



Original Article

No immediate or future extra costs of raising a virulent brood parasite chick

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Parental care is an adaptive behavior increasing the survival of a young. Virulent brood parasites, like the common cuckoo *Cuculus canorus*, avoid the parental care and leave the care for their nestlings to hosts. Although raising a cuckoo is always costly because it kills host's progeny, to date it is not known whether raising of a brood parasite itself represents any extra cost affecting host's fitness, that is, a cost above the baseline levels of care that are expended on raising the host own young anyway. We quantified costs of rearing a cuckoo nestling in the most frequent host, the reed warbler *Acrocephalus scirpaceus*. We measured changes in the host physical (body mass) and physiological conditions (stress levels quantified via heterophils/lymphocytes ratio) within the 1 breeding attempt (immediate cost) and retrapped some of these adults in the next breeding season to estimate return rates as a measure of their survival (future cost). In contrast to universal claims in the literature, raising a cuckoo nestling did not entail any extra immediate or future costs for hosts above natural costs of care for own offsprings. This counterintuitive result might partly reconcile theoretical expectations in the hosts with surprisingly low levels of counter-defences, including the reed warbler. Unexpectedly low raising costs of parasitism may also help explain a long-term maintenance of some host–parasite systems.

Key words: brood parasitism, coevolution, common cuckoo, reed warbler.

INTRODUCTION

Parental effort is costly in many respects (Royle et al. 2012). Such costs play a crucial role in the evolution of avian life histories (Stearns 1976) and shape the evolution of alternative nesting strategies. Brood parasites represent an extreme alternative breeding strategy: they evade costly parenthood by laying their eggs into foreign nests and manipulate host parents to foster nonrelated young, negatively affecting fitness of parasitized individuals (Davies 2000; Feeney et al. 2014).

Both theoretical models and empirical studies assume that the parasitism is highly costly for hosts (Davies 2000; Holen et al. 2001; Stokke et al. 2007a). Adult parasites can eliminate some or all host progeny during the egg stage (Wyllie 1981; Astie and Reboreda 2006) and nestling parasites can directly kill (Spottiswoode and Koorevaar 2012), evict (Honza et al. 2007; Grim et al. 2009a), or outcompete (Kilner et al. 2004) host nestlings (hereafter “lost progeny cost”). However, these are not the only costs hosts suffer: rearing a parasite can also impose extra physiological and physical costs via the parental effort increased above the levels necessary to

raise own offspring within a breeding attempt (hereafter “immediate costs”; Hauber and Montenegro 2002; Mark and Rubenstein 2013) and decreased parental survival (Payne and Payne 1998; Hoover and Reetz 2006; Koleček et al. 2015) or lower potential to reproduce in future (Hauber 2006) (hereafter “future costs”). Therefore, extra costs might negatively affect host's fitness in the next breeding attempts via trade-offs between the current and future reproduction and consequently influence evolutionary arms-race between brood parasites and their hosts. For example, selection on counter-defences should be stronger in a host population experiencing high immediate costs compared with the one with low immediate costs, assuming all other factors (such as lost progeny cost) being equal.

In one of the best studied brood parasites, the common cuckoo (*Cuculus canorus*; hereafter “cuckoo”), most studies focused on the lost progeny costs across various host species (Wyllie 1981; Brooke and Davies 1989; Øien et al. 1998; Moksnes et al. 2000; Samaš et al. 2016). Only a handful of studies quantified the immediate (Brooke and Davies 1989; Grim and Honza 1997; Kilner et al. 1999; Samaš et al. 2018) or future costs in hosts (Koleček et al. 2015). The rarity of such studies reflects logistical constraints: particularly challenging is studying future costs of raising the cuckoo,

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especially in hosts that are short-lived and/or show low breeding philopatry (Hoover and Hauber 2007).

Here, we quantified the immediate and future costs of raising a cuckoo in its regular host, the reed warbler (*Acrocephalus scirpaceus*) (Stoddard and Kilner 2013; Mikulica et al. 2017). Reed warbler is a small (12 g), regularly parasitized cuckoo host across the whole Europe (Stokke et al. 2007b; Moksnes et al. 2008) including our study site (parasitism rate 11%; Jelínek et al. 2016a). Reed warblers breed at our study site from May to early August and typically raises 3–4 nestlings per brood (range 1–6, average and mode 3.5; Brooke and Davies 1989; Grim and Honza 1997; this study). In parasitized broods, the young cuckoo always evicts all host eggs or nestlings and monopolizes the parental care (Honza et al. 2007).

To quantify immediate costs, we measured within-individual changes in the physical (body mass) and physiological (heterophils/lymphocytes ratio, hereafter “H/L ratio”) characteristics during the nestling stage in parents raising own and cuckoo nestlings. Body mass and H/L ratio are commonly used measures of physical and physiological stress during a breeding (Rands et al. 2006; Davis et al. 2008). We measured the changes within the two comparative time intervals; in the first week, posthatch (7 days posthatch for both reed warblers and cuckoo, hereafter “young cuckoos”) and after nestlings reach the growth asymptote (7 days posthatch for reed warblers and 16 days for cuckoos, hereafter “old cuckoos”). We estimated the energetic demands of own and cuckoo nestlings using the formula based on allometric relations between postnatal growth rate and energetics (Weathers 1992; see Methods). We predicted that raising the cuckoo should be on average 0.6 times less demanding within the first week posthatch, whereas 2.8 times more demanding after reaching growth asymptote compared with an average reed warbler brood. We assumed that these different energetic demands of a cuckoo and host nestlings will be similarly reflected in the physical and physiological states and in the feeding effort of their (foster) parents. Feeding effort was also measured to make our study quantitatively comparable with previous studies (Brooke and Davies 1989; Grim and Honza 1997; Kilner et al. 1999). To quantify future costs, we examined whether potential immediate costs of raising cuckoo nestlings can translate into future costs, that is, reduced return rates of their foster parents in the subsequent years.

METHODS

Fieldwork was conducted in Czech Republic at fishponds located between Hodonín and Mutěnice (48°53′ N, 17°03′ E) from May to July 2012–2016. We searched for nests in the littoral vegetation and monitored active nests to determine precise day of hatching. The natural parasitism rate of reed warbler nests decreased during the study period (2012—20%, $n = 113$; 2013—12%, $n = 98$; 2014—5%, $n = 168$) causing a very low natural cuckoo fledgling productivity, which prevented us to obtain sufficient sample sizes of naturally parasitized nests. Thus, we transferred majority of cuckoo hatchlings (23 of 27 cuckoo nestlings used in the study) from deserted or multiply parasitized great reed warbler nests (parasitism rate > 50%; Jelínek et al. 2015) into randomly chosen reed warbler nests. These cuckoos hatched either naturally in great reed warbler nests ($n = 5$) or in the incubator and these were transported into the focal reed warbler nests immediately after they hatched ($n = 18$). We did not manipulate a host clutch or brood after we transferred the cuckoo into a recipient nest (i.e., host progeny was removed

naturally via cuckoo eviction behavior). A previous experimental (cross-fostering) study in our study site confirmed that the cuckoo chick growth is determined rather by the host species identity and is not affected by a cuckoo genetic race (i.e., gens: Kleven et al. 1999; see Grim and Samaš 2016; Požgayová et al. 2018), suggesting that transfer of cuckoo eggs did not affect our results (see also Žabková 2016). Furthermore, adult cuckoos can target hosts nonrandomly as reported in related species, great reed warblers (i.e., selecting in terms of higher quality hosts; Poláčiková et al. 2009; and/or in terms of mimicry Honza et al. 2014). However, adult cuckoos probably did not parasitize parents of higher quality in our reed warbler population because we found no difference in adult body mass on nest hatching day between individuals naturally parasitized by cuckoos (mean \pm SD: 12.4 \pm 0.7 g, $n = 14$ individuals) or not (12.4 \pm 0.9 g, $n = 87$; Welch’s t -test $t_{20,2} = 0.07$, $P = 0.94$). This suggests that transferring cuckoo hatchlings into randomly chosen nests did not bias our results.

Timing of reed warbler capture

Within a single breeding attempt, we mist-netted reed warbler parents twice. All adults were caught on the day after nestlings hatched (range 0–2 days, 0 = hatching day of the first chick in the brood) and second time on the day 7 posthatch (median = 7, range 5–10; own or cuckoo) or on the day 16 posthatch (median = 16, range 13–17; cuckoos only because reed warblers fledge when 12 days old; Grim 2007). If the first mist-netting attempt was unsuccessful, we caught parents 1–2 days later. Parents fostering cuckoo nestlings were caught for a second time randomly either on the day 7 (first comparative period) or 16 (second comparative period) posthatch. All individuals were marked with a unique combination of a standard aluminum ring and up to 3 colored plastic rings. We set the timing of mist-netting of the 2 comparative periods (7- and 16-day intervals) for the following reasons.

First comparative period was set in a way that controlled for the temporal exposure, that is, reed warblers at parasitized and nonparasitized nests expended their care for the same length of time. Reed warbler nestlings become restless and may prematurely fledge due to a human disturbance (handling or setting the mist-net nearby the focal nest) when they are older than 9 days (Grim 2007; Leisler and Schulze-Hagen 2011). Therefore, we timed the latter mist-netting at the end of the period when it was safe to capture parents and at the same time we avoided the risks of premature fledging of their own nestlings. We also mist-netted hosts at parasitized nests so that we compared the same temporal period of parental care for both own and parasite nestlings. There was no difference in the age of reed warbler nestlings (mean \pm SE: 8.3 \pm 0.1 days) and young cuckoos during the first capture (8.5 \pm 0.2 days; Welch’s t -test $t_{41,0} = 0.62$, $P = 0.54$).

Second comparative period was set in a way enabling us to compare the total cost of care per whole nestling period which, however, inevitably differs markedly between our study species. Cuckoo (112 g) is a larger species than all host species including reed warblers (12 g; Leisler and Schulze-Hagen 2011). This leads to a longer period of growth manifested in a longer nestling period of cuckoo nestlings compared with their hosts. Natural fledging ages of cuckoos fostered by reed warbler varies between 17 and 21 days (Grim 2006) and only between 11 and 12 days in own nestlings (Grim 2007). This prevented the direct comparison in later stages of cuckoo nestling period as host own nestlings at such stage are already fledged.

This length of the second comparative period takes into account all parental effort needed to raise an own brood or a parasite nestling to fledging. As explained above, for nonparasitized broods, this period was limited to the first week posthatch. In contrast, cuckoo nestlings do not prematurely fledge due to a human-caused disturbance almost up to the moment of natural fledging (Grim et al. 2003; Grim 2007; Mikulica et al. 2017). To maximize data collection (i.e., to avoid losing data from cuckoos that fledged early), we set the timing of mist-netting of hosts caring for old cuckoo nestling (16.7 ± 0.4 days; range 13–20 days) at the lower end of the variation in fledging ages (17–21 days; Grim 2006). Importantly, the comparisons of own versus parasite treatments were also matched ontogenetically: to finish the linear phase of growth and to enter the asymptotic phase of growth (Grim et al. 2009b), the reed warbler nestlings need ca. 7 days (data from Grim 2007) and cuckoo nestlings need ca. 16 days (figure 1a in Grim 2006; this pattern holds for any cuckoos irrespective of the host species: figure 2 in Grim and Samaš 2016; Li et al. 2016; Požgayová et al. 2018). In both cases, this is shortly before both host own and parasite nestlings typically fledge (Grim 2007). All of these data come from our study population and thus are quantitatively directly comparable.

We also performed the extensive mist-netting using 100–200 m mist-net lines at several plots within our study site twice (in June and July in 2012–2016) per each breeding season with the consistent spatio-temporal effort each season. This allowed us to examine the return rate of reed warblers with a known parasitism status in the previous year (i.e., individual raising cuckoo or own brood). Additionally, we employed an alternative test using a survival model which explicitly corrected for the probability of (re)capture and considered the fate of each individual from the first capture onward (i.e., not only the next year after capture).

Body mass and H/L ratio

During the first and latter mist-netting of adults, we took blood samples and measured body mass (Pesola spring balance, precision 0.25 g). Body mass was used as the only measure of a physical condition because it best reflects a physical change within the same individual and during a short-term time interval (see below).

We used a syringe to take a drop (20 μ L) of blood from the brachial vein to make 2 blood smears immediately after capture of the adult. We left the fresh blood smears to dry out and stored it in a plastic, dark box and an experienced person (see Acknowledgments) later evaluated the number of heterophils and lymphocytes in the lab. We decided to analyze hematological parameters rather than glucocorticoids hormones, such as corticosterone because corticosterone levels rise immediately after the capture of wild animals (Romero and Reed 2005). Contrarily, leukocytes do not rise immediately after capture and H/L ratio is well-established as a common physiological indicator of a prolonged stress in wild animals (e.g., parental effort), with a documented positive relationship between H/L ratio and stress (Davis et al. 2008).

Feeding frequency

We used a camcorder (JVC GZ-MG 730E, 20E, or 155E) to video-record all focal nests twice: first, during the early nestling stage to confirm that each host parent was correctly assigned by us to its nest and, second, during the later nestling stage for analyses of feeding frequencies. We performed the second recordings when reed warbler broods were 7–11 days old (median = 9 days; $n = 21$ nests), young cuckoos 8–12 days (median = 11 days, $n = 11$), and

old cuckoos 15–20 days (median = 17.5 days, $n = 10$). Each of these video-recordings lasted 3–4 h but we always analyzed only 1 h. In each recording, we excluded at least the first 30 min to ensure sufficient habituation period of parents (for details see Jelinek et al. 2016b).

Nestlings energy demands

We used the known positive relationship between costs of parental care and nestling demands (e.g., Nur 1984) to predict how many times more or less demanding for host parents the raising a cuckoo nestling compared with an average host brood should be (see Introduction). We estimated energetic demands per nestling as daily metabolized energy (DME, $\text{kJ}\cdot\text{day}^{-1}$) according to the formula, $\text{DME} = 5.7 \times \text{mass}^{0.81}$ (Weathers 1992), where “mass” is an average nestling mass at the particular age. Population-average masses of cuckoo and reed warbler nestling were obtained from our study site (own measurements and Grim 2006 [cuckoos]; Grim 2007 [reed warblers]). To estimate energetic demands of raising the cuckoo (see Introduction), we quantified energy budgets (by summing up DMEs) for the specific brood type (cuckoo and own brood) and time periods (7 and 16 days posthatch). Energy budgets of own brood were calculated for an average brood size of 3.5 nestlings ($\text{SE} = 0.2$, $n = 28$ broods) which corresponds to an average brood size in our study population found in previous studies (3.5 nestlings in Grim and Honza 1997).

STATISTICAL ANALYSES

Immediate costs

Response variables of parental “change in body mass” (continuous; in grams) and “change in H/L ratio” (continuous) were calculated as difference scores of measurements, that is, the measurement at the second capture minus the measurement at the first capture (following Bonate 2000). The response variable of “feeding frequency” (counts; feeds delivered $\cdot \text{h}^{-1}$) had a right-skewed distribution and we used a negative binomial regression with log-link function, which fitted our data better than a Poisson regression (results not shown).

Before executing main analyses, we first tested only within reed warbler broods if variation in parental “change in body mass,” “change in H/L ratio” (dependent variables with normal distribution), and “feeding frequency” (negative binomial distribution) can be explained by the effect of “brood size” (range 2–6 nestlings for changes in body mass and H/L ratio and 3–5 for feeding frequency). Brood size could not be included in the main models because of high collinearity (see Zuur et al. 2010) with the predictor of main interest, “brood type” (categorical: reed warbler, young cuckoo, and old cuckoo): parasitized clutches always contained only a single cuckoo nestling (Honza et al. 2007), whereas nonparasitized broods always contained more than 1 nestling (see above). The full linear model contained the same set of predictors as in the main analyses (see below) except for “brood type.” Brood size from both full and final models showed a significant effect of this predictor on “parental body mass” (larger brood sizes were associated with higher decreases in parental body mass; brood size estimate = -0.18 ± 0.08 ; $F_{2,47} = 4.64$, $P = 0.04$) but not on “H/L ratio” (-0.01 ± 0.03 ; $F_{1,34} = 0.15$, $P = 0.70$) and “feeding frequency” (1.00 ± 2.37 ; $F_{1,19} = 0.18$, $P = 0.68$). We therefore reanalyzed all statistical models where we included only nests containing a cuckoo and an average reed warbler brood of 3 and 4 nestlings.

These reanalyses led to similar estimates and the same conclusions as the main analyses with all data pooled (see Results).

We tested effects of predictors “brood type” (see above) and “parental sex” (categorical; male vs. female) on the response variables of parental “change in body mass,” “change in H/L ratio,” and “feeding frequency” during the first week of the nestling period. Both were predictors of main interest and remained in all models regardless of their significance (Grafen and Hails 2002). We further included potential confounding variables: “year” (categorical) and “ordinal date of the first capture” (continuous; 1 = 1st January). The predictor “year” controlled for a temporal between-year variation and given the logic behind using random effects in statistics, it should also be treated as a random effect because we did not have any specific year-based prediction. However, we treated it in all analyses only as a fixed predictor because it had only 3 levels, whereas at least 5 levels are recommended for random effects (Bolker 2015).

In models with response variables, parental “change in body mass” and “change in H/L ratio,” we included also “initial mass” (continuous; parental body mass measured at the first capture) and “initial H/L ratio” (continuous; parental H/L ratio measured at the first capture), respectively. These controlled for effects of between-individual differences in parents. In the 2 respective models, we further added 2-way interactions “parental sex” with “initial mass” or “parental sex” with “initial H/L ratio” as both parental sexes usually differ in their effort during breeding (Kleindorfer et al. 1995; Jakubas et al. 2013; Požgayová et al. 2015).

We included the 2-way interaction between “brood type” and “parental sex” in all statistical models because parental sexes could differ in their care when nurturing own or brood parasite nestlings (Jakubas et al. 2013; Požgayová et al. 2015). In the models with “feeding frequency” as a response variable, we replaced “date of the first capture” by “hatching date” and additionally included the potential confounding variable “daytime” (continuous; hour video-recording started) and its quadratic polynomial term “daytime².” Predictor “parental sex” (continuous) was here coded as the proportion of feedings by male to overall number of feedings per hour because the response variable “feeding frequency” was a sum of male and female frequencies per nest and therefore it was not possible to use a categorical predictor (male vs. female) under such conditions.

Future costs

We examined return rates to the next breeding season in parents who raised an own brood ($n = 27$ females and 25 males) or a cuckoo nestling ($n = 26$ females and 23 males). We analyzed return rates using a generalized linear model with the binary response “parent

re-trapped” (yes or no) in the next breeding season. The predictor of main interest was the “brood type” being raised by an individual parent (categorical: own brood or cuckoo). In the full model, we included additional predictors of “parental sex” (categorical: male or female) and “year” of recapture or resighting (categorical: years 2013, 2014, and 2015). We additionally calculated a survival model to examine whether the apparent survival of parents (corrected for the probability of capture) differs according to “brood type” and “parental sex.” We used mist-netting data from seasons 2012–2016. “Brood type” was directly known only for the season when we examined parents/hosts for immediate costs. However, low natural parasitism rates suggest that the parents always reared own brood during the other seasons (note that majority of the broods containing a cuckoo were parasitized artificially by us anyway).

We report both full and final model outputs (Forstmeier and Schielzeth 2011). We selected final models by the backward elimination of nonsignificant terms (Grafen and Hails 2002). This was accomplished by examining the significance of predictors sequentially while keeping the predictors of main interest (see above) in the model regardless of its significance. All continuous predictors involved in interaction terms were centered around their means to make main effects biologically interpretable when included in interactions (Schielzeth 2010). Potential collinearity among covariates was satisfactory with variance inflation factors < 1.5 for all predictors (Zuur et al. 2010). We checked the distribution of residual errors in statistical models with identity link and assumed these approximately normally distributed (Grafen and Hails 2002).

All analyses were conducted in R 3.4.3 R Core Team 2017. Results are shown as estimates \pm s.e. from final models.

RESULTS

Immediate costs

Reed warbler parents rearing own broods and both young and old cuckoos decreased in body mass between the first and second captures (Tables 1 and 2). Parents decreased body mass in similar rate regardless of the brood type they raised (Tables 1 and 2). Females decreased their mass more than males and initially heavier parents decreased in mass significantly more (Table 2). The same conclusions were reached for the subset of data including only average brood size of own broods (Table 3).

Change in H/L ratio between the first and second capture did not differ between parents rearing own broods and both young and old cuckoos and neither differed between parental sexes (Tables 1 and 4). Parents with higher stress levels (H/L ratio) during the first capture (higher initial H/L ratio) showed lower increase in their stress levels regardless of the brood type raised (Table 4). The same

Table 1
Summary statistics for immediate cost measures calculated from the raw data

Brood type	Parental sex	Change in body mass		Change in H/L ratio		Feeding frequencies	
		<i>n</i>	mean \pm SE	<i>n</i>	mean \pm SE	<i>n</i>	mean \pm SE
Own brood	Female	27	-1.01 ± 0.16	16	0.02 ± 0.04	21	15.2 ± 1.1
	Male	23	-0.50 ± 0.17	20	0.07 ± 0.04	21	13.8 ± 1.4
Young cuckoo	Female	14	-1.39 ± 0.21	11	0.03 ± 0.04	11	15.5 ± 1.5
	Male	11	-0.70 ± 0.16	10	0.07 ± 0.03	11	9.1 ± 1.8
Old cuckoo	Female	11	-1.02 ± 0.23	10	0.05 ± 0.06	10	12.2 ± 2.4
	Male	8	-0.12 ± 0.21	8	0.04 ± 0.08	10	8.5 ± 3.6

Sample size (*n*) represents the number of cuckoos or reed warbler broods (i.e., own nestlings). SE = standard error of mean.

Table 2

Outputs of full and final models for the response variable of change in body mass of parents rearing the cuckoo ($n = 44$) or an own brood ($n = 50$; 2–6 nestlings)

Predictor	Full model			Final model		
	<i>F</i>	<i>P</i>	Estimate ± SE	<i>F</i>	<i>P</i>	Estimate ± SE
	Adjusted $R^2 = 0.48$			Adjusted $R^2 = 0.49$		
Intercept	16.64	0.0001	−0.72 ± 0.18	33.74	<0.0001	−0.63 ± 0.11
Brood type	0.68	0.51	—	0.90	0.41	—
Parental sex [M]	2.79	0.10	−0.29 ± 0.17	6.38	0.01	−0.32 ± 0.13
Initial body mass	19.00	<0.0001	−0.54 ± 0.12	60.82	<0.0001	−0.55 ± 0.07
Date	0.03	0.87	−0.001 ± 0.006	—	—	—
Year	1.21	0.30	—	—	—	—
Brood type*sex	0.39	0.68	—	—	—	—
Sex*Initial mass	0.06	0.81	0.04 ± 0.15	—	—	—

“Parental sex” and “brood type” are predictors of main interest and are kept in models regardless of their significance. The predictor “brood type” included 3 levels: an own brood (parental care of 7 days), a young cuckoo (7 days), and an old cuckoo (16 days). Numerator degrees of freedom is 1 in all cases except for “brood type” and “year” with $df = 2$. We did not report estimates (only F and P values given) for predictors with more than 2 categories. “[M]” = male is a reference level.

Table 3

Outputs of full and final models for the response variable of change in body mass of parents rearing the cuckoo or an average own brood ($n = 35$; 3 and 4 nestlings)

Predictor	Full model			Final model		
	<i>F</i>	<i>P</i>	Estimate ± SE	<i>F</i>	<i>P</i>	Estimate ± SE
	Adjusted $R^2 = 0.50$			Adjusted $R^2 = 0.52$		
Intercept	17.85	0.0001	−0.84 ± 0.20	31.83	<0.0001	−0.68 ± 0.12
Brood type	0.85	0.43	—	1.06	0.35	—
Parental sex [M]	6.76	0.06	−0.39 ± 0.20	7.94	0.006	−0.38 ± 0.13
Initial body mass	11.23	0.001	−0.43 ± 0.13	50.84	<0.0001	−0.52 ± 0.07
Date	0.11	0.74	0.002 ± 0.006	—	—	—
Year	1.18	0.31	—	—	—	—
Brood type*sex	0.45	0.64	—	—	—	—
Sex*Initial mass	0.58	0.45	−0.12 ± 0.16	—	—	—

“Parental sex” and “brood type” are predictors of main interest and are kept in models regardless of their significance. The predictor “brood type” included 3 levels: an own brood (parental care of 7 days), a young cuckoo (7 days), and an old cuckoo (16 days). Numerator degrees of freedom is 1 in all cases except for “brood type” and “year” with $df = 2$. We did not report estimates (only F and P values given) for predictors with more than 2 categories. “[M]” = male is a reference level.

conclusions were reached for the subset of data including only average brood size of own broods (Table 5).

Reed warbler broods were on average fed at higher frequencies than both young and old cuckoos (Tables 1 and 6). The differences in the feeding frequency were statistically significant only between own broods and old cuckoos (Table 6; Tukey post hoc test: estimate ± SE = 0.30 ± 0.09, $z = 3.32$, $P = 0.002$). Male parents fed on average with lower frequencies than females (Tables 1 and 6). The same conclusions were reached for the subset of data including only average brood size of own broods (Table 7).

Future costs

In total, we retrapped 16 (7 females and 9 males) out of 101 individuals the next season after they raised a cuckoo ($n = 9$ individuals) or an own brood ($n = 7$). Analysis of return rates did not show differences between individuals raising an own brood ($13.5 \pm 4.8\%$, $n = 53$) or a cuckoo ($18.4 \pm 5.6\%$, $n = 48$; $\chi^2 = 0.46$, $p = 0.50$). Neither parent sex ($\chi^2 = 0.60$, $p = 0.44$) nor year of retrap

($\chi^2 = 0.35$, $p = 0.84$) explained variation in return rates and these predictors were excluded from the final model.

We reanalyzed the data for the same set of individuals using a survival model correcting for the probability of capture. This reanalysis showed that the apparent survival estimates were very similar for parents rearing an own brood ($\phi = 0.370$, 95% CI: 0.217–0.554) and the cuckoo ($\phi = 0.367$, 95% CI: 0.216–0.549). Likewise, apparent survival estimates were similar for male ($\phi = 0.420$, 95% CI: 0.260–0.599) and female parents ($\phi = 0.305$, 95% CI: 0.168–0.488). Additionally, lowest AIC for the model without covariates (164.9) compared with the one which included the effect of brood type (167.0) or parental sex (165.7) suggested that the survival of parents was not significantly affected by any of these factors.

DISCUSSION

Several measures of immediate parental costs, namely, changes in body mass, H/L ratio (indicating stress level), and feeding

Table 4

Outputs of full and final models for the response variable of change in H/L ratio of parents rearing the cuckoo ($n = 39$) or an own brood ($n = 36$; 2–6 nestlings)

Predictor	Full model			Final model		
	F	P	Estimate \pm SE	F	P	Estimate \pm SE
	Adjusted $R^2 = 0.08$			Adjusted $R^2 = 0.05$		
Intercept	0.16	0.69	0.02 \pm 0.05	5.34	0.02	0.07 \pm 0.03
Brood type	0.03	0.97	—	0.003	0.99	—
Parental sex [M]	2.77	0.10	-0.09 \pm 0.05	1.44	0.23	-0.04 \pm 0.04
Initial H/L ratio	4.68	0.03	-0.34 \pm 0.16	7.38	0.008	-0.33 \pm 0.12
Initial body mass	0.05	0.82	-0.006 \pm 0.02	—	—	—
Date	1.47	0.23	-0.002 \pm 0.002	—	—	—
Year	1.68	0.20	—	—	—	—
Brood type*sex	0.34	0.71	—	—	—	—
Sex*Initial H/L	3.28	0.07	-0.52 \pm 0.29	—	—	—

“Parental sex” and “brood type” are predictors of main interest and are kept in models regardless of their significance. The predictor “brood type” includes 3 levels: own brood (parental care of 7 days), young cuckoo (7 days), and old cuckoo (16 days). Numerator degrees of freedom is 1 in all cases except for “brood type” and “year” with $df = 2$. We did not report estimates (only F and P values given) for predictors with more than 2 categories. “[M]” = male is a reference level.

Table 5

Outputs of full and final models for the response variable of change in H/L ratio of parents rearing the cuckoo or an average own brood ($n = 25$; 3 and 4 nestlings)

Predictor	Full model			Final model		
	F	P	Estimate \pm SE	F	P	Estimate \pm SE
	Adjusted $R^2 = 0.02$			Adjusted $R^2 = 0.07$		
Intercept	0.01	0.92	0.01 \pm 0.06	3.63	0.06	0.06 \pm 0.03
Brood type	0.09	0.92	—	0.18	0.83	—
Parental sex [M]	1.36	0.25	-0.08 \pm 0.07	1.04	0.31	-0.04 \pm 0.04
Initial H/L ratio	5.72	0.02	-0.48 \pm 0.20	4.57	0.04	-0.33 \pm 0.15
Initial body mass	0.40	0.53	-0.02 \pm 0.03	—	—	—
Date	1.09	0.30	-0.002 \pm 0.002	—	—	—
Year	0.60	0.55	—	—	—	—
Brood type*sex	0.28	0.76	—	—	—	—
Sex*Initial H/L	4.87	0.03	-0.72 \pm 0.33	5.34	0.02	-0.73 \pm 0.31

“Parental sex” and “brood type” are predictors of main interest and are kept in models regardless of their significance. The predictor “brood type” includes 3 levels: own brood (parental care of 7 days), young cuckoo (7 days), and old cuckoo (16 days). Numerator degrees of freedom is 1 in all cases except for “brood type” and “year” with $df = 2$. We did not report estimates (only F and P values given) for predictors with more than 2 categories. “[M]” = male is a reference level.

frequency, showed that there were no extra immediate costs of raising a cuckoo nestling above baseline levels that are expended by parents when not being parasitized by cuckoos anyway. Also similar return rates into subsequent breeding seasons of reed warbler parents rearing the cuckoo or an own brood suggest no future extra costs of the cuckoo parasitism in this frequent cuckoo host.

Specifically, based on avian energetics laws (Weathers 1992), for reed warblers the costs of rearing during the first 7 days posthatch should be on average 0.6 times *lower* when raising the cuckoo than an average reed warbler brood, and raising nestlings to the stage when they reach the growth asymptote (7 days in warblers, 16 days in cuckoos) should be on average 2.8 times more demanding for parents raising cuckoos. In contrast, caring for the cuckoo was on average 0.7 to 1.4 times more demanding during the first 7 days posthatch and only 0.2 to 1.3 times more demanding for the 16-day period (across parental sexes and cost measures: Figure 1a,b; Table

8); however, in all cases, the differences were statistically nonsignificant. Importantly, our present study in the reed warbler provides a more powerful test of extra costs of raising a brood parasite compared with a previous recent study (Samaš et al. 2018) in the common redstart (*Phoenicurus phoenicurus*); this is because in the redstarts an exact quantitative prediction was that raising the cuckoo over the whole nestling period should be only 1.1 to 1.2 times more demanding than raising an own average brood (cf. 2.8 times more demanding in reed warblers). Only few cuckoo hosts are smaller (as for their body size) and only marginally smaller than reed warblers; this suggests that the conclusions of the present study and of Samaš et al. (2018) are general.

Previous studies assessed costs in reed warbler-cuckoo system by comparing feeding frequencies between a host brood and a cuckoo nestling (Brooke and Davies 1989; Grim and Honza 1997; Kilner et al. 1999; Samaš et al. 2018). In line with conclusions of these

Table 6**Outputs of full and final models for feeding frequency of parents rearing the cuckoo ($n = 21$) or an own brood ($n = 21$; 3–5 nestlings)**

Predictor	Full model			Final model		
	χ^2	P	Estimate \pm SE	χ^2	P	Estimate \pm SE
	Adjusted $R^2 = 0.44$			Adjusted $R^2 = 0.38$		
Intercept	—	—	4.78 \pm 0.84	—	—	3.05 \pm 0.09
Brood type	8.55	0.01	—	11.51	0.003	—
Parental sex	4.70	0.03	0.85 \pm 0.39	8.05	0.005	0.41 \pm 0.15
Hatching date	3.26	0.07	-0.009 \pm 0.005	—	—	—
Daytime	0.22	0.64	-0.001 \pm 0.02	—	—	—
Daytime ²	0.39	0.53	0.004 \pm 0.006	—	—	—
Year	1.19	0.55	—	—	—	—
Brood type*sex	0.76	0.68	—	—	—	—

Numerator degrees of freedom is 1 in all cases except for “brood type” and “year” with $df = 2$. We did not report estimates (only F and P values given) for predictors with more than 2 categories.

Table 7**Outputs of full and final models for feeding frequency of parents rearing the cuckoo or an average own brood ($n = 17$; 3 and 4 nestlings)**

Predictor	Full model			Final model		
	χ^2	P	Estimate \pm SE	χ^2	P	Estimate \pm SE
	Adjusted $R^2 = 0.40$			Adjusted $R^2 = 0.17$		
Intercept	—	—	4.81 \pm 1.01	—	—	3.05 \pm 0.09
Brood type	6.77	0.03	—	8.80	0.01	—
Parental sex	4.09	0.04	0.84 \pm 0.42	7.17	0.007	0.41 \pm 0.15
Hatching date	2.35	0.12	-0.009 \pm 0.006	—	—	—
Daytime	0.21	0.65	-0.01 \pm 0.02	—	—	—
Daytime ²	0.46	0.50	0.004 \pm 0.007	—	—	—
Year	1.11	0.57	—	—	—	—
Brood type*sex	0.68	0.71	—	—	—	—

Numerator degrees of freedom is 1 in all cases except for “brood type” and “year” with $df = 2$. We did not report estimates (only F and P values given) for predictors with more than 2 categories.

studies, our results suggest that cuckoo nestling is not fed more often as own brood; in fact, cuckoos were fed even less than host broods. All these results congruently suggest that there is not an extra cost for reed warblers to rear a parasite cuckoo nestling. However, we are aware that feeding frequencies may not reflect load size (Royama 1966; Grim and Honza 2001) or energy content of nestling diet (e.g., secondary females of great reed warblers *Acrocephalus arundinaceus* bring larger mass of food to compensate lower male feeding effort, Sejberg et al. 2000; Požgayová et al. 2015). Specifically, data on load mass in our study population showed that the cuckoo and reed warbler chick of the same mass (compared across the range from 3 to 12 g) were fed at similar frequencies but the cuckoo received higher amount of food (mass of food loads: Grim and Honza 2001). Feeding frequencies themselves thus can be misleading measures of costs of parental effort. We nevertheless believe this is not the case in our study because Grim and Honza (1997) in the same study population found that cuckoos were fed with a similar food mass as an average-sized host brood.

Both parental sexes decreased in body mass and increased their stress level (measured as H/L ratio) during nestling stage. It has been shown that bird species exhibit such trends during the parent-hood for both body mass (reviewed in Rands et al. 2006) and stress

levels (e.g., Bonier et al. 2009; Bonier et al. 2011). Also in our study species, the reed warbler, it has been previously demonstrated that body mass decreases and H/L ratio increases in parents from the laying to nestling period (Jakubas et al. 2013). However, it remained unknown how these parameters change when hosts rear a parasitic cuckoo. Here we showed that the decrease in physical condition and the increase in physiological stress response were similar in parents raising both own brood and parasite nestling. The same conclusions were reported by Samaš et al. (2018) in the only cavity-nesting host of the cuckoo, the common redstart, regularly parasitized by the common cuckoo in Finland. Also in another brood parasite–host system, Canestrari et al. (2014) suggest that there are no extra costs for the carrion crow (*Corvus corone*) parents, a large host parasitized by the great spotted cuckoo (*Clamator glandarius*), because the parasitized brood required less provisioning effort, the period of dependence was shorter in the parasite than in the host and parasitism even increased nest success.

In a different brood parasite–host system, Mark and Rubenstein (2013) found that the rufous-and-white wrens' (*Thryophilus rufalbus*) parental body condition decreased and corticosterone levels increased from the incubation, through nestling to fledgling stages. Magnitudes of changes were similar for adults raising a

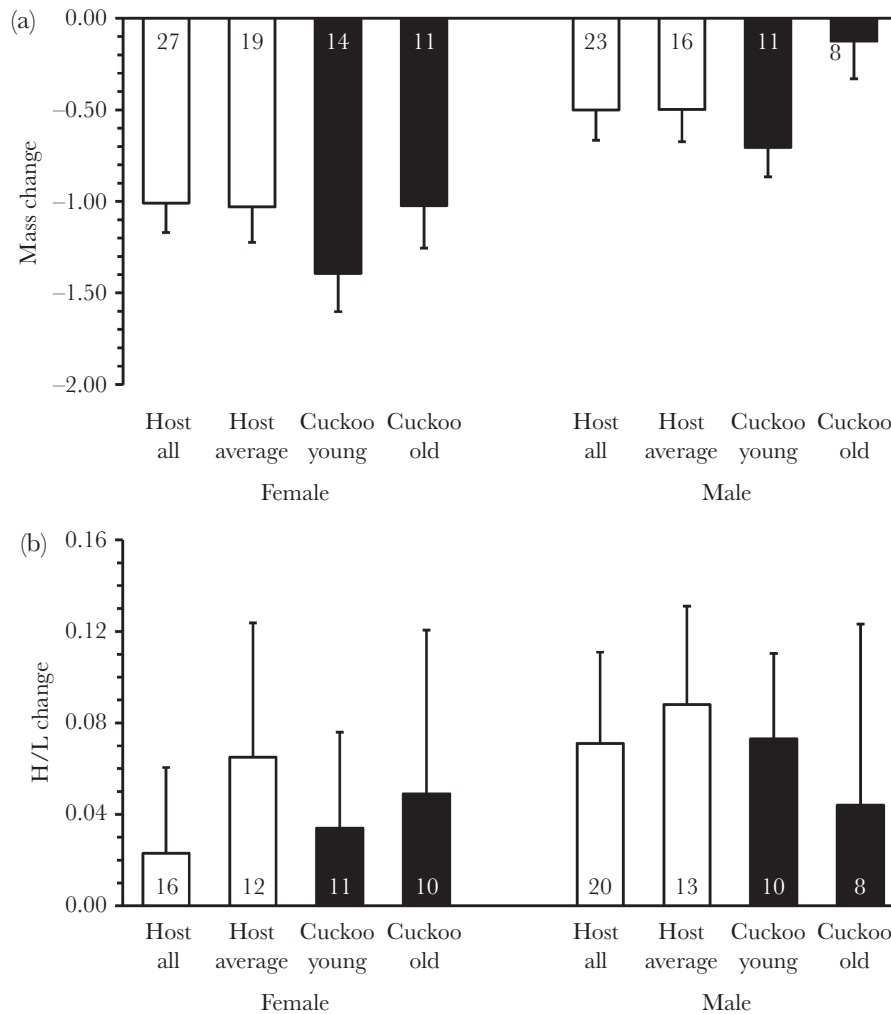


Figure 1
 Difference between the second and first capture (mean ± s.e., following Bonate 2000) in parental (a) mass change and (b) H/L change when raising an own reed warbler brood (white bars) in the first week posthatch and a cuckoo nestling (black bars) in the first week (young cuckoo) and 16 days (old cuckoo) posthatch. “Host all” includes all reed warbler broods, whereas “host average” includes only average broods with 3 and 4 nestlings. Sample sizes (no. of broods) are given within bars and differ between (a) and (b) because some blood smears could not be analyzed reliably.

Table 8
Summary of the costs imposed on parents rearing a cuckoo across parental sexes and cost measures

Cost parameter	Parent sex	Groups	Ratio	Cohen’s <i>d</i> (95% CI)
Body mass	Female	y-CC vs RW	1.2	0.33 (−0.39 to 1.06)
		o-CC vs RW	0.9	−0.12 (−0.89 to 0.66)
	Male	y-CC vs RW	1.4	0.31 (−0.50 to 1.13)
		o-CC vs RW	0.2	−0.63 (−1.54 to 0.29)
H/L ratio	Female	y-CC vs RW	0.9	−0.02 (−0.89 to 0.85)
		o-CC vs RW	1.3	0.07 (−0.82 to 0.96)
	Male	y-CC vs RW	0.7	−0.18 (−1.02 to 0.67)
		o-CC vs RW	0.5	−0.28 (−1.22 to 0.67)
Feeding effort	Female	y-CC vs RW	1.0	0.06 (−0.74 to 0.85)
		o-CC vs RW	0.8	−0.47 (−1.30 to 0.36)
	Male	y-CC vs RW	0.7	−0.63 (−1.44 to 0.19)
		o-CC vs RW	0.6	−0.54 (−1.37 to 0.29)

Ratios show how many times has been rearing a young (first week posthatch) or an old cuckoo (16 days posthatch) more demanding than raising an own average brood (first week posthatch). Cohen’s *d* represents effect size for corresponding ratio. RW = reed warbler brood; y-CC = young cuckoo; o-CC = old cuckoo.

nonparasitized own brood or brood parasite, the striped cuckoo (*Tapera naevia*). Comparison of their and our studies must be done with caution because Mark and Rubenstein (2013) measured changes in different cost parameters (mass/tarsus residuals and glucocorticoids vs. body mass and leukocytes here). Furthermore, they compared these changes across the incubation, nestling, and fledgling stages versus across nestling stage in our study. All studies nevertheless concur that raising a parasite is not more costly than raising an own brood.

Patterns found in the present study do not exclude a possibility that raising a parasite is extra costly during other nesting stages, such as incubation or postfledging (see Samaš et al. 2018). However, elevated costs during the incubation are unlikely because laying female cuckoos usually removes one or more host eggs (Moksnes et al. 2000; Šulc et al. 2016), thus compensating for the introduction of own egg which is—at least in some hosts—only slightly larger than a host egg (table 1 in Igc et al. 2015). Similarly, the only available systematic quantitative data on the postfledging period in reed warbler-cuckoos (table 32 in Wyllie 1981) and reed warblers (table 8.1 in Leisler and Schulze-Hagen 2011) showed that reed warblers care similarly long for cuckoos and their host own young

(16 and 13 days on average, respectively; see also Grim and Rutila 2017; Tyller et al. 2018). Samaš et al. (2018) even found that the postfledging care for cuckoo is about 2 days shorter compared with own nestlings in the common redstart host (17 and 19 days on average, respectively). A single cuckoo fledgling shows a higher mass than a whole reed warbler brood of the same age (Wyllie 1981) but may suffer higher risks of mortality which would relief hosts from extended care for the parasite (Wyllie 1981). These opposing pressures of unknown quantity thus make unclear whether care for parasites translates into substantial extra costs which could affect host survival and future reproduction at all.

We did not detect difference in the return rate of parents to the breeding site for individuals raising an own brood or a parasite nestling (but see lower sample size resulting from low overall return rate). In contrast, Koleček et al. (2015) reported reduced return rate in females of the great reed warbler after they raised a cuckoo chick (effect size with 95% CI: Cohen's $d = -0.33$ [0.02, -0.68] vs. our data $d = 0.24$ [1.15, -0.67]), suggesting that raising a cuckoo can lower fitness of hosts in subsequent years in other host species. Despite the great reed warbler being closely related to the reed warbler, both species notably differ in many parameters (e.g., body size, breeding parameters, breeding fidelity, and migration strategy) which prevents a meaningful comparison of just two species (i.e., pseudoreplication: Garland and Adolph 1994) and suggests other host species need to be tested to determine whether our conclusions hold in general.

CONCLUSIONS

Contrary to assumptions in traditional literature, we did not detect any significant extra immediate or future costs of raising the parasitic cuckoo nestling in the reed warbler host, that is, any costs above the standard level of costs that are imposed on hosts when raising their own progeny anyway. This conclusion was consistent for several measures, namely, changes in physical and physiological parameters of parents, feeding frequencies, and adult return rates into the next breeding season. Our results, together with a recent study of Samaš et al. (2018), question the traditional claim that a host care for a brood parasitic cuckoo nestling is unusually costly in terms of the parental effort and future survival, that is, additionally to the obvious lost progeny costs. Lower extra costs can also help explain the low levels of host counter-defences and may thus contribute to maintain a host–parasite system in a long term (Kruger 2011; Samaš et al. 2018). In contrast, it is theoretically possible that prohibitively large extra costs in some other hosts may prevent long-term host–parasite coevolution (because large costs of raising a brood parasite would diminish host survival and reproductive potential too severely). More studies examining especially the least known postfledging period (see Samaš et al. 2018; Tyller et al. 2018) and hosts with strong antiparasite defences are needed to better understand costs of raising brood parasites generally. We also suggest that future studies, instead of using surrogate measures (like feeding frequencies), should quantify direct physiological costs of host care for own progeny and misdirected care for parasites.

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Conflict of interest: We have no competing interests. This research complies with the "Association of Animal Behaviour" and the "Animal Behavior Society" guidelines for the treatment of animals in research. The study was carried out with permissions of regional conservation authorities (permit MUHO 2680/2014 OŽP). Bird captures and ringing was conducted under licence (numbers 906, 1050, and 1058) and followed rules issued by the Czech Bird Ringing Center.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Samaš et al. (2019).

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REFERENCES

- Astie A, Reboreda JC. 2006. Costs of egg punctures and parasitism by shiny cowbirds (*Molothrus bonariensis*) at creamy-bellied thrush (*Turdus amaurochalinus*) nests. *Auk*. 123:23–32.
- Bolker BM. 2015. Linear and generalized linear mixed models. In: Fox GA, Negrete-Yankelevich S, Sosa VJ, editors. *Ecological statistics: contemporary theory and application*. Oxford: Oxford University Press. p. 309–333.
- Bonate PL. 2000. *Analysis of the pretest–posttest designs*. Boca Raton: CRC Press.
- Bonier F, Moore IT, Martin PR, Robertson RJ. 2009. The relationship between fitness and baseline glucocorticoids in a passerine bird. *Gen Comp Endocrinol*. 163:208–213.
- Bonier F, Moore IT, Robertson RJ. 2011. The stress of parenthood? Increased glucocorticoids in birds with experimentally enlarged broods. *Biol Lett*. 7:944–946.
- Brooke MDL, Davies NB. 1989. Provisioning of nestling cuckoos *Cuculus canorus* by reed warbler *Acrocephalus scirpaceus* hosts. *Ibis*. 131:250–256.
- Canestrari D, Bolopo D, Turlings TC, Röder G, Marcos JM, Baglione V. 2014. From parasitism to mutualism: unexpected interactions between a cuckoo and its host. *Science*. 343:1350–1352.
- Davies NB. 2000. *Cuckoos, cowbirds and other cheats*. London: T & AD Poyser.
- Davis AK, Maney DL, Maerz JC. 2008. The use of leukocyte profiles to measure stress in vertebrates: a review for ecologists. *Funct Ecol*. 22:760–772.
- Feeney WE, Welbergen JA, Langmore NE. 2014. Advances in the study of coevolution between avian brood parasites and their hosts. *Annu Rev Ecol Syst*. 45:227–246.
- Forstmeier W, Schielzeth H. 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behav Ecol Sociobiol*. 65:47–55.
- Garland T, Adolph SC. 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. *Physiol Zool*. 67:797–828.
- Grafen A, Hails R. 2002. *Modern statistics for the life sciences*. Oxford: Oxford University Press.
- Grim T. 2006. Cuckoo growth performance in parasitized and unused hosts: not only host size matters. *Behav Ecol Sociobiol*. 60:716–723.
- Grim T. 2007. Experimental evidence for chick discrimination without recognition in a brood parasite host. *Proc Biol Sci*. 274:373–381.
- Grim T, Honza M. 1997. Differences in parental care of reed warbler (*Acrocephalus scirpaceus*) to its own nestlings and parasitic cuckoo (*Cuculus canorus*) chicks. *Folia Zool*. 46:135–142.
- Grim T, Honza M. 2001. Does supernormal stimulus influence parental behaviour of the cuckoo's host? *Behav Ecol Sociobiol*. 49:322–329.
- Grim T, Kleven O, Mikulica O. 2003. Nestling discrimination without recognition: a possible defence mechanism for hosts towards cuckoo parasitism? *Proc Biol Sci*. 270 (Suppl 1):S73–S75.
- Grim T, Rutila J. 2017. Cuckoo-host coevolutionary interactions across all breeding stages: unusual ecological setting of a cavity-nesting host. In: Soler M, editor. *Avian brood parasitism: behaviour, ecology, evolution and coevolution*. Cham: Springer International Publishing. p. 287–303.
- Grim T, Rutila J, Cassey P, Hauber ME. 2009a. The cost of virulence: an experimental study of egg eviction by brood parasitic chicks. *Behav Ecol*. 20:1138–1146.

- Grim T, Rutila J, Cassey P, Hauber ME. 2009b. Experimentally constrained virulence is costly for common cuckoo chicks. *Ethology*. 115:14–22.
- Grim T, Samaš P. 2016. Growth performance of nestling cuckoos *Cuculus canorus* in cavity nesting hosts. *Acta Ornithol.* 51:175–188.
- Hauber ME. 2006. A future cost of misdirected parental care for brood parasitic young? *Folia Zool.* 55:367–374.
- Hauber ME, Montenegro K. 2002. What are the costs of raising a brood parasite? Comparing host parental care at parasitized and non-parasitized broods. *Etologia.* 10:1–9.
- Holen ØH, Saetre GP, Slagsvold T, Stenseth NC. 2001. Parasites and supernormal manipulation. *Proc Biol Sci.* 268:2551–2558.
- Honza M, Šulc M, Jelínek V, Požgayová M, Procházka P. 2014. Brood parasites lay eggs matching the appearance of host clutches. *Proc R Soc B.* 281:1471–2954.
- Honza M, Vošlajerová K, Moskát C. 2007. Eviction behaviour of the common cuckoo *Cuculus canorus* chicks. *J Avian Biol.* 38:385–389.
- Hoover JP, Hauber ME. 2007. Individual patterns of habitat and nest-site use by hosts promote transgenerational transmission of avian brood parasitism status. *J Anim Ecol.* 76:1208–1214.
- Hoover JP, Reetz MJ. 2006. Brood parasitism increases provisioning rate, and reduces offspring recruitment and adult return rates, in a cowbird host. *Oecologia.* 149:165–173.
- Igic B, Zarate E, Sewell MA, Moskát C, Cassey P, Rutila J, Grim T, Shawkey MD, Hauber ME. 2015. A comparison of egg yolk lipid constituents between parasitic common cuckoos and their hosts. *Auk.* 132:817–825.
- Jakubas D, Wojczulanis-Jakubas K, Kulaszewicz I. 2013. Factors affecting haematological variables and body mass of reed warblers (*Acrocephalus scirpaceus*) and sedge warblers (*A. schoenobaenus*). *Ann Zool Fennici.* 50:146–157.
- Jelínek V, Karasová T, Weidinger K, Procházka P, Honza M. 2016a. Do common cuckoo chicks suffer nest predation more than host nestlings? *Behav Ecol Sociobiol.* 70:1975–1987.
- Jelínek V, Procházka P, Honza M. 2015. Experimental enlargement of nest size does not increase risk of predation or brood parasitism in the great reed warbler *Acrocephalus arundinaceus*. *Ibis.* 157:396–400.
- Jelínek V, Požgayová M, Honza M, Procházka P. 2016b. Nest as an extended phenotype signal of female quality in the great reed warbler. *J Avian Biol.* 47:428–437.
- Kilner RM, Madden JR, Hauber ME. 2004. Brood parasitic cowbird nestlings use host young to procure resources. *Science.* 305:877–879.
- Kilner RM, Noble DG, Davies NB. 1999. Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature.* 397:667–672.
- Kleindorfer S, Fessl B, Hoi H. 1995. More is not always better: male incubation in two acrocephalus warblers. *Behaviour.* 132:607–625.
- Kleven O, Moksnes A, Røskaft E, Honza M. 1999. Host species affects the growth rate of cuckoo (*Cuculus canorus*) chicks. *Behav Ecol Sociobiol.* 47:41–46.
- Koleček J, Jelínek V, Požgayová M, Trnka A, Baslerová P, Honza M, Procházka P. 2015. Breeding success and brood parasitism affect return rate and dispersal distances in the great reed warbler. *Behav Ecol Sociobiol.* 69:1845–1853.
- Krüger O. 2011. Brood parasitism selects for no defence in a cuckoo host. *Proc Biol Sci.* 278:2777–2783.
- Leisler B, Schulze-Hagen K. 2011. The reed warblers. Diversity in a uniform bird family. *Uitgeverij: KNNV.*
- Li D, Zhang Z, Grim T, Liang W, Stokke BG. 2016. Explaining variation in brood parasitism rates between potential host species with similar habitat requirements. *Evol Ecol.* 30:905–923.
- Mark MM, Rubenstein DR. 2013. Physiological costs and carry-over effects of avian interspecific brood parasitism influence reproductive tradeoffs. *Horm Behav.* 63:717–722.
- Mikulica O, Grim T, Schulze-Hagen K, Stokke BG. 2017. The cuckoo: the uninvited guest. *Plymouth: Wild Nature Press.*
- Moksnes A, Røskaft E, Hagen LG, Honza M, Mork C, Olsen PH. 2000. Common cuckoo *Cuculus canorus* and host behaviour at reed warbler *Acrocephalus scirpaceus* nests. *Ibis.* 142:247–258.
- Moksnes A, Røskaft E, Rudolfsen G, Skjelseth S, G. Stokke B, Kleven O, Lisle Gibbs H, Honza M, Taborsky B, Teuschl Y, et al. 2008. Individual female common cuckoos *Cuculus canorus* lay constant egg types but egg appearance cannot be used to assign eggs to females. *J Avian Biol.* 39:238–241.
- Nur N. 1984. Feeding frequencies of nestling blue tits (*Parus caeruleus*): costs, benefits and a model of optimal feeding frequency. *Oecologia.* 65:125–137.
- Øien J, Moksnes A, Røskaft E, Honza M. 1998. Costs of cuckoo *Cuculus canorus* parasitism to reed warblers *Acrocephalus scirpaceus*. *J Avian Biol.* 29:209–215.
- Payne RB, Payne LL. 1998. Brood parasitism by cowbirds: risks and effects on reproductive success and survival in indigo buntings. *Behav Ecol.* 9:64–73.
- Polačiková L, Procházka P, Cherry MI, Honza M. 2009. Choosing suitable hosts: common cuckoos *Cuculus canorus* parasitize great reed warblers *Acrocephalus arundinaceus* of high quality. *Evol Ecol.* 23:879–891.
- Požgayová M, Beňo R, Procházka P, Jelínek V, Abraham MM, Honza M. 2015. Lazy males and hardworking females? Sexual conflict over parental care in a brood parasite host and its consequences for chick growth. *Behav Ecol Sociobiol.* 69:1053–1061.
- Požgayová M, Piálková R, Honza M, Procházka P. 2018. Sex-specific nestling growth in an obligate brood parasite: common cuckoo males grow larger than females. *Auk.* 135:1033–1042.
- R Core Team. 2017. R: a language and environment for statistical computing. Version 3.4.3. Vienna (Austria): R Foundation for Statistical Computing. Available from: <https://www.R-project.org/>. Accessed 28 November 2018.
- Rands SA, Houston AI, Cuthill IC. 2006. Measurement of mass change in breeding birds: a bibliography and discussion of measurement techniques. *Ringing Migr.* 23:1–5.
- Romero LM, Reed JM. 2005. Collecting baseline corticosterone samples in the field: is under 3 min good enough? *Comp Biochem Physiol A Mol Integr Physiol.* 140:73–79.
- Royama T. 1966. Factors governing feeding rate, food requirement and brood size of nestling great tits *Parus major*. *Ibis.* 108:313–347.
- Royle N, Smiseth P, Kölliker M. 2012. The evolution of parental care. Oxford: Oxford University Press.
- Samaš P, Grim T, Jelínek V, Abraham M, Šulc M, Honza M. 2019. Data from: no immediate or future extra costs of raising a virulent brood parasite chick. Dryad Digital Repository. <https://doi.org/10.5061/dryad.s325n4d>.
- Samaš P, Rutila J, Grim T. 2016. The common redstart as a suitable model to study cuckoo-host coevolution in a unique ecological context. *BMC Evol Biol.* 16:255.
- Samaš P, Rutila J, Honza M, Kysučan M, Grim T. 2018. Rearing a virulent common cuckoo is not extra costly for its only cavity-nesting host. *Proc R Soc B.* 285:20181710.
- Schielzeth H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods Ecol Evol.* 1:103–113.
- Sejberg D, Bensch S, Hasselquist D. 2000. Nestling provisioning in polygynous great reed warblers (*Acrocephalus arundinaceus*): do males bring larger prey to compensate for fewer nest visits? *Behav Ecol Sociobiol.* 47:213–219.
- Spottiswoode CN, Koorevaar J. 2012. A stab in the dark: chick killing by brood parasitic honeyguides. *Biol Lett.* 8:241–244.
- Stearns SC. 1976. Life-history tactics: a review of the ideas. *Q Rev Biol.* 51:3–47.
- Stoddard MC, Kilner RM. 2013. The past, present and future of cuckoos versus reed warblers. *Anim Behav.* 85:693–699.
- Stokke BG, Hafstad I, Rudolfsen G, Bargain B, Beier J, Bigas Campàs D, Dyrce A, Honza M, Leisler B, L. Pap P, et al. 2007b. Host density predicts presence of cuckoo parasitism in reed warblers. *Oikos.* 116:913–922.
- Stokke BG, Takasu F, Moksnes A, Røskaft E. 2007a. The importance of clutch characteristics and learning for antiparasite adaptations in hosts of avian brood parasites. *Evolution.* 61:2212–2228.
- Šulc M, Procházka P, Capek M, Honza M. 2016. Common cuckoo females are not choosy when removing an egg during parasitism. *Behav Ecol.* 27:1642–1649.
- Tyler Z, Kysučan M, Grim T. 2018. Post-fledging behavior of the common cuckoo (*Cuculus canorus*) attended by the chaffinch (*Fringilla coelebs*): a comprehensive approach to study the least known stage of brood parasite-host coevolution. *Wilson J Ornithol.* 130:536–542.
- Weathers W. 1992. Scaling nestling energy requirements. *Ibis.* 134:142–153.
- Wyllie I. 1981. The cuckoo. London: Batsford.
- Žabková K. 2016. Vocalization of the common cuckoo chicks: ontogenesis and influence of the host species and acoustic environment. Prague, Czech Republic: Charles University.
- Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol.* 1:3–14.