Research

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Rearing a virulent common cuckoo is not extra costly for its only cavity-nesting host

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Virulent brood parasites refrain from arduous parental care, often kill host progeny and inflict rearing costs upon their hosts. Quantifying the magnitude of such costs across the whole period of care (from incubation through to parasite fledgling independence) is essential for understanding the selection pressures on hosts to evolve antiparasitic defences. Despite the central importance of such costs for our understanding of coevolutionary dynamics, they have not yet been comprehensively quantified in any host of any avian brood parasite. We quantified parasite-rearing costs in common redstarts *Phoenicurus phoenicurus* raising either parasitic common cuckoo *Cuculus canorus* or their own chicks throughout the complete breeding cycle, and used multiple cost parameters for each breeding stage: incubation, brooding and feeding effort; length of parental/host care; parent/host body condition; and heterophil/lymphocyte ratio (stress-level indicator). Contrary to traditional assumptions, rearing the parasite *per se* was not associated with overall higher physiological or physical costs to hosts above the natural levels imposed by efforts to rear their own progeny. The low parasite-rearing costs imposed on hosts may, in part, explain the low levels of known host counter-defences in this unusually frequently parasitized cuckoo host.

1. Introduction

Avian brood parasites avoid parenthood by laying their eggs into foreign nests [1]. Hosts targeted by brood parasites suffer multiple kinds of costs. Some hosts of interspecific parasites lose some or all of their progeny, which are killed by laying parasite females [2], or directly killed [3], evicted [4] or outcompeted [5] by parasite offspring (hereafter: lost progeny cost). By contrast, *all* hosts of both interspecific [6] and conspecific [7] parasites misdirect their care to genetically unrelated individuals, leading to additional fitness losses. From the life-history perspective, there are two types of misdirected rearing costs. These include immediate costs such as the degree of care for the parasite increased above the natural care for their own offspring [8,9] and future costs such as the host's reduced potential to invest into the future reproduction [10], diminished host's survival [11] or decreased survival of the host's own fledged offspring [12]. Both theoretical models and empirical studies assume that these costs are substantial (supernormal) for hosts [1,13,14].

However, there is a lack of empirical studies quantifying immediate or future costs of being parasitized thus creating a gap between theory and evidence. For instance, in one of the otherwise most studied brood parasites, the common cuckoo *Cuculus canorus* (hereafter: cuckoo), only a few studies have quantified immediate [2,15–17] or future costs [18]. Furthermore, all studies quantified immediate costs incompletely—they focused only on a part of the breeding period (e.g. the nestling period), leaving the costs of other parts (e.g. the fledgling period) unquantified. Overall, it is crucial for theoretical

models to take into account quantitative estimates of *complete* immediate costs of parasitism to allow for realistic modelling and prediction of coevolutionary dynamics [19].

Here, we studied the costs of rearing the cuckoo for the common redstart *Phoenicurus phoenicurus* (hereafter: redstart), the only cavity-nesting host regularly parasitized by this brood parasite [16,20]. This host–parasite system shares some common characteristics with other cuckoo–host systems [1,2]. The egg colour of the cuckoo that primarily parasitizes redstarts (hereafter: redstart-cuckoo) is similar to that of its host (egg mimicry): [21], a cuckoo nestling is distinctly heavier (approx. six times) than a host nestling or adult [22] and cuckoo hatchlings evict host progeny [4], thus decreasing the host fitness approximately 8.4 times: this decrease is similar to other hosts [23]. This system also exhibits some unique features: redstart-cuckoos typically do *not* remove a host egg when laying [23], cavity nests impede successful eviction of the host's progeny and the cuckoo is sometimes forced to grow alongside redstarts (hereafter: mixed brood). Despite all the obstacles the cuckoo faces [24], the redstart-cuckoo–host system has persisted over two million years [25] and various redstart populations currently experience consistently high parasitism rates (approx. 30% in parasitized populations: [16]).

For the first time, we measured and quantified the immediate costs of raising a cuckoo across *all* developmental stages. However, we did not manage to quantify future costs (see Material and methods). For parasitized broods, we predicted longer incubation [26] and nestling periods [22], and lower success at hatching [27] and fledging for the host nestlings [16]. For the nestling stage, we formulated exact quantitative predictions according to allometric relationships among avian growth parameters and avian energetics (see Material and methods). We were unable to formulate any specific predictions for the fledgling stage, because neither of the two published studies about the cuckoo fledgling stage reported any data on host fledglings [2,28].

2. Material and methods

(a) Study area and experimental procedures

Fieldwork was conducted at Ruokolahti (61°24′ N, 28°37′ E), Finland, May–August 2012–2016. We used 350 nest-boxes designed for redstarts [16]. During the laying and incubation stages, we checked nests daily to determine clutch size and parasitism status, and to estimate hatching dates by candling. The majority of cuckoo eggs (52 out of total $n = 82$) were cross-fostered (see electronic supplementary material for justification and details).

(b) Parental fitness

In 2012–2014, we sought to catch redstart adults twice in non-parasitized broods and three times in parasitized broods within a single breeding attempt (see figure 1 for sample sizes). We repeatedly caught both parental sexes at the same nest in 30 out of 64 nests and only one of the sexes in the remaining nests. Owing to a low occurrence of mixed broods ($n = 8$), we successfully captured only one male and four females twice, and thus we could not estimate parental parameters for the mixed brood treatment. Out of 157 nestlings and 67 adults ringed in the first year of the study, only one adult returned to the study area in the next breeding season; this prevented us from quantifying future costs.

We caught most adults on hatching day (0 = hatching day of the first chick in the brood; median = 0, range 0–2 days) and for a second time on day 10 post-hatch (median = 10, range 10–12; own or cuckoo) or on day 18 post-hatch (median = 18, range 16–19; cuckoo only because redstarts fledge at 14 days old). If the first catching attempt was unsuccessful, we caught parents 1–2 days later. We set the timing of catching for the two comparative periods (10 and 18 days intervals) because we aimed to control for (i) temporal exposure (the same length of time) and (ii) comparison of the total cost of care per nestling period (i.e. when chicks reach their growth asymptote). We caught parents about 3 days before the expected fledging date to decrease the risk of missing earlier fledging broods.

Adults were primarily caught during the afternoon (median = 3 p.m., inter-quartile range = 5 h, $n = 310$ catchings). We caught birds at the nest-box by a guillotine-type trap operated wirelessly from 10 to 80 m away or by mist-netting. The trap was made of metal with dimensions to fit inside the nest-box (fig. 2b in [16]). After the redstart entered the focal nest-box, we sent a wireless signal to trap and the plastic rectangle blocked the entrance hole. Immediately after we caught the bird, we processed it to avoid any spurious variation in measured parameters due to varying time since capture.

We banded the adult with a numbered aluminium ring, took a blood sample (see below) and measured its body mass (digital scale, precision 0.1 g) and tarsus length (digital calliper, precision 0.1 mm). To assess parental body condition, we used the scaled mass index based on body mass and tarsus length according to the study of Peig & Green [30]. To assess parental stress level, we used the heterophil-to-lymphocyte ratio (hereafter: H/L ratio) as a common physiological indicator of a prolonged stress (e.g. parental feeding effort), with a known positive relationship between the H/L ratio and stress [31]. We used a syringe to take 20 μl of blood from the under-wing vein to make a blood smear within the first few minutes after capture. Two experienced researchers (referred to in the acknowledgements section) counted the number of heterophils and lymphocytes (to produce the H/L ratio) later in the laboratory. Repeatability of heterophil and lymphocyte counts between observers was high ($r \sim 0.80$, $n = 20$ smears).

(c) Video-recording

We recorded host parental feeding effort and brooding effort using Panasonic HDC-HS80 camcorders on nests with 0–14-day-old redstart nestlings and 0–25-day-old cuckoo nestlings, covering the full length of the nestling period for both species. The camcorder was placed at the top of the nest-box attached to a wooden box extension (fig. 2b in [16]). To quantify feeding rates, we counted a 60 min feeding period 30 min after the recording began to allow for habituation of host parents to the camcorder. Brooding effort was quantified as the proportion of time spent brooding during the recording session. Each session started with the first nest visitation by parents and lasted 0.5–5 h (median = 2 h) until the end of recording. Because the length of brooding bouts varied greatly, we decided to record sequences for as long as possible, to get samples which would be more representative and less biased due to random events (e.g. self-feeding off-bout or disturbance by weather or forest animals). The length of recordings varied because some recordings were limited by inclement weather or for logistical reasons.

(d) Chick growth

Each chick was individually marked on the hatching day with a non-toxic marker. Chicks were weighed (digital scale, precision 0.1 g), but where applicable (see below), it was always after the video-recording was finished. All chicks were measured every 2–3 days from hatching day throughout the nestling period.
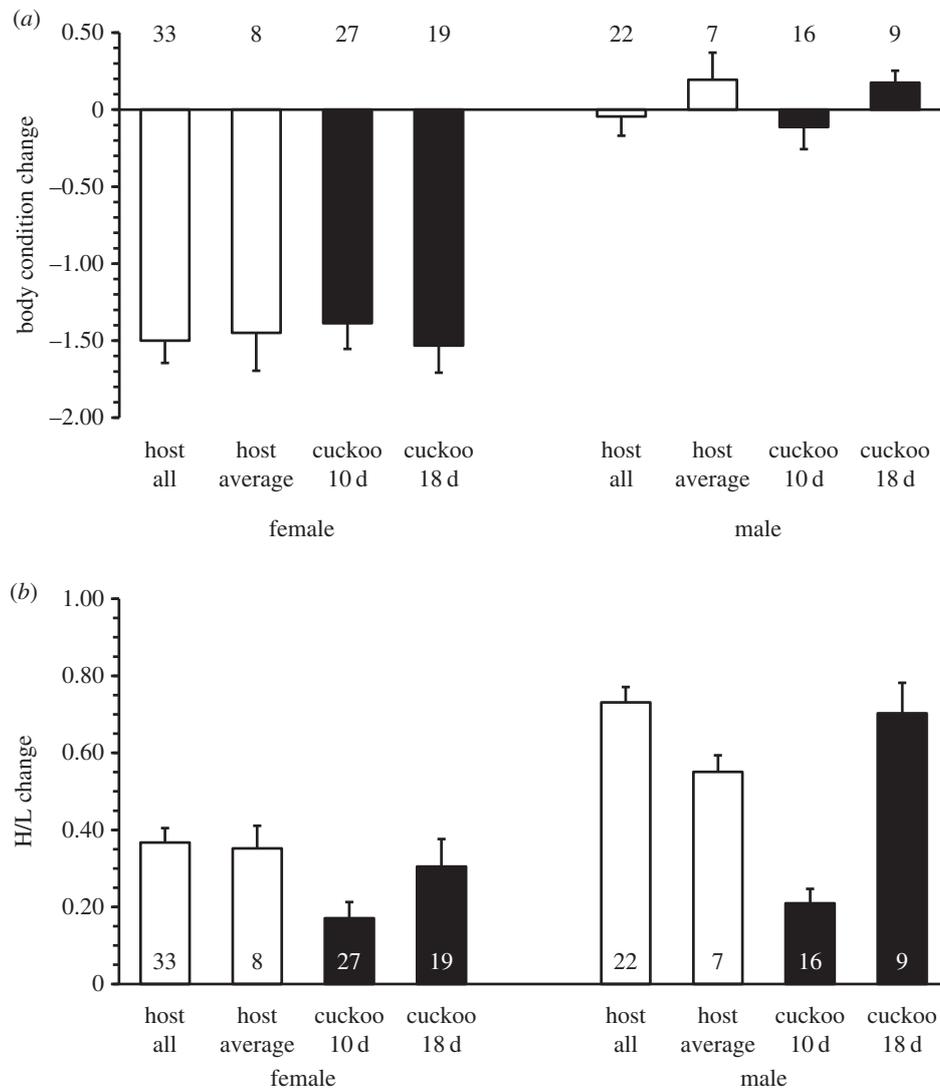
Figure 1. Difference between the second and first catchings (raw mean $\pm$ s.e., following [29]) in parental (*a*) body mass and (*b*) H/L ratio when raising their own redstart brood (white bars) in the first 10 days post-hatch and cuckoo nestling (black bars) in the first 10 days (cuckoo 10 d) and 18 days (cuckoo 18 d) post-hatch. 'Host all' includes all redstart broods while 'host average' includes only average broods with six nestlings. Sample sizes (number of broods) are given above (*a*) or within bars (*b*).

Redstart chicks were measured until the age of 10–14 days and cuckoo chicks until they fledged as handling does not trigger premature fledging [22,32].

To estimate the energy metabolized by each brood, daily metabolized energy (DME) was calculated according to the formula $DME(kJ) = 5.86 \times mass^{0.81}$ ('mass' is a specific nestling's mass at the particular age [33]). For days without mass measurements, DME was estimated using mass predictions from a growth curve calculated from the available mass measurements (following [34]). We summed DMEs of all nestlings in each brood according to the exact number of days between captures of the particular parent. Hereafter, individual total metabolized energy (individual TME) refers to metabolized energy calculated for a particular brood reared by a particular host parent.

To formulate quantitative predictions, we quantified energy budgets (summed DMEs) per an average brood size (mean $\pm$ s.d. $= 6.1 \pm 1.1$ redstart nestlings, $n = 143$ broods in our study population) and specific nestling periods: (i) the same period for both cuckoos and redstarts (0–10 days post-hatch) and (ii) the period in which nestlings reach their growth asymptote (0–10 days in redstarts and 0–18 days in cuckoos). Specifically, in the first 10 days post-hatch, rearing the cuckoo was estimated to be on average 0.4 times *less* demanding than rearing an average redstart brood. Rearing nestlings to the stage where they reach the growth asymptote was estimated to be on average 1.1

times more demanding for hosts rearing the cuckoo compared to their own average brood. We applied these exact predictions on changes in adult body condition, H/L ratio and feeding effort. Specifically for feeding effort, we additionally predicted that rearing an average mixed brood (one cuckoo plus two redstart nestlings) should be 0.5 *less* and 1.2 *more* times demanding than rearing an average redstart brood in the first 10 days post-hatch and to the stage where they reach the growth asymptote, respectively (we did not manage to catch enough host parents to perform this comparison for adult body condition and H/L ratio). We also examined covariation among sex-specific host feeding frequencies, adult body condition changes and H/L ratio changes.

(e) Radio-tracking

Radio-tracking started immediately after any of the nestlings fledged using a portable 4 MHz Sika receiver with a hand-held Lintec flexible three-element Yagi antenna (138 MHz) from Biotrack Ltd. A wing loop (figure-of-eight) backpack harness made of a cotton-nylon elastic string [35] was used to attach the transmitters to cuckoos (model PiP3 Ag393, 2.1 g) and redstarts (PicoPip Ag376, 0.7 g). Fledglings were radio-tracked daily until they started to fly and then followed at least every third day until independence or death (predation or starvation).

Fledglings reached independence if they stopped begging [36] and adults ceased feeding [37] and producing alarm calls towards the researcher or any other potential threat [28]. We visually confirmed the status for all independent fledglings.

To quantify feeding effort of parents during the post-fledging period, nestlings were located via radio-tracking and the feeding of fledglings by redstart parents was observed using binoculars from a hide (distance depended on the habitat structure). Feedings were typically recorded for 60 min (in 65% of cases, range 30–90 min) or until visual contact with the focal fledgling(s) was lost. Within each brood, some redstart fledglings were not followed due to disappearance for unknown reasons. For example, out of 159 fledglings, 28% lost signal (i.e. we did not receive any signal from the transmitter) and 35% lost transmitter (i.e. we found an undamaged transmitter without a fledgling suggesting that the fledgling lost the transmitter). Moreover, in mixed broods, one of the parents followed only the cuckoo while the other only the redstart(s) fledglings (brood division). This precluded the use of the treatments 'redstart brood', 'mixed brood' and 'solitary cuckoo' as in other analyses and instead a single 'redstart' from a non-parasitized brood was compared with a single 'mixed redstart', 'mixed cuckoo' and 'solitary cuckoo' in the post-fledging analyses.

(f) Statistical analyses

(i) Egg stage

Comparison of incubation effort (i.e. period length; continuous; in days) between parasitized and non-parasitized clutches (i.e. parasitism status; cuckoo egg present or not) was analysed by a linear model with additional predictors of ordinal date of starting incubation (continuous; 1 = 1 January), final clutch size at the start of incubation (continuous; for parasitized clutches, the cuckoo egg was included) and interaction of parasitism status with clutch size. For the incubation period, day 1 was defined as the day when the female laid the last egg and the final day was the hatching day of either the cuckoo or the first host nestling(s).

A logistic binomial regression was used to analyse the effects of cuckoo parasitism on the hatching success of host eggs using the same set of predictors as for the analyses of incubation effort (parasitism status, date of starting incubation, final clutch size and the interaction of parasitism status with clutch size). Hatchability was traditionally defined as the percentage of eggs surviving to the time of hatching that produced a chick [38]. Applying this definition in a non-parasitized nest is straightforward. However, in about every fifth parasitized nest, the cuckoo female removed a host egg (and thus such eggs had no chance to develop and hatch [16]). To avoid confounding the hatchability estimates with egg removal, we defined hatchability as the number of host eggs that hatched divided by the number of host eggs incubated (i.e. not removed by a female cuckoo or destroyed for other reasons) × 100.

(ii) Nestling stage

We first calculated Pearson's correlation coefficients with 95% asymptotic confidence intervals to assess the relationship between the studied variables of body condition, H/L ratio and feeding frequency separately for each parental sex and nestling species. Our measures of costs did not correlate with each other (electronic supplementary material, figure S1) and each provided independent information, and thus they were analysed separately.

During the first 10 days post-hatch, the effect of nestling species (categorical; redstarts versus cuckoo) and parental sex (categorical; male versus female) on the change in parental body condition and H/L ratio (both dependent variables with a normal distribution) was tested. We employed linear models with identity link. Response variables were calculated as the difference scores within measurements [29]. Additional predictors included the number of days that had elapsed between the first and second capture (continuous; range 7–12 days), the date of the first capture (continuous; 1 = 1 January), final clutch size (continuous; only redstart eggs counted as a proxy of hosts' original reproductive investment), individual TME (continuous; in kilojoules), initial parental body condition (continuous; parental body condition at first catching) and initial H/L ratio (continuous; only in models with H/L ratio as the response variable). Potential collinearity among the covariates was satisfactory, and variance inflation factors were less than two for all predictors [39]. Two-way interactions included nestling species with parental sex, nestling species with individual TME, nestling species with clutch size and parental sex with initial parental body condition.

The above analyses were re-ran for parents rearing the cuckoo and redstart nestlings for almost the full nesting period (i.e. 18 and 10 days, respectively). Full models contained the same set of predictors as above. The models were also recalculated with the response of change in body condition (computed as the scaled mass index) substituted for change in body mass (raw body mass at first capture minus the mass at next capture) to test the robustness of our results (see Results and electronic supplementary material).

Next, parental feeding effort (feedings h^{-1}) between nests with a solitary cuckoo ($n = 338$ feeding hours in 63 nests, age 0–22 days, excluding a few greater than 22-day-old cuckoos due to less than three recordings per a day of age), a mixed brood ($n = 124$ h in 17 nests, age 0–22 days) or redstart nestlings ($n = 210$ h in 70 nests, age 0–14 days) were compared using generalized linear mixed models with a negative binomial distribution and a log link. To account for multiple video-recordings of the same nests at different ages, we employed random slope mixed-effect models with 'nest ID' as random intercepts and 'brood age' as random slopes. The full model included the response variable of feedings per hour (counts) and predictors of nestling species (binary; cuckoo or redstart), brood mass (continuous; mass of all nestlings in nest), time of day (continuous; hour) and the interaction of nestling species with brood mass. To compare feeding effort directly with the prediction (see Introduction), we further recalculated the above specified model with redstart and cuckoo nestlings for the time-standardized period (first 10 days post-hatch) and extracted covariate-adjusted means of feeding frequencies.

We estimated total energy metabolized by cuckoo nestlings and redstart broods (sum of all redstart nestlings in a nest) until fledging as total metabolizable energy (TME) in kilojoules according to the formula TME (kJ) $= 6.65 \times M^{0.85} \times t_{fl}^{0.71}$, where M is the fledging mass in grams and t_{fl} is the nestling period in days (see equation (8) in [33]).

Brooding effort was analysed using a linear model. The response variable (proportion of time spent by brooding) was predicted by nestling species (categorical; redstarts versus cuckoo), average diurnal temperature on the day of recording (continuous; °C), brood age (continuous; days from hatching), daytime (continuous; hour) and its squared term to test for nonlinear trends. We included the random effect of 'nest ID' to account for multiple video-recordings of the same nests.

(iii) Fledgling stage

The effect of cuckoo parasitism on fledging success was analysed using a logistic binomial regression. The response variable (fledging success) was predicted by the presence of a cuckoo hatchling in the nest (present or absent), the date that incubation commenced (continuous; 1 = 1 January) and the final clutch size at the start of incubation (continuous). Fledging success was quantified as the percentage of hatchlings that fledged [40]. This definition was easily applicable to non-parasitized nests but parasitized nests were influenced by a cuckoo eviction

behaviour. Some host eggs failed to hatch and hatchlings failed to fledge because they were evicted by the cuckoo nestling. Therefore, we defined fledging success as the number of host chicks that fledged (successfully left the nest) divided by the number of hatchlings × 100.

We compared parental feeding effort (feedings h^{-1}) between fledgling species during the post-fledging period (0–14 days after leaving nest), using the same model structure as for the nestling stage, but the predictor of brood mass (not measured) and the interaction term were dropped. As explained above, we compared a solitary and mixed cuckoo with a single redstart fledgling (not brood as we did for nestling stage). Both full and final model outputs are presented in the electronic supplementary material [41]. The final models were selected using backward elimination of non-significant terms [42]. First, we sequentially examined the significance of predictors and kept the predictors of main interest (nestling species and parental sex) in the models regardless of their significance. All predictors in the statistical models were centred around their mean to make biologically interpretable main effects when involved in interactions. We always checked the assumption of normality of residual errors, linearity of effect and homogeneity of variances by visual inspection in models with identity link [42].

All analyses were conducted in R v. 3.4.3 [43] using R package lme4 v. 1.1–15 [44]. Potential collinearity of predictors was assessed with R package car v. 2.1–6 [45]. Results are shown as raw means ± s.e. unless stated otherwise.

3. Results

(a) Egg stage

The incubation period of redstart eggs was about half a day shorter in non-parasitized (covariate-adjusted mean 13.3 ± 0.1, $n = 67$; day 1 = the day the last host egg was laid) than in parasitized clutches (13.9 ± 0.1, $n = 50$; $\chi^2 = 8.76$, $p = 0.003$; table 1), controlling for significant predictors of date in breeding season and clutch size. The incubation period decreased with advancing date in breeding season ($\chi^2 = 11.70$, $p = 0.001$; incubation period = 13.4(± 0.1) + 0.3(± 0.2) × parasitized clutch − 0.2(± 0.1) × clutch size − 0.03(± 0.008) × date).

The incubation period of the cuckoo egg (13.2 ± 0.2, $n = 50$) was shorter than that of the redstart eggs in the same clutch (13.7 ± 0.2, $n = 50$; paired t-test, $t_{49} = 3.48$, $p = 0.001$). The hatching success of redstart eggs was higher in non-parasitized (93.6 ± 1.1%, $n = 106$ broods) than parasitized nests (73.3 ± 2.5%, $n = 100$ broods; $\chi^2 = 116.55$, $p < 0.0001$; table 1).

(b) Nestling stage

First, change in the parental body condition did not differ when rearing a redstart brood or a cuckoo nestling during the first 10 days post-hatch ($\chi^2 = 0.13$, $p = 0.72$; figure 1a; electronic supplementary material, table S1a). Females decreased their body condition significantly more than males ($\chi^2 = 28.48$, $p < 0.0001$; electronic supplementary material, table S1a). The results remained similar when we used change in parental body mass instead of the response variable change in parental body condition (electronic supplementary material, table S3a). Both females and males increased their H/L ratio (i.e. increased stress) at a similar rate ($\chi^2 = 2.37$, $p = 0.12$; figure 1b; electronic supplementary material, table S1b). Parents rearing redstart broods increased their H/L ratio more than those rearing a cuckoo nestling

($\chi^2 = 6.33$, $p = 0.01$; figure 1b; electronic supplementary material, table S1b). Parents with initially higher H/L ratios showed less increase during rearing of any nestling species ($\chi^2 = 10.52$, $p = 0.001$).

Second, during the full nestling period (i.e. the first 10 days of redstart and 18 days of cuckoo nestling life), patterns remained the same as reported above for change in parental body condition during the standardized 10-day post-hatch period (table 1; electronic supplementary material, table S2a). Again, the same conclusions were reached when we replaced the response variable of change in parental body condition with the change in parental body mass (electronic supplementary material, table S3b). Parents rearing nestlings for the full nestling period increased their H/L ratios similarly when rearing a cuckoo or redstart brood ($\chi^2 = 0.35$, $p = 0.55$; figure 1b and table 1; electronic supplementary material, table S2b). Again, parents with initially higher H/L ratios showed less increase during rearing of any nestling species ($\chi^2 = 6.34$, $p = 0.01$; electronic supplementary material, table S2b).

Analyses of feeding frequencies (controlling for brood mass) showed that during the period of the first 10 days post-hatch, redstart broods (14.9 ± 0.7 feeds h^{-1}) were fed more often than a solitary cuckoo nestling (8.4 ± 0.4; Tukey's post hoc test: $z = 2.83$, $p = 0.01$) but similar to a mixed brood (10.9 ± 0.8; $z = 0.89$, $p = 0.65$) (figure 2). Mixed broods were fed at similar frequencies to a solitary cuckoo ($z = 1.40$, $p = 0.34$) (figure 2). For the full nestling period, redstart broods of 2–8 nestlings were, on average, fed at higher frequencies (16.8 ± 0.6 feeds h^{-1}) than both a solitary cuckoo nestling (11.5 ± 0.4; Tukey's test: $z = 7.05$, $p < 0.0001$) and a mixed brood (11.8 ± 0.7; $z = 4.36$, $p < 0.0001$) (figure 2 and table 1; electronic supplementary material, table S4a). Again, the mixed broods and solitary cuckoos were fed at similar rates ($z = 0.49$, $p = 0.87$). Average redstart broods of six nestlings were fed with higher frequency (17.9 ± 1.2 feeds h^{-1}) than a single cuckoo nestling (electronic supplementary material, table S4b).

The average TME for a redstart brood (2673 ± 103 kJ, $n = 39$ nests) was similar to that of a solitary cuckoo (2644 ± 55, $n = 32$; Tukey's test: $t = 0.24$, $p = 0.97$). A mixed brood (3289 ± 127, $n = 13$) had higher TME compared with both a redstart brood ($t = 3.75$, $p < 0.0001$) and a solitary cuckoo ($t = 3.83$, $p < 0.0001$; table 1). Redstart females spent significantly less time at the nest for brooding of redstarts (mean ± s.e.: 33.4 ± 2.9%) compared with a solitary cuckoo (52.0 ± 1.6%; Tukey's test: $z = 8.36$, $p < 0.0001$) and mixed broods (52.0 ± 3.6%; $z = 5.45$, $p < 0.0001$) (figure 3). However, mixed broods and solitary cuckoos were brooded similarly ($z = 0.17$, $p = 0.98$) (figure 3). We controlled for a significant decreasing effect of brood age ($\chi^2 = 233.65$, $p < 0.0001$) and quadratic trend of daytime (nestlings were brooded less during midday; $\chi^2 = 4.05$, $p = 0.04$). The non-significant effect of day temperature ($p = 0.12$) was dropped from the final model. Cuckoo and redstart nestlings were brooded at maximum until day 11 and 12 post-hatch, respectively. Redstarts raising solitary cuckoos (20.1 ± 0.3 days, $n = 55$) and mixed broods (20.1 ± 0.7, $n = 15$) prolonged their parental effort for about a week during the nestling stage compared with those raising redstart broods (13.8 ± 0.1, $n = 97$; Tukey's test: $t = 22.08$ and 13.52, $p < 0.0001$; table 1). Nestling periods were similar for solitary cuckoos and mixed broods ($t = 0.09$, $p = 0.99$; table 1).

Table 1. Summary of the costs incurred by common redstarts from cuckoo parasitism. Sample sizes are given separately for host broods (i.e. non-parasitized), broods with a solitary cuckoo and mixed broods (i.e. redstarts sharing a nest with a cuckoo). Standardized effect sizes (r) are given with their 95% confidence intervals (CI). Negative effect sizes suggest that raising the solitary cuckoos or mixed broods is less costly than raising non-parasitized broods. Effect sizes for the fledgling period measure the magnitude of difference between a cuckoo nestling (either solitary or mixed) and a single redstart fledgling (either solitary or mixed) (see Material and methods for details). Sample sizes varied for various reasons (e.g. some chicks died before fledging and thus we have data on feeding frequency but not on growth or post-fledging period).

period	method	sample size			type of cost	r (CI)	
		host	cuckoo	mixed		host versus solitary cuckoo	host versus mixed cuckoo
incubation	observations	67	50	—	incubation effort	0.15 (−0.03 to 0.33)	—
incubation	observations	106	100	—	hatching success	0.47 (0.36 to 0.57)	—
nestling	mist-netting	39	24	—	parental body condition	0.00 (−0.22 to 0.22)	—
nestling	mist-netting	39	24	—	parental condition—H/L ratio	−0.09 (−0.13 to 0.31)	—
nestling	video-recording	68	59	17	nestling feeding frequency	−0.33 (−0.48 to −0.17)	−0.24 (−0.43 to −0.02)
nestling	video-recording	47	52	10	brooding effort	0.33 (0.17 to 0.52)	0.27 (0.00 to 0.50)
nestling	growth measurements	34	38	12	metabolizable energy	0.03 (−0.21 to 0.26)	0.40 (0.13 to 0.61)
nestling	observations	97	55	15	nestling period length	0.89 (0.85 to 0.92)	0.83 (0.76 to 0.88)
nestling	observations	53	112	15	fledging success	0.95 (0.94 to 0.97)	0.59 (0.41 to 0.73)
fledgling	observations	27[a]	35[a]	6	post-fledging feeding frequency	0.37 (0.13 to 0.57)	0.27 (0.05 to 0.74)
fledgling	observations	9[a]	14[a]	2	post-fledging period length	−0.44 (−0.73 to 0.00)	0.05 (−0.56 to 0.50)

[a]Samples sizes are either the number of nests or the number of individuals included in the analysis.

7

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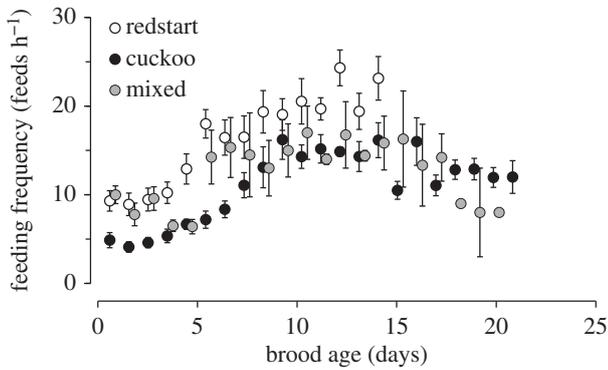
Figure 2. Feedings per hour (raw means $\pm$ s.e.) delivered to a solitary cuckoo, mixed broods of a cuckoo with redstarts and redstart broods (2 – 8 nestlings) during the nestling stage. Mean sample size per nest per day is 14 (range 8 – 35) for solitary cuckoo and redstart broods, and 5 (range 1 – 12) for mixed broods.
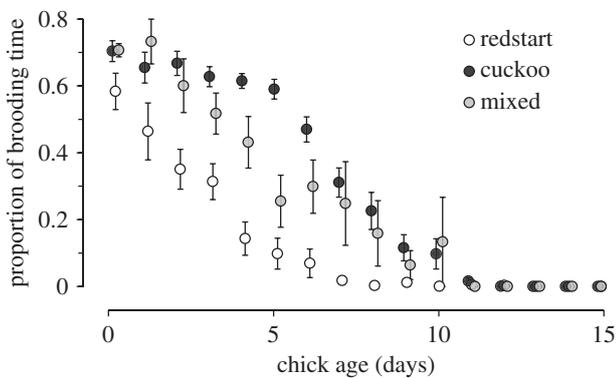
Figure 3. Brooding effort (raw means $\pm$ s.e.) by redstart females in relation to chick age. Average sample size (number of nests day) was 13 (range 7 – 23).

(c) Fledgling stage

Fledging success of redstart nestlings was higher from non-parasitized broods (90.9 $\pm$ 2.2%, $n = 112$ broods) than from mixed broods (44.3 $\pm$ 33.8%, $n = 15$; $\chi^2 = 305.30$, $p < 0.0001$; table 1).

After fledging, a single redstart from a non-parasitized brood (8.8 $\pm$ 0.4 feeds h^{-1}, $n = 54$ samples from 35 nestlings from 15 nests) was fed less often than a solitary cuckoo (12.9 $\pm$ 0.8 feeds h^{-1}, $n = 76$ samples from 27 cuckoos; Tukey's test: $z = 2.79$, $p = 0.03$) but similar to a mixed cuckoo (11.9 $\pm$ 2.9 feeds h^{-1}, $n = 8$ samples from six cuckoos; $z = 0.84$, $p = 0.83$) and a single mixed redstart (10.1 $\pm$ 0.8 feeds h^{-1}, $n = 7$ samples from seven nestlings from four nests; $z = 0.17$, $p = 0.99$). Non-significant effects of time of day ($p = 0.51$) and ordinal date ($p = 0.68$) were dropped from the final model.

The duration of dependence on host parents after fledging was similar between a single redstart from a non-parasitized brood (18.7 $\pm$ 0.5 days, $n = 14$ fledglings from nine broods), a solitary cuckoo (16.8 $\pm$ 0.7 days, $n = 9$; ANOVA, Tukey's test: $t = 1.66$, $p = 0.35$), a mixed cuckoo (19.0 $\pm$ 3.0 days, $n = 2$; $t = 0.14$, $p = 0.99$) and a single mixed redstart (19.6 $\pm$ 2.2 days, $n = 5$ fledglings from four nests; $t = 0.62$, $p = 0.92$).

4. Discussion

The fundamental brood parasite–host coevolutionary paradigm assumes that host care for the parasite is dramatically more costly than care for their own progeny [1]. Our quantitative estimates of costs across the *complete* period of host care for the parasite challenge this paradigm by showing that parental care by one of the major cuckoo hosts, the redstart, is not more costly when invested into the parasitic cuckoo rather than their own offspring. Counterintuitively, some of the multiple parental care parameters were even *lower* for the parasite than for a host progeny. This conclusion holds even for mixed broods, where the cuckoo shares the nest with host nestling(s). This might be because a single cuckoo nestling in a mixed brood does not (over)compensate the needs (feeding, brooding, etc.) of the host nestlings that it evicted. Paradoxically, the presence of the parasite thus might *increase* host survival and future reproduction via life-history trade-offs between current and future reproduction. This exciting scenario provides an impetus for future studies.

(a) Quantitative predictions versus estimated costs

As predicted, the presence of a parasitic cuckoo nestling in a redstart nest was associated with decreased hatching and fledging success of host progeny (see also [16]), more brooding effort and five extra days of care during the complete breeding cycle. However, parental body condition or physiological stress did not differ between parents raising their own brood, a mixed brood (predicted to be 1.2 times more costly) and solitary parasitic nestling (predicted to be 1.1 times more costly) when compared across the full nestling period (see also [8,9]). This was probably because parents reduced their feeding effort for cuckoo nestlings to about two-thirds of the feeding effort for a host brood of similar weight, which contrasts with findings from other host–parasite systems [11] (but see [8,9]). Cuckoos in mixed broods were fed at similar frequencies to solitary cuckoos; this confirms previous conclusions [16,23,27,32] that redstart-cuckoo nestlings do not use the host's own young to attract more fosterer care (cf. [5]).

During the post-fledging stage, the cuckoo received approximately 34% more feeds per hour than a single redstart fledgling, but such a difference does not reflect the fact that the cuckoo fledgling is about six times heavier than a single redstart fledgling (fig. 1 in [24]). It is also very likely that parents usually feed more than one redstart fledgling because non-parasitized nests usually fledge 5.7 redstarts [16]. However, unlike parental effort indicators of body condition and H/L ratio, feeding frequency is only a proxy indicator as it may not reflect the true load size [46]. Still, redstarts feed nestlings, both their own and parasitic, with similar prey types which does not suggest any differences in prey or load size [24] (note that prey size differences in diet delivered to own versus cuckoo nestlings covary with diet composition differences [47]). Surprisingly, cuckoo fledglings reached independence 2 days earlier than redstarts, while they required seven extra days of parenting during the nestling stage. These results cannot be compared with others because no study so far has studied these parameters in both host and parasite fledglings.

(b) Estimating different types of costs

Costs of parasitism entail both lost progeny costs [2–5] and rearing costs; the latter type of costs can be separated into immediate costs (physiological and physical [8,9]) and

future costs (survival and future fecundity [10–12]; see Introduction). Estimating lost progeny costs is easy because each egg, nestling and fledgling represents a unit. Therefore, fitness can be indirectly measured as, for instance, the number of fledged chicks per egg laid; comparing such measures between parasitized and non-parasitized nests provides a quantitative estimate of lost progeny costs [23]. For example, an average parasitized redstart brood has 8.4 times lower fitness than an average non-parasitized brood [23].

Estimating overall rearing costs is not that straightforward. This is because different measures of costs are suitable and measurable at different developmental stages. For example, there are no brooding costs during the fledgling stage and costs of feeding unrelated nestlings obviously cannot apply during the incubation stage; this precludes a meaningful overall estimate of rearing costs. Theoretically, physiological costs (like H/L ratio) could be estimated for any developmental stage; practically, this was not feasible in our study system because redstarts always desert a nest when captured during the egg-laying period.

For redstarts that lose all their offspring due to cuckoo eviction, the costs of rearing the cuckoo might seem irrelevant. The rearing costs would only become important if they affected host future reproduction [11]. Indeed, such a pattern was found, for example, in a tropical parasite host system: increased investment into current reproduction while parasitized by the striped cuckoo *Tapera naevia* was associated with the host's (the rufous-and-white wren *Thryophilus rufalbus*) delayed re-nesting and a reduced probability of nesting in the next breeding season [9] (but see [8,10,12]). In the common cuckoo, only a single published study has examined the effect of rearing the cuckoo on the host's future reproduction: female great reed warblers *Acrocephalus arundinaceus* that reared a cuckoo survived less than non-parasitized females [18]. However, for the great reed warbler, there is currently no estimate of immediate costs. By contrast, for the redstarts we have estimates of immediate costs but no estimates of future costs. This calls for more studies in this surprisingly neglected research area.

A recent interspecific comparative study [48] showed that lost progeny costs explain interspecific variation in host resistance (egg rejection rates). Future studies should therefore focus on estimating rearing costs (table 1) across various host species—this will allow for interspecific comparative studies to elucidate whether and how varying immediate and future rearing costs explain varying host defences across species additional to lost progeny costs [48].

(c) Maintenance of the redstart-cuckoo system

Cuckoo parasitism decreased redstarts' hatching and fledging success only slightly compared with other cuckoo hosts which experience almost nil breeding success (because the cuckoo chick usually evicts all host progeny in open-nesting hosts [2,17]). Lower cuckoo virulence observed in redstarts can be attributed to their different breeding strategy—the redstart is the only regular cavity breeding cuckoo host [23]. Only a third of cuckoo eggs end up inside the nest cup after cuckoo laying attempts [23,27]. Even after successful parasitism, cuckoo nestlings often struggle to evict host eggs and chicks [4]. Such hindrances, not present in open-nesting hosts [2,17], decrease the cuckoo's chances of eliminating host

progeny. Indeed, cuckoo nestlings grow alongside redstart chicks more often than in any other host species [32].

Despite these cumulative effects, the redstart–cuckoo host–parasite system has persisted for more than 2.5 Myr [25]. Low parasite success [16] combined with low costs for redstart hosts (this study) might explain low to absent levels of redstart antiparasitic behaviour against all parasite developmental stages (i.e. adult cuckoos, their eggs, nestlings and fledglings) across the many studied populations [16,20,23,27]. Negligible antiparasitic defences would otherwise be hard to explain in a host that suffers parasitism rates that are unusually high among cuckoo hosts (consistently approx. 30% in parasitized populations [16], compared with typically less than 15% in most parasitized populations of the most common cuckoo host [49]). The surprisingly low immediate costs to breeding redstarts that we quantified in this study, combined with perfect mimicry in redstart-cuckoo eggs [23] and the absence of second breeding attempts in redstarts [23], might thus constrain the evolution of antiparasitic behaviour and help cuckoos to maintain this host–parasite system long term (see also [50]).

(d) Reduced parasite virulence and increased host tolerance?

General theory of host–pathogen coevolution [19] encompasses a scenario of reduced pathogen virulence coupled with reduced host resistance (fig. 1 in [51]). Such increased host tolerance was documented in a different brood parasite–host system [52] and might potentially be occurring in the redstart–cuckoo system where surprisingly low costs of cuckoo parasitism to redstarts (i.e. low 'pathogen virulence': this study) are coupled with very weak host resistance [23]. However, we suggest that this pattern is more parsimoniously explained by constraints rather than coevolution (similar to other apparent cases of reduced pathogen/parasite virulence and host resistance [51].

Low virulence of redstart-cuckoos most probably reflects simple physical constraints, namely nest cup location far from the nest entrance (which limits cuckoo female laying success [16]) and nest cup design (which limits cuckoo nestling eviction success [4]) rather than specifically evolved 'reduced pathogen virulence'. In theory, low virulence might evolve, for example, in the form of reduced eviction effort (i.e. tolerating cohabitation with host chicks); if anything, the reality is the opposite (e.g. prolonged period of eviction activity in redstart-cuckoo nestlings [4]).

Although redstarts show very low resistance [16,23], coevolved 'decreased host resistance' or 'tolerance' [51,52] does not seem to apply in the redstart–cuckoo system. This is because, by definition, 'tolerance does not inhibit the parasites' growth or reproduction, but minimizes the impact of parasite attacks' [52]—and ample evidence [16,20,22–24,27,32] shows that cuckoos in redstart nests suffer both dramatically reduced growth and reproduction.

Overall, available data suggest a different scenario, specifically 'lower pathogenicity' leading to 'reduced selection for host resistance' (fig. 1 in [51]). Future research should address the topic of tolerance versus resistance via the study of multiple populations which would allow quantification of the potential tolerance in redstart hosts following the methods described in [52].

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Rearing a virulent common cuckoo is not extra costly for its only cavity-nesting host

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Supplementary Results

During a previous study [1], we cross-fostered cuckoo eggs (52 out of total n=82) into randomly chosen synchronous redstart host nests, randomizing parasitism status of particular host pairs. The cross-fostering of eggs is a standard established method used in brood parasitism studies to disentangle the potential cues that hosts can use to recognize and reject foreign eggs [2]. However, this could be problematic if cuckoo parasitism in nature is non-random with respect to host age [3] or phenotypes [4]. In a previous study we found that cuckoos selected redstart pairs randomly with respect to host phenotypes and that cross-fostering was also done randomly in respect to host phenotypes [5].

In the present study, we found no difference between the scaled mass index (a measure of body condition, calculated from mass and tarsus on nest hatching day: [6]) of redstarts naturally parasitised by cuckoos (mean±SD: 15.40±1.32g, n=34 individuals) and those that were not parasitised (15.36±1.24g, n=111; Welsch's t-test $t_{52.1}$=0.16, p=0.87). Also, redstart parents fed cuckoos in naturally parasitised nests at similar rates (mean±SD: 9.6±5.3 feeds.hour^{-1}, n=21 nests) as cuckoos that were cross-fostered into unparasitised nests (11.1±4.0 feeds.hour^{-1}, n=49; $F_{1,40}$=2.46, p=0.12) after controlling for a significant non-linear effect of nestling age ($F_{1,40}$=36.06, p<0.0001). Additionally, clutch size did not differ between naturally parasitised (mean±SD: 6.4±0.9 eggs, n=54) and non-parasitised nests (6.7±0.9 eggs, n=219; Welsch's t-test t_{80}=1.56, p=0.12; figure S2). Thus, we found no evidence that cuckoos choose redstart hosts according to host phenotypes.

Although the cross-fostered cuckoo eggs were placed in randomly selected non-parasitised nests, we directly tested for any potential biases due to cross-fostering activities statistically. We found no difference in the initial host body condition between redstarts raising cross-fostered cuckoos (mean±SD: 15.25±1.33 g, n=50 individuals) and the rest of the host population in our sample (15.44±1.22 g, n=95; Welsch's t-test $t_{92.4}$=0.84, p=0.40). Redstart parents fed cross-fostered cuckoos at similar rates (mean±SD: 11.2±4.1 feeds.hour^{-1}, n=48 nests) as cuckoos in naturally parasitised nests (10.3±4.2 feeds.hour^{-1}, n=22; $F_{1,40}$=1.47, p=0.23) after controlling for a significant non-linear effect of nestling age ($F_{1,40}$=55.7, p<0.0001). Host clutch size was also similar between nests with a cross-fostered cuckoo (mean±SD: 6.6±0.9, n=74) and naturally parasitised nests without cross-fostering (6.7±0.9, n=198; Welsch's t-test $t_{126.3}$=0.62, p=0.53). Thus, in all tested parameters the nests that received cross-fostered cuckoos were representative of the host population.

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Figure S1. Pearson's correlations with 95% confidence intervals (see below) for sex-specific host feeding frequencies (FF), adult body condition changes (BC), and H/L ratio changes (H/L) calculated separately for cuckoo nestlings and redstart broods. Confidence intervals overlapping with dashed line suggest non-significant difference from zero (because all CIs overlap with 0 there was no need for Bonferroni correction). Females = open circles, males = closed circles.
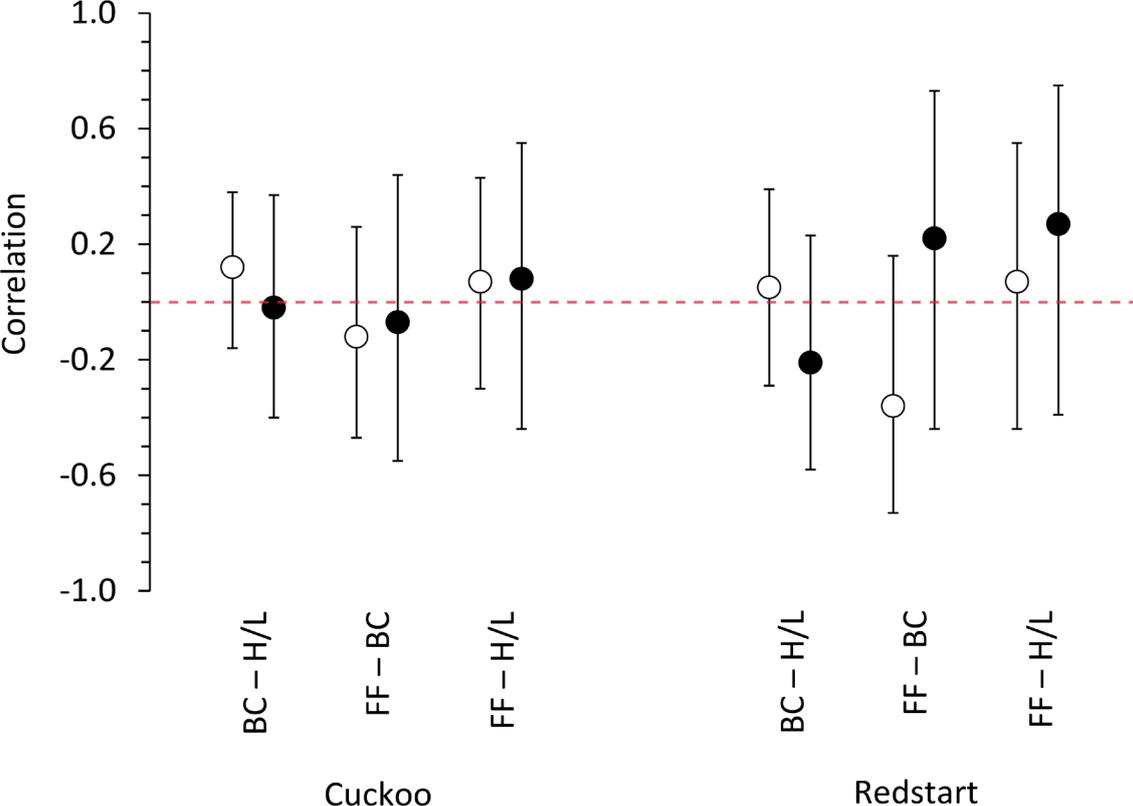
Figure S2. Distribution of final clutch size of common redstart hosts which were parasitised (grey bars; *n*=54; median=7, mean=6.4±0.1) or were not naturally parasitised by the common cuckoo (black bars; *n*=219; median=7, mean=6.7±0.1).
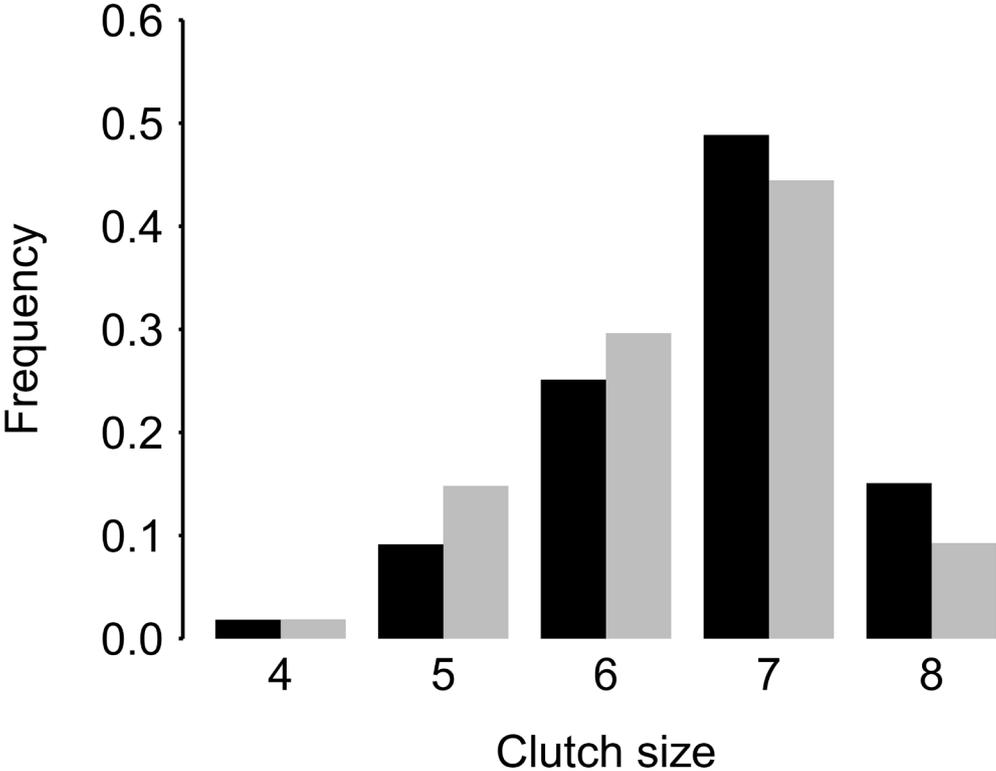
Table S1. Outputs of full and final models for (a) change in body condition and (b) H/L ratio of parents/hosts rearing either own redstart brood or a cuckoo nestling during first 10 days from hatching (i.e., time-standardised cost of rearing). Parental sex ('sex' in interaction term) and nestling species ('species' in interaction term) were predictors of key interest and were kept in model regardless of their significance. 'Individual TME' = total metabolizable energy, 'R' = redstart as reference level, 'M' = male redstart as reference level.

(a)

Predictor	Full model $F_{11,86}=14.55$, $p<0.01$, $R^2=0.61$, $AIC_c=201.2$			Final model $F_{3,94}=49.29$, $p<0.01$, $R^2=0.60$, $AIC_c=191.9$		
	χ^2	p	Estimate±SE	χ^2	p	Estimate±SE
Intercept	–	–	−0.86±0.08	–	–	−0.92±0.06
Nestling species [R]	0.57	0.45	−0.10±0.14	0.13	0.72	−0.04±0.13
Parental sex [M]	26.26	<0.0001	−0.91±0.22	28.48	<0.0001	−0.87±0.16
Individual TME	0.10	0.75	−0.0001±0.0002	–	–	–
Initial condition	26.85	<0.0001	−0.33±0.06	30.41	<0.0001	−0.35±0.06
Day span	0.02	0.89	0.01±0.10	–	–	–
Date	2.66	0.11	0.010±0.007	–	–	–
Clutch size	5.02	0.03	0.22±0.10	–	–	–
Species*sex	1.72	0.19	−0.34±0.27	–	–	–
Species*TME	0.42	0.52	−0.0003±0.0005	–	–	–
Species*clutch size	0.76	0.38	0.15±0.18	–	–	–
Sex*Initial condition	1.32	0.25	−0.15±0.14	–	–	–

(b)

Predictor	Full model $F_{12,85}=2.45$, $p=0.008$, $R^2=0.15$, $AIC_c=204.3$			Final model $F_{3,94}=7.33$, $p<0.01$, $R^2=0.16$, $AIC_c=190.4$		
	χ^2	p	Estimate±SE	χ^2	p	Estimate±SE
Intercept	–	–	0.30±0.08	–	–	0.35±0.06
Nestling species [R]	7.83	0.005	−0.05±0.18	6.33	0.01	−0.32±0.13
Parental sex [M]	0.07	0.79	−0.37±0.14	2.37	0.12	−0.20±0.13
Individual TME	0.47	0.49	0.0002±0.0002	–	–	–
Initial H/L ratio	12.15	0.0005	−0.51±0.15	10.52	0.001	−0.48±0.15
Initial mass	2.51	0.11	0.10±0.06	–	–	–
Day span	1.04	0.31	0.10±0.11	–	–	–
Date	0.01	0.94	0.001±0.01	–	–	–
Clutch size	0.02	0.90	0.01±0.10	–	–	–
Species*sex	3.38	0.07	−0.49±0.28	–	–	–
Species*TME	0.79	0.37	−0.0004±0.0005	–	–	–
Species*clutch size	0.67	0.41	0.14±0.18	–	–	–
Sex*Initial mass	1.17	0.28	0.15±0.14	–	–	–

Table S2. Outputs of full and final models for (a) change in body condition and (b) H/L ratio of parents/hosts rearing either own redstart brood during the first 10 days post-hatch or a cuckoo nestling during 18 days (i.e., full rearing cost across the nestling period). Parental sex ('sex' in interaction term) and nestling species ('species' in interaction term) were predictors of key interest and were kept in models regardless of their significance. 'TME' = total metabolizable energy, 'R' = redstart as reference level, 'M' = male redstart as reference level.

(a)

Predictor	Full model $F_{11,71}=12.92$, $p<0.01$, $R^2=0.62$, $AIC_c=178.7$			Final model $F_{3,79}=46.09$, $p<0.01$, $R^2=0.62$, $AIC_c=165.5$		
	χ^2	p	Estimate±SE	χ^2	p	Estimate±SE
Intercept	–	–	−0.82±0.09	–	–	−0.94±0.07
Nestling species [R]	0.14	0.71	−0.06±0.18	0.00	0.97	−0.005±0.15
Parental sex [M]	30.51	<0.0001	−1.14±0.20	21.34	<0.0001	−1.01±0.21
Individual TME	1.10	0.29	−0.0002±0.0002	–	–	–
Initial condition	16.05	<0.0001	−0.29±0.07	13.01	0.0003	−0.39±0.11
Day span	0.28	0.60	−0.06±0.12	–	–	–
Date	1.63	0.20	0.009±0.008	–	–	–
Clutch size	4.14	0.04	0.23±0.12	–	–	–
Species*sex	0.02	0.89	−0.04±0.34	–	–	–
Species*TME	0.01	0.91	−0.0001±0.0004	–	–	–
Species*clutch size	0.25	0.62	−0.10±0.22	–	–	–
Sex*Initial condition	1.43	0.23	−0.18±0.16	–	–	–

(b)

Predictor	Full model $F_{12,70}=1.96$, $p=0.04$, $R^2=0.12$, $AIC_c=195.5$			Final model $F_{3,79}=4.60$, $p<0.01$, $R^2=0.12$, $AIC_c=182.8$		
	χ^2	p	Estimate±SE	χ^2	p	Estimate±SE
Intercept	–	–	0.44±0.10	–	–	0.46±0.08
Nestling species [R]	0.71	0.40	−0.16±0.20	0.35	0.55	−0.32±0.13
Parental sex [M]	2.38	0.12	−0.32±0.22	5.70	0.01	−0.20±0.13
Individual TME	0.68	0.41	0.0001±0.0002	–	–	–
Initial H/L ratio	6.73	0.009	−0.46±0.19	6.34	0.01	−0.48±0.15
Initial condition	1.03	0.31	−0.08±0.08	–	–	–
Day span	0.23	0.63	0.06±0.13	–	–	–
Date	0.29	0.59	0.004±0.01	–	–	–
Clutch size	0.11	0.75	0.04±0.13	–	–	–
Species*sex	0.15	0.70	−0.13±0.38	–	–	–
Species*TME	1.28	0.26	−0.0005±0.0004	–	–	–
Species*clutch size	2.89	0.09	−0.37±0.24	–	–	–
Sex*Initial condition	0.25	0.62	0.08±0.18	–	–	–

Table S3. Outputs of full and final models for response variable of change in body mass of parents/hosts rearing (a) own redstart brood and a cuckoo nestling the first 10 days from hatching (i.e., time-standardised cost of rearing) and (b) own redstart brood during the first 10 days post-hatch and a cuckoo nestling during 18 days (i.e., cost of rearing for full nestling period). Parental sex ('sex' in interaction term) and nestling species ('species' in interaction term) were predictors of key interest and were kept in model regardless of their significance. 'Individual TME' = total metabolizable energy, 'R' = redstart as reference level, 'M' = male redstart as reference level.

(a)

Predictor	Full model $F_{11,86}=15.50$, $p<0.01$, $R^2=0.62$, $AIC_c=170.6$			Final model $F_{4,93}=42.33$, $p<0.01$, $R^2=0.63$, $AIC_c=158.6$		
	χ^2	p	Estimate±SE	χ^2	p	Estimate±SE
Intercept	–	–	−0.81±0.08	–	–	−0.78±0.08
Nestling species [R]	1.14	0.29	−0.11±0.11	0.42	0.51	−0.07±0.11
Parental sex [M]	27.80	<0.0001	−0.94±0.18	30.38	<0.0001	−0.99±0.17
Individual TME	1.58	0.21	−0.0003±0.0002	–	–	–
Initial mass	17.51	<0.0001	−0.35±0.09	15.58	<0.0001	−0.33±0.08
Day span	0.59	0.44	0.07±0.09	–	–	–
Date	0.94	0.33	0.005±0.006	–	–	–
Clutch size	3.61	0.06	0.16±0.09	–	–	–
Species*sex	0.01	0.93	−0.02±0.23	–	–	–
Species*TME	2.44	0.12	−0.0006±0.0004	–	–	–
Species*clutch size	0.00	0.97	0.005±0.15	–	–	–
Sex*Initial mass	4.73	0.03	−0.40±0.19	8.04	0.005	−0.50±0.18

(b)

Predictor	Full model $F_{11,71}=13.41$, $p<0.01$, $R^2=0.62$, $AIC_c=153.4$			Final model $F_{3,79}=45.6$, $p<0.01$, $R^2=0.62$, $AIC_c=142.4$		
	χ^2	p	Estimate±SE	χ^2	p	Estimate±SE
Intercept	–	–	−0.87±0.09	–	–	−0.95±0.06
Nestling species [R]	0.79	0.37	−0.13±0.15	0.05	0.83	−0.03±0.13
Parental sex [M]	27.46	<0.0001	−1.05±0.20	27.49	<0.0001	−0.96±0.17
Individual TME	0.28	0.59	−0.0001±0.0001	–	–	–
Initial mass	11.39	0.0007	−0.30±0.09	12.55	0.0004	−0.32±0.09
Day span	0.26	0.61	0.05±0.10	–	–	–
Date	2.39	0.12	0.009±0.006	–	–	–
Clutch size	3.90	0.05	0.19±0.11	–	–	–
Species*sex	0.60	0.44	−0.20±0.28	–	–	–
Species*TME	0.40	0.53	−0.0002±0.0003	–	–	–
Species*clutch size	0.01	0.91	−0.20±0.19	–	–	–
Sex*Initial mass	1.66	0.20	−0.25±0.21	–	–	–

Table S4. Outputs of full and final models for feeding frequency of parents rearing (a) cuckoo nestling or all redstart broods (range: 2–8 nestlings) and (b) cuckoo nestling or modal redstart broods (6 nestlings). Nominator degrees of freedom are 4 for 'Year' and 2 for 'Brood type'. Model fits are summarised using marginal (R^2_m) and conditional (R^2_c) R-squared accompanied with AIC_c.

(a)

Predictor	Full model R^2_m=0.29, R^2_c=0.47, AIC_c=3761			Final model R^2_m=0.30, R^2_c=0.44, AIC_c=3756		
	χ^2	p	Log(estimate±SE)	χ^2	p	Log(estimate±SE)
Intercept	−	−	2.53±0.06	−	−	2.52 ± 0.06
Brood type	50.6	<0.0001	−	53.3	<0.0001	−
Brood mass	92.4	<0.0001	0.010±0.001	182.3	<0.0001	0.009±0.001
Year	13.6	0.009	−	15.5	0.004	−
Date	0.00	0.96	−0.0001±0.002	−	−	−
Daytime	1.74	0.19	−0.003±0.006	−	−	−
Brood type*mass	4.56	0.10	−	−	−	−

(b)

Predictor	Full model R^2_m=0.28, R^2_c=0.45, AIC_c=2862			Final model R^2_m=0.30, R^2_c=0.48, AIC_c=2868		
	χ^2	p	Log(estimate±SE)	χ^2	p	Log(estimate±SE)
Intercept	−	−	2.54±0.07	−	−	2.53 ± 0.07
Brood type	19.7	<0.0001	−	23.2	<0.0001	−
Brood mass	88.9	<0.0001	0.010±0.001	118.0	<0.0001	0.009±0.001
Year	13.8	0.008	−	15.5	0.004	−
Date	0.01	0.92	−0.0002±0.002	−	−	−
Daytime	0.14	0.71	−0.002±0.007	−	−	−
Brood type*mass	4.10	0.13	−	−	−	−