, as they were based on different host species (redstart: Grim et al., 2009a; rufous bush robin *Cercotrichas galactotes*: Martín-Gálvez et al., 2005; great reed warbler: Hauber and Moskát, 2008), or on different breeding stages (hatchlings: Anderson et al., 2009; from hatching to fledging: Grim et al., 2009b; after eviction until near fledging of host chicks: Hauber and Moskát, 2008; after eviction until fledging of cuckoos: present study). Although these studies have revealed several costly aspects of shared parental care for the cuckoo chicks relative to host nestlings, further research, in addition to the current study, is still needed to clarify the mechanisms underpinning the different outcomes among these studies. In addition, physiological and behavioural costs not revealed by the analysis of growth and fledging date of compensatory growth (e.g. immunological or cognitive costs: Fisher et al., 2006) also remain to be explored for this and other host-parasite systems. For example, the present study revealed no difference in the size of food items delivered to the host and cuckoo chicks, irrespective of treatment type, i.e. mixed brood with one chick of both species, or controls with only one chick either of the cuckoo or the great reed warbler host. In contrast, food items were consistently greater for cuckoos than for great reed warblers in the study by Hauber and Moskát (2008), when mixed broods containing one cuckoo and two hosts, and control nests containing three host nestlings were examined. These differences in results suggest that greater numbers of host nestlings seem to be more comparable with the larger and more aggressive cuckoo chick, by demanding more food, and host parents are able to discriminate between the two types of nestlings when the number of host chicks is above a certain threshold. Finally, our results revealed that nestlings of both species were able to grow satisfactorily on the common food type, even if differences in food types delivered may cause problems in development of nestlings in brood parasitism if one species cannot utilize properly the delivered food (Turtumøygard and Slagsvold, 2010). Future work should examine whether and how (foster) parents may respond to the different signals of need exhibited by host and parasite nestlings in singleton or

mixed broods, and whether the size of food items delivered is a suitable proxy for the caloric and nutritional content of the food items delivered, fed, and consumed by the different chicks (Grodzinski et al., 2009).

In conclusion, by generating experimentally mixed broods with an equal numbers of brood parasites and hosts, we have shown that it is temporarily costly for evictor brood parasitic cuckoos to share a nest with even just a singleton host nestling. This direct competition leads to reduced provisioning rates to both parasite and host nestlings, and to reduced growth trajectories in the cuckoo nestling while sharing the nest. However, cuckoo chicks appear to be able to compensate once the host chick fledged, although experimental support to disentangle the potential confound of parasite age, size, and host nestmate absence are yet to be generated. Our new data on the flexible growth dynamics of parasitic cuckoo chicks contrast with the results of previous studies, which suggested that chick competition in mixed broods would lead to irrecoverable costs for the cuckoo chick. These results also show that cuckoo chicks possess plasticity in their growth patterns, which may be an adaptation in response to the ecological uncertainty of being a generalist brood parasite whose nestlings have to rely on the variable provisioning abilities of foster parents within and across different host species.

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