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ORIGINAL PAPER

# Lazy males and hardworking females? Sexual conflict over parental care in a brood parasite host and its consequences for chick growth

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**Abstract** Due to the costs of parental care, a conflict of interests often arises between mates wherein each prefers the other to invest more. As with parents raising their own offspring, hosts of brood parasites also exhibit negotiations over investment, becoming particularly intensive when parasite demands are high. Lack of cooperation between the partners may eventually affect the condition and fledging success of the young. Here, we investigate the magnitude of sexual conflict over food provisioning in socially polygynous great reed warblers (*Acrocephalus arundinaceus*) rearing either a parasitic common cuckoo (*Cuculus canorus*) or their own nestlings and its consequences for chick growth. We found that, overall, males provided less food than females, and that polygynous males provided less food per nest than monogamous males. Moreover, polygynous males provisioning two simultaneous broods supplied their own offspring in relation to age and type (cuckoo/host) of the other brood. Females, unlike males, delivered food amount almost irrespective of social status. The difference in contribution between polygynous males and their mates was most pronounced in nests with a cuckoo. In any case, reduced paternal assistance had no significant effect on growth performance of nestlings. In cuckoos, however, this result may be biased as we could not consider a relatively high proportion of secondary cuckoos that died before their growth parameters could be ascertained. Although not detected in chick growth, host sexual conflict over food provisioning may impose a cost on cuckoos in terms of increased mortality in secondary nests.

**Keywords** *Acrocephalus arundinaceus* · Brood parasitism · *Cuculus canorus* · Feeding · Parental investment · Social polygyny

## Introduction

Parental care has evolved to enhance the survival and future reproductive success of progeny and, therefore, the fitness of the parents themselves (Maynard Smith 1977; Clutton-Brock 1991). Parental care also carries costs to the parents, however, since it requires both time and energy and may impose risks, thus reducing their survival and further mating opportunities (Balshine-Earn et al. 2002). Care providers, therefore, should optimise their investment to achieve a balance between the costs and benefits (Maynard Smith 1977; Montgomerie and Weatherhead 1988; Clutton-Brock 1991). As the optimal care level is specific to the individual, however, a conflict of interests can arise between the partners in species with bi-parental care, with each preferring the other to invest more (Houston et al. 2005).

Sexual conflict over parental care has been investigated in a range of animal taxa, including birds with their elaborate social systems and behaviours (Ligon 1999; Olson et al. 2008). In socially polygynous birds, the main concern of males is to increase their own fitness by producing several simultaneous broods, each with a different female. The parental contribution of such males per individual nest is usually lower than that of monogamous males and is related to the female's social status (Johnson et al. 1993; Forstmeier et al. 2001a). Nestlings of higher ranked (i.e. primary) females benefit from generally

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higher male feeding rates than nestlings of lower order (i.e. secondary, tertiary etc.) females (Alatalo et al. 1981; Yasukawa et al. 1990; Johnson et al. 1993). As a result, the parents may disagree on the amount of parental care that males should provide, with females usually becoming the losers in this game. To compensate for low male investment, the females are expected to increase their own workload (Sejberg et al. 2000; Forstmeier et al. 2001b; Redpath et al. 2006), though this is often not completely within their power. As a consequence, fewer or lower quality young usually fledge from nests with reduced or no male assistance compared with fully male-assisted nests (Pinxten and Eens 1990; Johnson and Kermott 1993, but see Bensch 1996). Due to the costs of polygyny, females strive to maintain their males in monogamous bonds through aggressive behaviour towards other females or destruction of other female's nests (Sandell 1998; Veiga 2004; Trnka et al. 2010).

The high costs associated with rearing offspring have led some species (or individuals) to evolve an alternative reproductive strategy, freeing them from parental responsibility. Brood parasitism (Payne 1977; Rothstein 1990) is based on the exploitation of parental care of other individuals (the hosts). As with parents raising their own offspring, hosts of brood parasites also exhibit sexual conflict over care (Grayson et al. 2013). This conflict may sometimes escalate more than in non-parasitised parents, particularly when the demands of the parasite are high (Grayson et al. 2013). Lack of cooperation between the host parents may then affect fledging success or the condition of the parasitic chick and, eventually, the fitness of the adult parasite (see Trnka et al. 2012). In this context, socially polygynous hosts of brood parasites represent a non-trivial system for exploring the magnitude of sexual conflict over paternal care.

Here, we investigate (1) differences in parental contribution to nestling provisioning and (2) chick growth under sexual conflict regimes typical of the socially polygynous great reed warbler *Acrocephalus arundinaceus* (Hasselquist 1998; Leisler and Wink 2000; Trnka et al. 2010). In this passerine species, polygynous males provide less food per nest than their monogamous counterparts (Dyrcz 1986; Sejberg et al. 2000), which often decreases fledging success, especially in lower ranking young (Catchpole et al. 1985; Dyrcz 1986; Bensch and Hasselquist 1991; our unpublished data). Moreover, the great reed warbler is a major common cuckoo (*Cuculus canorus*, hereafter cuckoo) host (Moskát and Honza 2002; Campobello and Sealy 2009; Jelínek et al. 2014). Although it is a high-quality host compared to other potential species (in terms of cuckoo growth and fledging success; Kleven et al. 1999, 2004), the number of cuckoos fledging from secondary nests (compared with monogamous hosts) is more than two times lower (33 vs. 76 %) because of the costs of polygyny (Trnka et al. 2012).

In both parasitised and non-parasitised broods, we assume that the difference in mate contribution to chick provisioning on nests of polygynous rather than monogamous males, and on secondary rather than primary nests, will be consistently greater. Consequently, we predict that it will be with secondary cuckoos or secondary host nestlings where sexual conflict over male assistance with feeding will be the most pronounced. Moreover, we expect that this will have a serious impact on the growth of cuckoos and host nestlings of polygynous males, especially in secondary nests.

## Methods

### Data collection

Between late April and late July 2009–2014, we studied a great reed warbler population based on two nearby fishpond systems situated between Hodonín (48° 51′ N, 17° 07′ E) and Mutěnice (48° 54′ N, 17° 02′ E) in the Czech Republic. The population consisted of approximately 100 to 120 breeding pairs exhibiting 20–30 % male polygyny (Požgayová et al. 2013) and a 30–50 % cuckoo parasitism rate (Jelínek et al. 2014).

Nests were continuously searched for in the littoral vegetation fringing the fishponds and subsequently monitored at 1 to 4-day intervals (for more details about nest checking, see Požgayová et al. 2013 and Jelínek et al. 2014). Adults were caught by mist-netting and colour ringed with a unique combination of a standard aluminium ring and up to three colour plastic rings. Bird identity and social status were verified based on re-sightings of the unique colour ring combinations at nests during checks or from video recordings (see below). As the social status of both males and females may change due to settlement of new females or because of nest failure (Bensch 1996), we used actual status on the day of filming in our analysis. Accordingly, a female was registered as monogamous when she was the only female of a monogamous male. A primary female was the first mated female of a polygynous male, sharing her territory simultaneously with a secondary female. A secondary female was the second mated female of the polygynous male, sharing her territory simultaneously with the primary female. In the same way, we also classified the nests and chicks as monogamous, primary or secondary.

An average great reed warbler brood consists of four nestlings that stay in the nest for 10 to 14 days (Procházka and Hudec 2011). Cuckoo chicks, on the other hand, remain in the host nest for 19 to 25 days (our unpublished data). When the nestlings (either host or cuckoo) reached the age of 7.7±1.1 days (mean±SD, range 6–10 days), we installed a video recorder setup near the focal nest consisting of a sheltered camcorder (JVC GZ-MG 730E, 20E or 155E) and a tripod placed 2–5 m from the nest, level with the nest rim or slightly raised above and camouflaged with plant material from the nest's surroundings. Each nest was then recorded continuously for 4.9±1.2 h (mean±SD, range 2–8 h). The first 0.5 h of each recording was ignored to allow for bird habituation and was not considered in the analysis. In almost all cases, the (foster) parents resumed normal behaviour within several minutes of the onset of recording. On only 8 (6.3 %) of 126 nests did they appear to hesitate for some time (perhaps in response to the setup). In these cases, we prolonged habituation to 1–1.5 h. Before the camcorder was switched on at 10:12±01:48 hours CET (mean±SD, range 07:40–17:45 hours), all nestlings were weighed using a digital pocket scale (OHAUS YA Gold Series, accuracy=0.05 g). In total, we filmed 126 nests: 42 with cuckoo and 84 with host nestlings. Of the 42 nests with a cuckoo, 18 were monogamous, 14 primary and 10 secondary. Of the 84 nests with host nestlings, 47 were monogamous, 19 primary and 18 secondary.

In addition to filming, we measured the growth rate of 65 cuckoos from 65 nests and 141 host chicks from 44 nests. Starting on hatching day (i.e. the first day of age), each nestling was weighed at one to 3-day intervals until the age of 9 (host chick) or 18 (cuckoo) days. Host nestlings were uniquely marked on their toes using a waterproof marker pen for individual identification. At each visit, the marking was renewed, and from the 6th day of age, the nestlings were recognisable based on ring number. The maximum age at weighing was chosen for ethical reasons in order to prevent undesirable premature fledging of the chicks, which could negatively affect their survival chances. Of the 65 cuckoos where growth was measured, 27 were monogamous, 26 primary and 12 secondary. Of the 44 nests where host nestling growth was measured, 22 were monogamous, 11 primary and 11 secondary. As chick social status may change over time (see above), we only considered the status that lasted longest (in days) over the measurement period.

## Data analysis

Video recordings were analysed at low speed by extracting the size of food brought by a bird on each feeding visit over the filming period (after habituation). In all cases, video analysis was undertaken by the same person (RB), individually for adult males and females (each recognised on the basis of their colour rings). Food size was quantified relative to the bird's bill size on an image scale of food size categories ranging from 0.25 to 10 (see Sejberg et al. 2000; Hauber and Moskát 2008; Geltsch et al. 2012 for a similar approach). By summarising all food sizes delivered by each of the partners, we obtained sex-specific estimates of food amount delivered. The total amount of food was defined as the sum of food amounts brought by both pair members. Sex-specific and total amounts of food brought were calculated per hour.

All statistical procedures were conducted in R, version 2.15.2 (R Core Team 2012). To explain the differences in adult feeding behaviour, we fitted linear mixed models (LMM) with normal error distribution for cuckoo and for host nestlings separately. The amount of food brought per hour (continuous; either sex-specific or total) was entered into these models as a dependent variable. Nestling social status (nominal; levels: monogamous, primary, secondary), host/parent sex (nominal; levels: male, female; not used for total amount), number of nestlings (continuous; not used for cuckoos), age (continuous; days) and hatching date (continuous; 1 May=day 1), time of filming (here: a midpoint of the recorded interval; continuous) and interaction between nestling social status and host/parent sex were treated as fixed effects. To improve the interpretability of model parameters, the fixed-effect predictors were centred (Schielzeth 2010). As the dataset comprised both (host) parents from each nest, a random effect of nest identity (ID; not used for total amount) was entered into the models. Some individuals (both male and female) were filmed on more than one nest due to polygyny and inter-annual breeding site fidelity; hence, we also included bird ID as a random effect in all models. Sampling year was included as a further random effect in order to take potential inter-annual variation in the data into account.

In polygynous males caring for two broods simultaneously, we explored how age and type (own or cuckoo chick) of one brood influenced the amount of food delivered by the male to the other brood. For 18 focal cuckoos and 24 focal host broods raised simultaneously with another brood, we fitted two LMM with amount of food brought by the male to the focal brood as a dependent variable, size of the focal brood, and age and type (cuckoo/host) of the simultaneous brood as predictors. Male identity was entered into the models as a random effect. All models were fitted using the glmmADMB function in the glmmADMB package (Fournier et al. 2012). We present ANOVA tables (type III) of fixed effects from full initial models.

Growth curves for individual nestlings were fitted using the drm function in the drc package (Ritz and Streibig 2005). We applied the general asymmetric three-parameter logistic model based on the following function: $f(x)=d/(1+\exp(b(x-e)))$, where $f(x)$ is chick mass at age $x$, $d$ the asymptotic mass, $b$ a measure of nestling growth rate (with an opposite sign) and $e$ the inflection point on the growth curve. The differences in the three growth parameters ($b$, $d$, $e$) with respect to nestling social status were tested using Kruskal–Wallis ANOVA. For host chicks, we used medians and quartiles of the parameters per brood.

## Results

### Host provisioning behaviour

The amount of food delivered to cuckoos varied significantly with their social status, host sex and interaction of these two terms (Table 1). Monogamous males brought higher amounts of food to cuckoos than did polygynous males, whether on primary or secondary nests (Fig. 1). Overall, while females fed cuckoos more food than males (especially females of polygynous males), there was no significant difference in the amount of food that females delivered to monogamous, primary and secondary cuckoos (Fig. 1). The total amount of food brought to cuckoos did not differ significantly between the three nest status categories ($F=2.71$, $df=2$, $P=0.258$; estimate±SE 24.28±1.83 (monogamous), 22.84±2.09 (primary), 19.92±2.41 (secondary)). On the other hand, total amount of food delivered showed a significant positive increase with cuckoo age ($F=4.29$, $df=1$, $P=0.038$; 2.58±1.25) and a marginally non-significant decrease with cuckoo hatching date ($F=3.71$, $df=1$, $P=0.054$; −0.23±0.12).

Similarly, food delivered to host chicks varied significantly with brood social status, parental sex and their interaction (Table 1). Moreover, there was also an increase with increasing number of nestlings (3.48±0.48; Table 1) and a marginally non-significant increase with nestling age (1.07±0.55; Table 1). Males fed nestlings more on monogamous and primary nests than on secondary nests (Fig. 1). Females delivered more food than males, and unlike males, most supplied secondary broods (Fig. 1). The total amount of food delivered to host chicks by both parents did not differ between the three nest status categories ($F=1.11$, $df=2$, $P=0.336$; 32.82±1.20 (monogamous), 35.11±1.85 (primary), 30.33±2.01 (secondary)). Total amount of food was, however, positively affected by chick number ($F=63.68$, $df=1$, $P<0.001$; 6.88±0.86) and age ($F=4.93$, $df=1$, $P=0.030$; 2.18±98).

The amount of food brought by polygynous males to their own nestlings (but not to cuckoos) in the focal nest differed significantly with age and type of brood in the simultaneous nest (Table 2), i.e. the older the simultaneous brood, the less food the male delivered to its own nestlings in the focal nest (−0.34±0.14; Table 2). Moreover, when the simultaneous brood consisted of host chicks, host nestlings in the focal nest were fed less by the male than when a cuckoo was raised in the simultaneous nest (−7.08±2.27; Table 2).

### Nestling growth

Asymptotic mass and inflection point (parameters $d$ and $e$, respectively) did not differ significantly in cuckoos reared in monogamous, primary or secondary nests (Table 3; Fig. 2). Growth rate (parameter $b$) of primary cuckoos, however, was higher than that for monogamous and secondary cuckoos, though the difference was marginally non-significant (Table 3; Fig. 2). Host nestlings of the three social status groups did not differ significantly in any of the growth parameters (Table 3; Fig. 2).

## Discussion

As predicted, difference in host/parental contribution to nestling provisioning was most pronounced on secondary nests. The amount of food delivered to these nests by males was extremely low compared to that delivered by females, and especially so on the secondary nests with a cuckoo chick. What we did not expect, however, was the low level of male investment in primary cuckoos, which was as low as male investment in secondary cuckoos. Primary host young, on the other hand, received significantly more food from males than secondary host young. Further, we found that when males were caring for two broods simultaneously, the older the one brood, the lower amount the males delivered to the other brood with own nestlings. Moreover, the males brought less food to their own focal nestlings when there were host chicks in the simultaneous nest, compared to when there was a

**Table 1** Food amount delivered to cuckoo and host nestlings by individual hosts/parents

| | | Cuckoo | | Host | |
|---|---|---|---|---|---|
| Food amount/1 h~ | *df* | *F* | *P* | *F* | *P* |
| *Social status of nestlings* | *2* | *8.56* | *<0.001* | *3.57* | *0.031* |
| *Host/parent sex* | *1* | *16.59* | *<0.001* | *14.98* | *<0.001* |
| *Number of nestlings* | *1* | *–* | *–* | *53.20* | *<0.001* |
| Hatching date of nestlings | 1 | 2.05 | 0.157 | 0.35 | 0.556 |
| Age of nestlings | 1 | 2.46 | 0.121 | 3.84 | 0.052 |
| Time of filming | 1 | 0.03 | 0.872 | 0.00 | 0.966 |
| *Social status of nestlings: host/parent sex* | *2* | *7.52* | *0.001* | *8.85* | *<0.001* |

Significant predictors are given in *italics*. For model contrasts, see Fig. 1

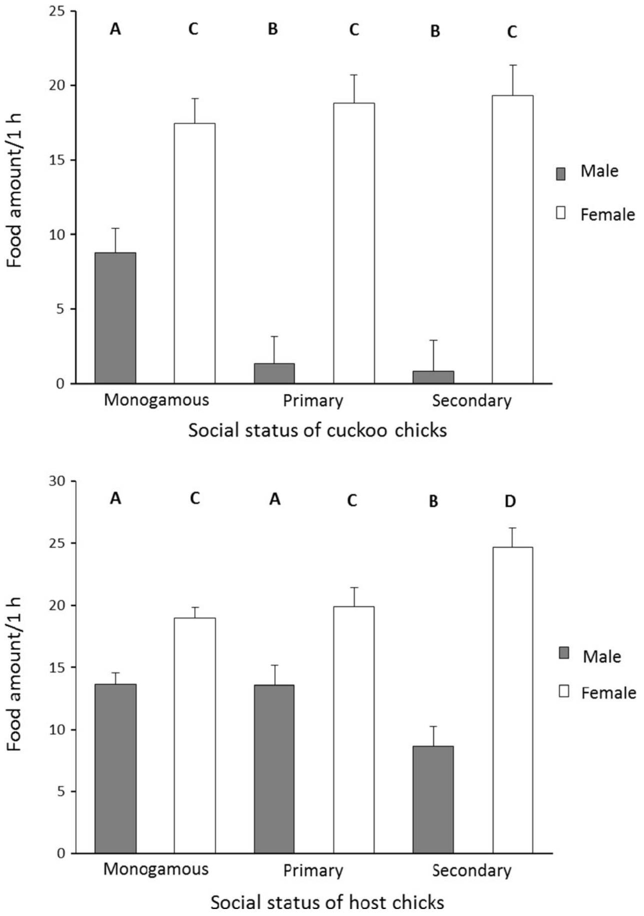

**Fig. 1** Host/parent sex-specific differences in amount of food delivered to cuckoo and host chicks for three social status categories (means+SE from full models). Statistical significance ($P<0.05$) is indicated by *different letters above the bars*

cuckoo in the simultaneous nest. In contrast to males, females generally brought a similar amount of food to broods of different social status, with the exception of secondary females and their own nestlings, where females compensated for poor male investment by providing more food. Though the total amount of food supplied to cuckoo and host chicks did not differ with social status, secondary cuckoos tended to receive the lowest total amount of food.

Compared with monogamous males, polygynous males may not physically be able to allocate their investment equally when provisioning two simultaneous broods. As a result, they prefer primary broods to those of socially lower ranked females (Johnson et al. 1993; Rodrigues 1996; Sejberg et al. 2000; Forstmeier et al. 2001a; but see Pinxten and Eens 1994), possibly because of the higher potential reproductive value of the former or simply because hatching order acts as a cue. In this respect, our findings on host nestlings correspond well with those reported for other great reed warbler populations (Dyrcz 1986; Bensch and Hasselquist 1994; Sejberg et al. 2000) or other socially polygynous species (e.g. Alatalo et al. 1981; Urano 1990; Smith and Sandell 1998). Nevertheless, we showed that when males provisioned two broods simultaneously, the older the one brood, the less food they brought to their own nestlings in the other brood. The males fed their own offspring more, however, when the simultaneous nest contained a cuckoo. This preference for its own chicks over the brood parasite is the most likely explanation for the extremely low amount of food provided by polygynous males to cuckoos. This lack of male investment in cuckoo chicks is opposite to the findings of Grayson et al. (2013) in socially polygynous red-winged blackbirds (*Agelaius phoeniceus*). They observed that presence of a parasite in a brood of host chicks was associated with a higher incidence of paternal host care (even in polygynous males) than when the parasite was absent. The brood parasite in this case, however, was the brown-headed cowbird (*Molothrus ater*), which is reared alongside the host's offspring (unlike the cuckoo). As non-evicting parasites are stronger competitors than their host nest-mates, parasitised adults should benefit from investing more in mixed broods as it is likely to be the only way to promote survival of at least some of their own nestlings (Holen and Johnstone 2007). Alternatively, mixed broods of host and parasitic chicks may be larger or may beg more loudly than non-parasitised broods, which could force the foster parents to invest more in provisioning the parasite. In either case, the extra male contribution to feeding is likely to alleviate the costs of parasitism (Grayson et al. 2013).

In some socially polygynous species, females of monogamous and polygynous males differ in their inherent characteristics (Forstmeier et al. 2001a, b; Moreno et al. 2002; Griggio et al. 2003; Pilastro et al. 2003), which can affect female reproductive output irrespective of male help (Moreno et al.

**Table 2** Amount of food brought to the focal nest by polygynous males in relation to age and type (cuckoo/host) of the simultaneous brood

| | | Focal nest | | | |
|---|---|---|---|---|---|
| | | Cuckoo | | Host | |
| Food brought by polygynous male/1 h~ | *df* | *F* | *P* | *F* | *P* |
| *Number of nestlings in focal nest* | 1 | – | – | *11.96* | *0.003* |
| *Age of simultaneous brood* | 1 | 0.63 | 0.440 | *5.90* | *0.026* |
| *Type of simultaneous brood (cuckoo/host)* | 1 | 0.40 | 0.537 | *9.76* | *0.006* |

Significant predictors are given in *italics*

**Table 3** Results of Kruskal–Wallis ANOVA, median and 25 and 75 % quantiles for growth parameters of cuckoo and host chicks reared in monogamous, primary and secondary nests

| | Monogamous | | | Primary | | | Secondary | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 25 % | Median | 75 % | 25 % | Median | 75 % | 25 % | Median | 75 % | $\chi^2$ | *P* |
| Cuckoo chicks | | | | | | | | | | | |
| *b* | −0.39 | −0.35 | −0.32 | −0.42 | −0.40 | −0.37 | −0.41 | −0.35 | −0.34 | 6.00 | 0.050 |
| *d* | 76.55 | 86.00 | 92.31 | 71.56 | 79.79 | 87.63 | 57.75 | 71.36 | 87.06 | 4.20 | 0.122 |
| *e* | 8.52 | 8.94 | 9.64 | 8.28 | 8.93 | 9.63 | 7.80 | 9.12 | 9.78 | 0.02 | 0.991 |
| Host chicks | | | | | | | | | | | |
| *b* | −0.57 | −0.53 | −0.50 | −0.61 | −0.57 | −0.44 | −0.58 | −0.55 | −0.53 | 0.51 | 0.776 |
| *d* | 23.78 | 25.55 | 27.74 | 22.08 | 25.49 | 29.14 | 22.38 | 25.31 | 27.44 | 0.67 | 0.714 |
| *e* | 4.98 | 5.41 | 6.01 | 4.56 | 5.27 | 6.24 | 5.01 | 5.20 | 5.46 | 1.04 | 0.594 |

Parameters were derived from the three-parameter logistic model: *d* asymptotic mass, *b* measure of nestling growth rate, and *e* inflection point on the growth curve. For more details, see “Methods” section

2002). In this respect, some females are better suited to raising their progeny without male assistance than others and polygynous males then adjust their paternal effort to the female’s ability (Forstmeier et al. 2001b). While none of the female great reed warbler social status categories differ in body mass and intensity of egg shell coloration (Honza et al. 2011; Trnka and Prokop 2011), they may still differ in other traits (not measured by us) or parenting quality. If so, then adjustment of male care in response to female traits might explain the decreased investments of polygynous males in our study.

We expected that the females of polygynous males (especially secondary females) would provide more food to nestlings in response to lower male investment (Sejberg et al. 2000; Forstmeier et al. 2001b; Redpath et al. 2006). Nevertheless, only secondary females exhibited such behavioural compensation when feeding their own young. Surprisingly, primary and secondary females caring for a cuckoo did not increase the amount of food delivered. It would appear that they manage to provide for the cuckoo singlehandedly, without the need to compensate for reduced male assistance. Our unpublished data support this assumption, with a 9-day-old cuckoo weighing around 44.6±6.3 g (mean±SD; $n$=53), half the weight of an average host brood (four nestlings) of the same age (89.1±8.4 g; $n$=16). Moreover, the young parasite was supplied with less food (29.9±9.9; $n$=14) than the average host brood (45.6±11.7; $n$=13), suggesting that it is cheaper for the hosts to nurture the cuckoo, at least in terms of provisioning effort exerted at this age. How great the host

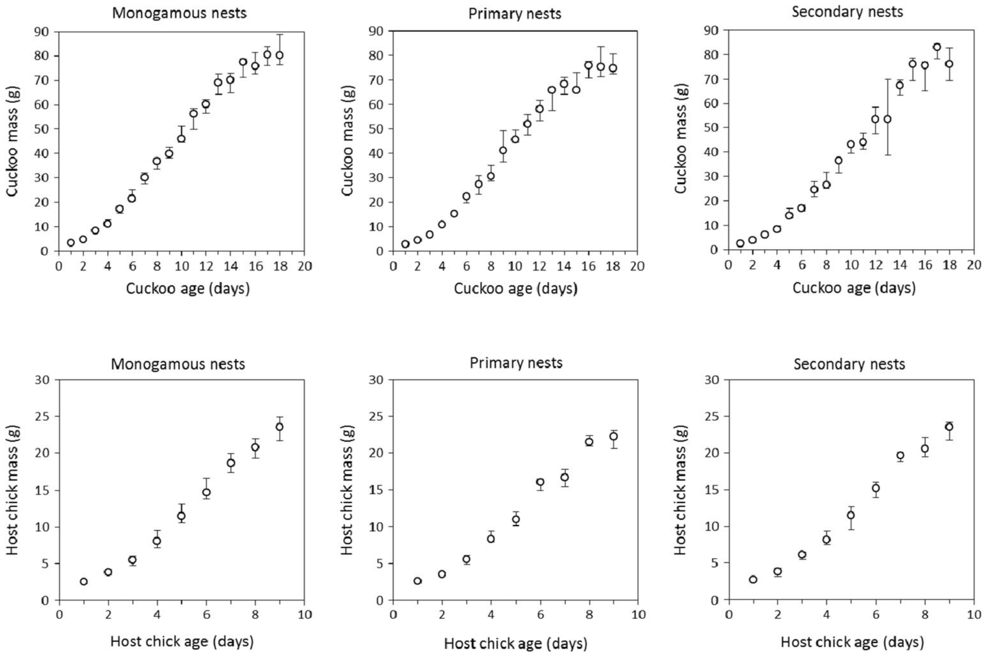

**Fig. 2** Growth performances of cuckoo and host chicks for three social status categories. *Circles* denote medians and *whiskers* interquartile ranges. For more details, see “Methods” section

work load becomes later, when the brood parasite reaches a similar mass to the average host brood, and what effect it has on foster parent's physical state deserve further examination.

Studies on socially polygynous species suggest that reduced paternal feeding decreases current female reproductive success (Yasukawa et al. 1990; Patterson 1991; Pinxten and Eens 1994). While this may sometimes also concern primary females (Huk and Winkel 2006; Ferretti and Winkler 2009; but see Czapka and Johnson 2000), it is most often the secondary females that suffer the higher costs of polygyny, raising fewer or lower quality (under-sized or under-weight) young (Whittingham 1989; Yasukawa et al. 1990; Johnson et al. 1993). Here, we explored nestling growth under conditions of parental conflict over male care, which we showed to be most pronounced in secondary nests. Contrary to our expectations, we did not find any significant difference in growth performance between either cuckoos or host nestlings of three social status categories. Only primary cuckoos tended to grow more rapidly, though this did not speed up their fledging times compared to that of monogamous or secondary cuckoos (our unpublished data). Indeed, support for a deterioration in nestling growth rate or for lower fledgling mass in secondary nests is generally mixed (Leonard 1990; Patterson 1991; Johnson et al. 1993; Bensch 1996; Smith and Sandell 1998; Forstmeier et al. 2001a; Grønstøl et al. 2013). In cuckoos, however, the results may be biased by the secondary chicks that died before their growth parameters could be obtained (and hence were not considered in the analysis). As secondary cuckoos exhibited much lower fledging success than monogamous cuckoos (33 vs. 76 %; Trnka et al. 2012), we cannot exclude the possibility that sexual conflict over paternal care has an effect on growth. Although statistically non-significant, secondary cuckoos received the lowest total amount of food per hour (see "Results" section). Over the long term, however, a reduced food supply may have a biologically significant impact on their viability. Moreover, food quality (in addition to quantity) is known to positively influence chick growth, its subsequent survival and reproduction (Martin 1987; Starck and Ricklefs 1998). Higher investment by polygynous males, therefore, may be beneficial to nestlings and particularly cuckoos.

Despite the failure of secondary cuckoos (see above), the brood parasite still obtains benefit from exploiting the great reed warbler. Compared to the sympatric, but three times smaller, reed warbler (*Acrocephalus scirpaceus*), even secondary cuckoos of great reed warblers achieve a higher asymptotic mass (71.4 g; Table 3) than those fostered by reed warblers (median, interquartile range 64.4 g, 56.7–74.7 g, *n*=34; our unpublished data). Probably, it is the high amount or nutritional value of food and more aggressive nest defence which make the great reed warbler a good-quality host (Kleven et al. 1999, 2004; Grim 2006). Further exploration of these issues within the context of polygyny or sexual conflict will be a challenging task for future studies.

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**Conflict of interest** The authors declare that they have no conflict of interest.

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