



Post-fledging interactions between the Common Cuckoo *Cuculus canorus* and its cavity-nesting Common Redstart *Phoenicurus phoenicurus* host

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Brood parasite–host interactions during the incubation and nestling stages have been well studied, but the post-fledging period remains virtually unknown. Using radiotracking, we provide the first detailed data on post-fledging interactions between the Common Cuckoo *Cuculus canorus* and its only regular cavity-nesting host, the Common Redstart *Phoenicurus phoenicurus*. Cuckoos raised alone ('solitary') fledged at higher mass, with higher wing and tarsus length and started to fly at a younger age than Cuckoos raised alongside young Redstarts ('mixed'). However, a further 23 fledging and post-fledging parameters measured at five pre-determined times (fledging, first-flight, predation, starvation, independence) did not differ between solitary and mixed Cuckoos. In addition, none of the parameters measured during the post-fledging period (growth, dispersal distances, number of flights) differed between solitary and mixed Cuckoos. Redstart fledglings from non-parasitized broods ('solitary') showed generally similar fledging and post-fledging parameters to fledglings reared alongside a Cuckoo ('mixed'). Surprisingly, there were no significant differences in post-fledging predation rate, starvation or overall survival rates between mixed and solitary Cuckoos or mixed and solitary Redstarts. Thus, during the post-fledging period, mixed Cuckoo fledglings successfully compensated for the poorer performance experienced during the nestling stage whereas mixed and solitary Redstarts did not differ in any measured parameters. This suggests that the regular occurrence of mixed broods in this host–parasite system – which is unique among the many Cuckoo hosts – is evolutionarily stable for both hosts and parasites.

Keywords: brood parasitism, fledgling survival, independence, post-fledging, predation, radiotracking, starvation.

The post-fledging period is the time after young birds leave the nest and before they achieve independence, disperse or migrate (Cox *et al.* 2014). The first weeks after fledging are the most critical for development and survival of most birds (Anders *et al.* 1997, Cox *et al.* 2014, Soler *et al.* 2014a, Martin *et al.* 2018). The post-fledging period, as the last phase of avian parental care, also determines the success of prior parental investment (Grüebler & Naef-Daenzer 2010).

Data on fledgling survival are thus crucial for estimating population productivity (Anders *et al.* 1997). Despite its fundamental importance, the post-fledging period remains poorly studied, especially compared with other avian developmental stages (Cox *et al.* 2014). The main reason is the difficulty of following and observing young mobile birds after they have left the nest (Kershner *et al.* 2004, Thompson & Ridley 2013).

Avian brood parasites are no exception. An additional difficulty is that higher numbers of nests must be monitored (compared with non-parasitic birds) to ensure sufficient sample sizes because

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only a small proportion of host nests are usually parasitized (Davies 2000, Grim *et al.* 2011) and the long nestling periods of parasites relative to hosts may reduce the probability of successful fledging (at least in some hosts: Jelínek *et al.* 2016). Except for the parasitic cowbirds (*Molothrus* spp.) and their hosts (Woodward 1983, Rasmussen & Sealy 2006, De Mársico *et al.* 2012) and the Great Spotted Cuckoo *Clamator glandarius* and its Eurasian Magpie *Pica pica* host (Soler *et al.* 1994, 2014a), very little is known about the interactions between hosts and fledged brood parasites (De Mársico *et al.* 2017). Especially striking is the lack of data for the otherwise best-studied brood parasite, the Common Cuckoo *Cuculus canorus* (hereafter: Cuckoo) (Davies 2000, Mikulica *et al.* 2017).

Compared with hundreds of egg studies and dozens of nestling studies (Grim 2007a), only three studies have been published on the Cuckoo post-fledging period. Wyllie (1981) studied a reasonable sample size of Cuckoos raised by Eurasian Reed Warblers *Acrocephalus scirpaceus* (hereafter: 'Reed Warbler') but he reported only the ages at first flight, survival rate and length of post-fledging period, but no other information about fledgling biology. Vega *et al.* (2016) followed post-fledging and migratory movements of Cuckoo fledglings raised by Common Redstarts *Phoenicurus phoenicurus* (hereafter: 'Redstart') using satellite tracking, but they reported only the survival rate and length of post-fledging dependent period (estimated indirectly from satellite data). Tyller *et al.* (2018) provided detailed data on post-fledging care by a host Common Chaffinch *Fringilla coelebs* but their study was based only on a single Cuckoo fledgling. None of these three studies reported comparative data on hosts' own fledglings. Without quantification of reproductive output and host care for their own progeny it is impossible to determine how costly host care is for the parasite relative to baseline parental effort delivered to the host's own young (Rasmussen & Sealy 2006, Samaš *et al.* 2018). Such costs affect selection pressures on the evolution of host defences and are central to our understanding of parasite–host coevolution (Takasu *et al.* 1993, Davies 2000, Soler *et al.* 2014a, Soler 2017).

To help fill these knowledge gaps, we studied post-fledging care provided to Cuckoo and host chicks by Redstarts. The Redstart is the only known European cavity-nesting passerine that is regularly parasitized by the Cuckoo (Samaš *et al.*

2016, Yang *et al.* 2016), and has recently become a model system for the study of Cuckoo–host interactions (reviewed by Grim & Rutila 2017). Nests placed in a cavity make egg-laying difficult for female Cuckoos and significantly reduce their laying success (Rutila *et al.* 2002, Samaš *et al.* 2016, Thomson *et al.* 2016), and also make eviction of host eggs or chicks more difficult for Cuckoo hatchlings compared with open nests (Rutila *et al.* 2002, Grim *et al.* 2009a), often resulting in mixed broods (Samaš *et al.* 2016, Thomson *et al.* 2016). In such broods the Cuckoo shares the nest with Redstarts, often leading to early death of the Cuckoo nestling (Samaš *et al.* 2016, Thomson *et al.* 2016; see also Grim *et al.* 2011). Also, food composition of Redstarts may contribute to poor Cuckoo nestling performance, because Redstarts may in addition to invertebrates, feed the nestlings unusual (for otherwise purely insectivorous Cuckoo nestlings: Grim & Honza 2001) diet items, including fruits and lizards, which negatively affects Cuckoo fitness (Grim *et al.* 2017). Nevertheless, nothing is known about the Cuckoo and Redstart interactions during the post-fledging period.

As in recent studies (Rutila *et al.* 2002, Grim *et al.* 2009a,b, Samaš *et al.* 2016, 2018, Thomson *et al.* 2016), we took advantage of variation in brood composition by comparing broods where Cuckoos or Redstarts were raised alone ('solitary Cuckoos' and 'solitary Redstarts'), with those where they are raised together ('mixed broods').

We predicted that fledglings from mixed broods would fledge, start to fly and achieve independence later than solitary Cuckoos or solitary Redstart broods. Further, we expected lower values of measured performance parameters (see Methods) and lower survival rate in fledglings from mixed broods. In interspecific comparisons, we predicted that Cuckoos would fledge, start to fly and achieve independence when older than Redstarts, due to the greater developmental demands of the larger species (fig. 1 in Grim *et al.* 2017). Similarly, other physiological differences between the two species (e.g. poorly adapted digestive system of Cuckoos to Redstart food composition, see Grim *et al.* 2017), should slow the Cuckoo chick in its post-fledging development.

In addition, as in other host–parasite systems (Fraga 1998, Grim 2011, De Mársico *et al.* 2012, 2017), there is the possibility that Redstart hosts can distinguish a Cuckoo fledgling from their own

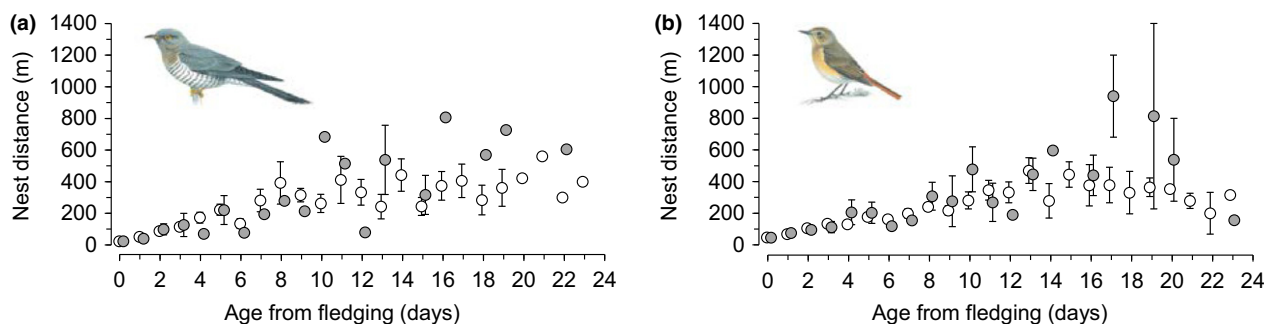


Figure 1. The post-fledging nest distances (i.e. dispersal distances from the natal nest; mean \pm se, from fledging = day 0) of Cuckoos (a) and Redstarts (b) reared in solitary broods (open circles; Cuckoos: $n = 31$, Redstarts: $n = 27$) or in mixed broods (grey circles; Cuckoos: $n = 9$, Redstarts: $n = 10$). Redstart data represent brood means. [Colour figure can be viewed at wileyonlinelibrary.com]

fledglings and discriminate against it. Therefore, we predicted lower values of breeding performance parameters and a lower survival rate in Cuckoos than in Redstarts.

METHODS

Study site and population

We conducted this research during three consecutive breeding seasons (June–August 2014–2016) in southeastern Finland close to Ruokolahti (61°24' N, 28°37' E). The study site comprises cultivated Scots Pine *Pinus sylvestris* forest with low ground vegetation (Samaš *et al.* 2016).

Redstarts and Cuckoos in our study area have been studied for more than 30 years (Samaš *et al.* 2016) and, except for one natural nest, we studied an established host nestbox population (Samaš *et al.* 2016) because natural nests are very difficult to find (J. Haikola pers. comm., M. Kysučan *et al.* unpubl. data). All nestboxes were specifically designed for the study with an entrance diameter of 60–80 mm to facilitate both Cuckoo female laying and Cuckoo chick fledging. For further technical details, description of general field procedures and overall population analysis during the egg-laying, incubation and nestling stages, see Samaš *et al.* (2016) and Grim *et al.* (2017).

We studied four treatment groups. 'Solitary Cuckoo' fledglings ($n = 31$) were reared without nest-mates (31 broods). 'Mixed Cuckoo' fledglings ($n = 11$) were raised alongside Redstart chicks (nine broods, one Cuckoo per nest/brood), while the remaining two Cuckoo chicks shared one nest/brood without Redstart nest-mates ($n = 10$ broods). 'Mixed Redstart' fledglings ($n = 22$,

mean \pm se = 2.3 ± 0.3 Redstart fledglings per nest) were those that were raised alongside the 10 Cuckoos ($n = 10$ broods, one Cuckoo per nest). One Cuckoo died due to starvation 2 days before its Redstart nest-mates fledged and thus is not included in the Mixed Cuckoo group. Two Cuckoos sharing the same nest were included in the mixed group due to their mutual competition, which is similar to that in Cuckoo–Redstart mixed groups (Samaš *et al.* 2018). Both Cuckoos were treated as independent data points, as (1) before fledging, there were no signs of pseudoreplication because of the very different growth trajectories of the two chicks (resulting in divergent masses of 85 and 65 g at the equal age of 20 days) and (2) after fledging, each Cuckoo was attended independently by a different parent (male vs. female Redstart) and not cared for by the other host parent (i.e. brood division). 'Solitary Redstart' fledglings ($n = 137$ from 27 broods, mean \pm se = 5.1 ± 0.3 fledglings per nest) were raised in unparasitized broods, in other words without a Cuckoo.

Transmitter attachment and ringing

In contrast to other radiotracking (Soler *et al.* 1994, 1995, 2014a,b, Tyller *et al.* 2018) or satellite-tracking (Vega *et al.* 2016) studies of avian brood parasites, we tracked both parasite and host offspring. In total, 42 Cuckoo nestlings from 41 different broods and 159 Redstart nestlings from 37 different broods that were fitted with transmitters successfully fledged (File S2).

To minimize potential transmitter effects, we chose the transmitters weighing <5% of chick mass, as recommended for small birds (Barron *et al.* 2010). Therefore, we used two types of glue-

mounted transmitters (Biotrack Ltd., Wareham, UK). For Cuckoos we used 2.1-g (2.3% of Cuckoo mass during tagging: 91.7 ± 2.4 g, $n = 42$) PiP3 Ag393 tags with a 15-cm-long wire antenna and a detection range of 200–600 m ground to ground and 500–1200 m above ground. For Redstarts we used 0.7-g (4.7% of Redstart mass during tagging: 15.8 ± 0.1 g, $n = 159$) PicoPip Ag376 tags with a 12-cm-long wire antenna and a detection range of 80–300 m ground to ground and 150–600 m above ground. We attached the transmitters with cyanoacrylate superglue to clipped and degreased (by acetone) back feathers (following Diemer *et al.* 2014).

We attached the transmitters 2–3 days before the estimated fledging date to maximize the number of tagged fledglings and allow the chicks to become accustomed to transmitters (following Soler *et al.* 2014a). Presumed fledging dates of Cuckoos (18 days post-hatch) and Redstarts (13 days post-hatch) were calculated based on data from 11 breeding seasons from our study site (Samaš *et al.* 2016). We set hatching day as 0 (following Grim & Samaš 2016). In retrospect, the transmitters were attached 2.2 ± 0.1 days (mean \pm se, $n = 201$; precision: days) before the real fledging date, which we determined from nest checks and video-recordings. Thus, we tagged the fledglings at maximum body size and age and, at the same time, avoided the threat of premature fledging which could be caused by late tagging (Ausprey & Rodewald 2011).

Transmitter loss was expected with moulting (Diemer *et al.* 2014) of young Cuckoos prior to migration (Verheyen 1950, Stresemann & Stresemann 1961, Rohwer & Broms 2013). Nevertheless, during the first field season (2014) five of 16 Cuckoos and 40 of 73 Redstarts lost their transmitters before attaining independence (average transmitter attachment duration from fledging: Cuckoos: mean \pm se = 10.2 ± 2.7 days, $n = 5$; Redstarts: 5.0 ± 0.7 days, $n = 40$). Therefore, in the next two field seasons, in addition to glue attachment we used a modified wing loop (figure-of-eight) back-pack harness (following Anders *et al.* 1997, Hill *et al.* 1999) made of a cotton-nylon elastic string (following Rappole & Tipton 1991). We could not use the most recommended figure-of-eight leg loop (Raim 1978) due to still undeveloped nestling bodies (especially tail feathers), which caused transmitter loss when we tried to follow such a procedure. Thus, the harness was tied under each wing, leaving room for sufficient

motion range and growth of the chicks' wings and pectoral muscles (Anders *et al.* 1997). This method has been effective in small and medium-sized birds, without interfering with their behaviour (Hill *et al.* 1999). As a result, during 2015 none of 13 Cuckoo fledglings and only 16 of 60 Redstart fledglings lost their transmitter (average transmitter attachment duration: 4.6 ± 1.4 days, $n = 16$). In 2016, none of 13 Cuckoos and none of 26 Redstarts lost transmitters.

During transmitter attachment, we banded the right leg (left in one case) of each fledgling with a numbered metal ring (Finnish Museum of Natural History). Both legs were further banded with a unique combination of colour plastic rings (Eco-tone Plain colour rings) for individual long-distance visual recognition of fledglings from the same brood or from nearby nests. We also measured physical parameters of body mass, wing length and tarsus length in all chicks during each nest visit from tagging until fledging.

Determining the exact date of fledging events

Using motion-activated infrared SpyCamera CCTV cameras, we video-recorded 63 nests at the end of the nestling stage to determine the exact date of fledging events (29 solitary Cuckoo broods, 24 unparasitized Redstart broods and 10 mixed broods). To distinguish particular Redstart chicks during fledging events we individually marked 49 nestlings from 14 complete broods (seven unparasitized and seven mixed) with differently shaped white paper stickers glued to the transmitters (following Porkert & Špinka 2004).

Altogether, 201 tagged nestlings (42 Cuckoos and 159 Redstarts) successfully fledged. We obtained the exact fledging date from video-recordings of 163 fledglings: 39 Cuckoos and 124 Redstarts. Seventy-five of these 124 Redstarts were unmarked but their broods ($n = 15$) completely fledged within a single day and therefore we were able to obtain their exact fledging dates. For the remaining fledglings (three Cuckoos and 35 Redstarts), which were not recorded or were not marked and whose brood fledged over the course of more than a single day, we estimated the fledging date with a precision of 32 h (i.e. we consistently used a mid-point between the last nest check when the chick was present in the nest and the first nest check when the chick was already fledged: Grim 2007b).

To prevent premature fledging of nestlings (Grim 2007b), we installed the cameras while the transmitter attachments, ringing and nestling measurements were being conducted. To minimize disturbance at video-recorded nests we used car-batteries to power the cameras and a wooden box extension for camera placement (fig. 2b in Samaš *et al.* 2016). We conducted video-recordings from tagging day until the last chick in the nest fledged.

Post-fledging period study procedures

From the expected fledging date, we visited the nest area once or twice a day and started radio-tracking when we noticed that fledging had begun. We used a portable 4-MHz Sika receiver with hand-held Lintec flexible three-element Yagi antenna (138 MHz) to radiotrack the fledglings. The following parameters were recorded consistently by the same person (M.K.).

First, after the visual contact with a tracked fledgling, the observer recorded its GPS position ('original point', precision 2–6 m) using the mobile application Locus Map Version 2.10.1 to measure 'nest distance' (i.e. distance in metres between the fledgling's original point and its natal nest) and 'daily dispersal distance' (i.e. distance between locations on successive days). Data from non-consecutive days were excluded to make temporal periods consistent (always 1 day) and thus comparable.

Secondly, the observer approached the fledgling. When the presence of the observer or an attempt to capture the fledgling (see below) flushed it from its original point, we recorded the 'fleeing distance' (in metres) from the original

point (following Hanley *et al.* 2015). Further, the observer recorded the 'number of flights per hour' without flushing the fledgling (i.e. number of flights during 1 h of observation when the observer was covered by a camouflage net and vegetation and maintained visual contact with the focal fledgling; following Soler *et al.* 1994). This parameter was impossible to record when the fledglings started to fly well, so we have no data for fledglings after independence.

Thirdly, the observer caught and measured the fledgling. During the first days after leaving a nest, most chicks remain motionless, cannot fly or fly clumsily (Wyllie 1981), and can be easily caught by an observer (Tyller *et al.* 2018). For such fledglings, we measured their body mass with a portable electronic balance (precision 0.1 g), their wing length with a ruler (following fig. 4.4 in Sutherland *et al.* 2004; precision 1 mm) and tarsus length with a digital calliper ('maximum tarsus length', following fig. 4.5a in Sutherland *et al.* 2004; precision 0.1 mm). Additionally, we report, as a baseline, 'fledging mass', i.e. the first measurement of chick body mass after a fledging event (this did not necessarily happen on the fledging day, see section Determining the exact date of fledging events).

Radiotracking was conducted daily until a fledgling started to fly well. Then, the fledgling was located at least every third day until its death (predation or starvation), or the first sign of its independence, which was judged by cessation of begging behaviour and lack of feeding and alarm calls from the adult Redstarts (following Tyller *et al.* 2018, see also Woodward 1983, Tarwater *et al.* 2011). We managed to confirm our assessment of

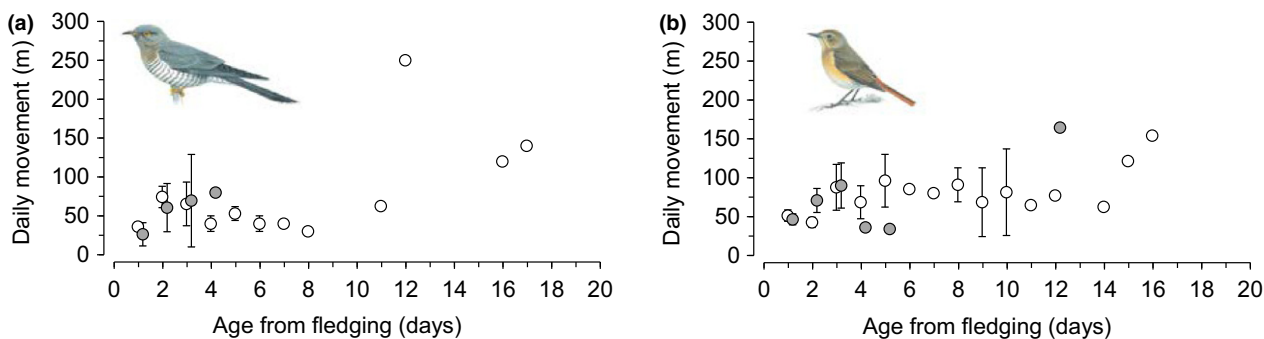


Figure 2. Post-fledging daily dispersal distances (i.e. daily movements; mean \pm se; from fledging = day 0) of Cuckoos (a) and Redstarts (b) reared in solitary broods (open circles; Cuckoos: $n = 25$, Redstarts: $n = 17$) or in mixed broods (grey circles; Cuckoos: $n = 5$, Redstarts: $n = 7$). Redstart data represent brood means. 0 = day of fledging. [Colour figure can be viewed at wileyonlinelibrary.com]

independence in seven (five solitary and two mixed) Cuckoos and eight (three solitary and five mixed) Redstarts several days after the estimated independence (mean \pm se = 3.3 ± 0.4 days, $n = 15$).

We scored fledglings as gaining independence (confirmed visually) or not. We scored the fledgling's status as 'unknown' when the fledgling lost its transmitter ($n = 61$), the transmitter signal could not be located (lost signal, $n = 51$) or we finished data collection before the fledgling achieved independence ($n = 7$). Fledglings with unknown status were excluded from calculation of post-fledging predation, starvation and survival rates.

We identified five pre-determined situations in the post-fledging period; these included two time-points and three possible outcomes: 'Fledging' was the day when a chick left the nest, i.e. the start of the post-fledging period; 'First flight' was the day when a Cuckoo chick flew further than 3 m or a Redstart chick flew further than 2 m, which enabled them to escape from ground predators (Wyllie 1981). When fledglings did not survive until independence, we recorded the two causes of its death. 'Predation' means that we found the remains of a fledgling's body or the transmitter in an active raptor nest or with some other indication of predation (such as antenna damage, presence of bitten feathers or blood). 'Starvation' means that we found the fledgling dead with obvious signs of malnutrition and no signs of predation (Grim 2007b). Finally, 'independence' means that the fledgling had no remaining contact with the adult Redstarts that had raised it and was alive. At each situation, we always recorded 'age from hatching' as the number of days from hatching (hatching day = 0, precision = 1 day) and 'age from fledging' as the number of days from fledging (fledging day = 0, precision = 1 day).

Physical parameters of body mass, wing length and tarsus length were measured in all catchable fledglings during the radiotracking phase between fledging and independence, disappearance or death. We attempted to reduce disturbance of fledglings as much as possible and measured only flightless fledglings; flying fledglings were solely observed from a distance.

Data analysis

All analyses were conducted with R 3.5.0 (R Core Team 2018) and STATISTICA 13 (TIBCO

Software Inc. 2017). We compared multiple parameters among fledgling groups and performed two major analyses: (1) we examined change of focal parameters across the post-fledging period and (2) we compared focal parameters in the five pre-determined situations of biological interest (fledging, first flight, predation, starvation, independence). We did not apply Bonferroni corrections because our study is necessarily exploratory and, due to the number of compared parameters, any correction for multiple tests would lead to too strict alpha-values and would greatly increase the risks of type II errors (Nakagawa 2004).

Tests over the post-fledging period

We tested fixed effects of 'group' (categorical; solitary Cuckoo, mixed Cuckoo, solitary Redstart, mixed Redstart) and 'age' (continuous; fledgling age) on the four response variables: nest distance (continuous, log-transformed), daily dispersal distance (continuous, log-transformed), number of flights per hour (counts) and body mass (continuous). In all cases we employed a linear mixed model with identity link except for the response variable number of flights per hour, which was modelled using a marginal model with Poisson error distribution and log link. In all full models we additionally included 'age²' (continuous; quadratic term to test for potential non-linear effects of fledgling age) and the interactions of 'group' with 'age' and 'group' with 'age²'. In all but one statistical model (see below) we controlled for fledgling age, nestling identity (ID) and brood ID variation by employing a nested random slope model (i.e. random effect for slopes of fledgling age assigned to random effects of nestling ID nested within brood ID). To account for temporally correlated data (repeated measurements), we used a continuous first-order autoregressive correlation structure which allows observations that are further apart from each other to be less strongly correlated.

We used a four-level predictor 'group' (see above) in all models except the one analysing post-fledging body mass. In the latter case we employed two linear mixed models (one for each species) because each species markedly differed in fledging mass (Grim *et al.* 2017). One model included only Cuckoos (categorical; solitary Cuckoo, mixed Cuckoo), another only Redstarts

Table 1. Definitions of terms.

Term	Definition
Pre-determined time points	
Fledging	Day when a chick left the nest.
First flight	Redstart flew >2 m, Cuckoo flew >3 m.
Predation	Rest of fledgling's body or transmitter with some indication of predation found.
Starvation	Fledgling found dead with obvious signs of malnutrition and no signs of predation.
Independence	Fledgling had no remaining contact with the adult Redstarts that had raised it and was alive.
Post-fledging parameters	
Age from hatching	Fledgling's age from hatching day (in days; 0 = hatching day).
Age from fledging	Fledgling's age from the day it left its nest (in days; 0 = fledging day).
Nest distance	Distance from the nestbox (in metres; precision 1 m).
Daily dispersal distance	Distances between fledgling's locations on successive days (in metres; precision 1 m).
Fleeing distance	Distance that the fledgling flew after being flushed by the approaching observer (in metres; precision 1 m).
Number of flights per hour	Number of flights during 1 h of observation.
Fledging mass	The first measurement of chick's body mass after fledging event (precision 0.1 g).
Wing length	The length of fledgling's wing (in mm; precision 1 mm).
Tarsus length	Maximum tarsus length (in mm; precision 0.1 mm).

(categorical; solitary Redstart, mixed Redstart). For Cuckoos, we excluded the random effect of brood ID because all broods contained only a single Cuckoo, except one case when two Cuckoos shared one nest – these were treated as two individual Cuckoos and both assigned to the 'group' mixed Cuckoo (exclusion of one of these Cuckoos from the shared nest did not affect analytical outcomes).

We present outputs from both the full (recommended by Forstmeier & Schielzeth 2011) and final reduced models (recommended by Grafen & Hails 2002). We used backward elimination of non-significant ($\alpha = 0.05$) terms but kept the main predictors of interest 'group' and 'age' in the models regardless of their significance (as recommended by Grafen & Hails 2002).

We used the packages nlme (version 3.1-131, Pinheiro *et al.* 2017) for statistical models with

normal error distribution and geepack (version 1.2-1, Halekoh *et al.* 2006) for the marginal model with Poisson error distribution.

Tests at time points of biological interest

We tested effects of 'group' (categorical; solitary Cuckoo, mixed Cuckoo, solitary Redstart, mixed Redstart) on the 27 fledging and post-fledging parameters (Table 1) categorized into five pre-determined time points of biological interest (fledging, first flight, predation, starvation, independence; Table 1). Before analyses, we averaged each Redstart parameter per brood ID in nests containing multiple Redstarts. Each Cuckoo was treated as an individual, including one case when two Cuckoos shared one nest (both assigned into the mixed Cuckoo group). We employed a linear model with identity link and normal distribution and in some cases used a log transformation of a response variable to meet the assumptions of normality for model residuals. We used Tukey's post-hoc test (package multcomp, version 1.4.8, Hothorn *et al.* 2008) to test for differences between groups, specifically solitary Cuckoo vs. mixed Cuckoo, solitary Redstart vs. mixed Redstart, solitary Cuckoo vs. solitary Redstart and mixed Cuckoo vs. mixed Redstart. For the three parameters of predation, starvation and survival rate we applied a Cox proportional-hazards model (Cox 1972) using the package survival (version 2.41.3, Therneau & Grambsch 2000) and again used Tukey's post-hoc test for between-group comparisons.

RESULTS

The post-fledging period

The average nest distance during the post-fledging period did not differ between the groups ($\chi^2 = 5.4$, $P = 0.14$, $n = 189$ fledglings) but it increased non-linearly with age in all fledgling groups ($\chi^2 = 179.6$, $P < 0.001$; Fig. 1, Supporting Information Table S1 in File S1). Fledglings from mixed broods increased their distance from nest with advancing age at higher rates than Cuckoos or Redstarts from solitary broods ($\chi^2 = 20.3$, $P < 0.001$; Fig. 1, Table S1 in File S1).

The daily dispersal distance during the post-fledging period increased with age in all fledgling groups ($\chi^2 = 3.5$, $P = 0.05$, $n = 113$ fledglings; Fig. 2, Table S2 in File S1). Groups did not

significantly differ in average daily dispersal distances: solitary Cuckoo (adjusted mean = 41 m, 95% CI 29–57), mixed Cuckoo (mean = 23, 95% CI 13–44), solitary Redstart (mean = 46, 95% CI 34–62) and mixed Redstart (mean = 48, 95% CI 29–81) ($\chi^2 = 6.1$, $P = 0.11$; Table S2 in File S1).

The number of flights per hour during the post-fledging period differed between groups ($\chi^2 = 23.0$, $P < 0.001$, $n = 76$ fledglings; Table S3 in File S1). The number of flights showed an increasing trend with advancing fledgling age in solitary Cuckoo, mixed Cuckoo and mixed Redstart groups but a decreasing trend in solitary Redstarts ($\chi^2 = 18.7$, $P = 0.0003$; Fig. 3, Table S3 in File S1).

For Cuckoo fledglings ($n = 32$), body mass was higher in solitary Cuckoos ($\chi^2 = 26.1$, $P < 0.001$) and in both groups (solitary and mixed) body mass decreased non-linearly with advancing age throughout the post-fledging period ($\chi^2 = 4.3$, $P = 0.04$; Fig. 4a, Table S4a in File S1). Both Redstart fledgling groups ($n = 120$ fledglings) had a similar body mass ($\chi^2 = 2.9$, $P = 0.09$) and decreased mass linearly with advancing age ($\chi^2 = 10.2$, $P = 0.001$; Fig. 4b, Table S4b in File S1).

Time points of biological interest

On fledging day, solitary Cuckoos ($n = 31$) were the same age as mixed Cuckoos ($n = 10$) but weighed more and had longer wings and tarsi (Fig. 5, Table S5 in File S1). Solitary Cuckoos fledged at a greater age than did solitary Redstarts ($n = 27$). Similarly, in mixed broods, Cuckoos fledged at a greater age than Redstarts ($n = 10$). However, there were no significant differences in

age, mass, wing or tarsus length between solitary Redstarts and those in mixed broods (Fig. 5, Table S5 in File S1).

When they first flew, solitary Cuckoos ($n = 25$) were younger (from hatching) than Cuckoos from mixed broods ($n = 4$); nevertheless, age from fledging, nest distance, fleeing distance, mass, wing and tarsus length did not differ between the Cuckoo groups (Fig. 5, Table S5 in File S1). Solitary Cuckoos first flew at a greater age (from hatching) and performed longer fleeing distances than solitary Redstarts ($n = 23$), whereas age from fledging and nest distance were higher in solitary Redstarts. Cuckoos from mixed broods first flew when older than Redstarts from mixed broods ($n = 9$). However, age from fledging, nest distance and fleeing distance at first flight did not differ between the two groups. Solitary Redstarts first flew when younger (from hatching) than Redstarts from mixed broods. In contrast, age from fledging, nest distance, fleeing distance, mass, wing and tarsus length did not differ between the Redstart groups (Fig. 5, Table S5 in File S1).

Predated ($n = 28$) and starved fledglings ($n = 11$) did not differ in age from hatching, age from fledging, nest distance, predation or starvation rates among all fledgling groups. Starved solitary Cuckoos did not differ in mass, wing or tarsus length from starved Cuckoos from mixed broods. Similarly, starved Redstarts from solitary broods did not differ in these body parameters from starved Redstarts from mixed broods (Fig. 5, Table S5 in File S1).

At independence, solitary Cuckoos did not differ in their age from hatching from Cuckoos from

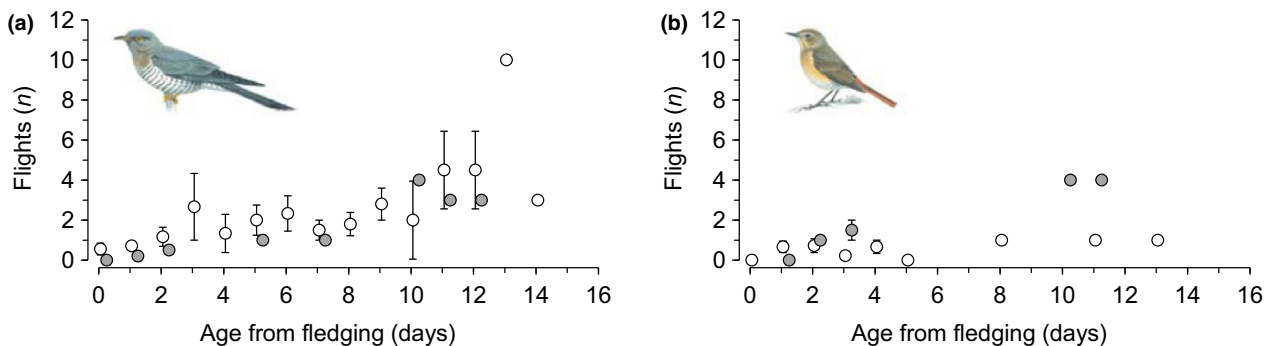


Figure 3. The post-fledging number of flights per hour (mean \pm se; from fledging = day 0) after the first flushing, of Cuckoos (a) and Redstarts (b) reared in solitary broods (open circles; Cuckoos: $n = 27$, Redstarts: $n = 14$) or in mixed broods (grey circles; Cuckoos: $n = 7$, Redstarts: $n = 4$). Redstart data represent brood means. [Colour figure can be viewed at wileyonlinelibrary.com]

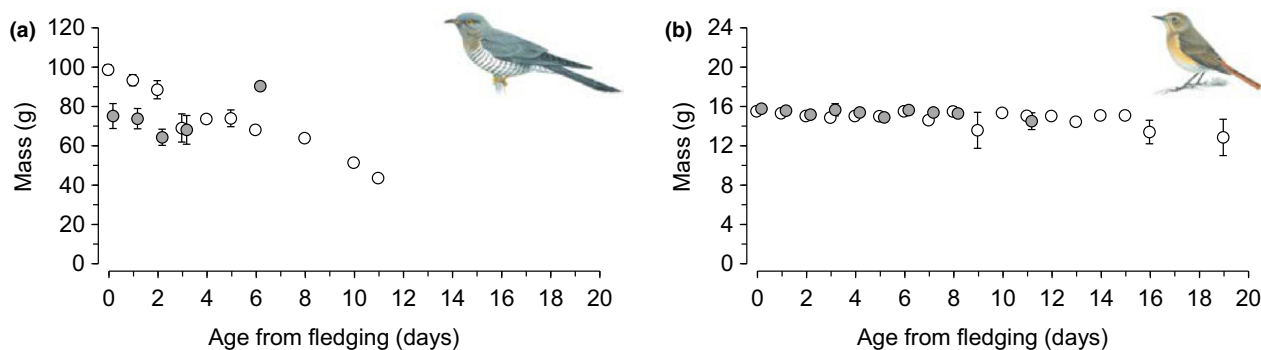


Figure 4. The post-fledging mass growth rate (mean \pm se), of Cuckoos (a) and Redstarts (b) reared in solitary broods (open circles; Cuckoos: $n = 25$, Redstarts: $n = 22$) or in mixed broods (grey circles; Cuckoos: $n = 7$, Redstarts: $n = 10$). Redstart data represent brood means. 0 = day of fledging. [Colour figure can be viewed at wileyonlinelibrary.com]

mixed broods. In Redstarts as well, the age from hatching did not differ between chicks from mixed or solitary broods. Nevertheless, solitary Cuckoos ($n = 9$) achieved independence at a greater age than Redstarts from solitary broods ($n = 8$), and mixed Cuckoos ($n = 2$) achieved independence at a greater age than mixed Redstarts ($n = 5$). Age from fledging, nest distance, fleeing distance and survival rates did not differ among the fledgling groups (Fig. 5, Table S5 in File S1).

DISCUSSION

Surprisingly, Cuckoo fledglings reared alongside Redstart chicks fledged at similar ages as solitary Cuckoos. However, and as predicted, Cuckoos from mixed broods showed delayed age at first flight and lower fledging masses, shorter wings and tarsi compared with solitary Cuckoo fledglings, although these effects lasted only for the first 3 days after fledging. Over the course of the post-fledging period, Cuckoo fledglings from mixed broods compensated for their biometric shortfall at fledging and did not differ from solitary Cuckoos in any measured parameters at independence. This pattern parallels a similar compensatory response by Cuckoo nestlings which follows an energetically demanding period of eviction of host eggs or chicks in both Redstart–Cuckoo (Grim *et al.* 2009a) and other systems (Anderson *et al.* 2009). We therefore did not find any support for parasite fledgling discrimination in Cuckoo–Redstart mixed broods (cf. De Mársico *et al.* 2012). Unexpectedly, Redstart fledglings from mixed broods did not suffer from sharing the nest with a Cuckoo, and fledged at similar ages, at similar masses and with similar wing and tarsus lengths as

Redstarts from solitary broods. Despite of delayed age at first flight, Redstarts from mixed broods compensated for this delay and achieved independence with similar parameters to those whose broods were not parasitized.

Solitary Cuckoos fledged, started to fly and achieved independence later after hatching compared with Redstarts from solitary broods. However, age from fledging at independence did not differ between the groups. Similarly, Cuckoos from mixed broods fledged, started to fly and achieved independence later after hatching compared with Redstarts from these broods. Nevertheless, age from fledging did not differ between the groups at either first flight or independence. Surprisingly, there was no significant difference in post-fledging predation rate, starvation and overall survival rates among all fledgling groups. Thus, our results suggest that the regular occurrence of mixed broods in this host–parasite system may be evolutionarily stable for both hosts and parasites (see also Samaš *et al.* 2018).

The ability of Cuckoos in mixed broods to compensate during the post-fledging period for smaller size and delayed ability to fly after leaving the host nest can perhaps be explained by the brood division we regularly observed in the Redstart study population. In mixed broods one of the adult Redstarts followed only Redstart fledglings which fledged (on average) almost 1 week earlier than the Cuckoo. This is advantageous for the Cuckoo, which receives undivided care from the second adult Redstart. An average Cuckoo nestling in a Redstart nest is fed at frequencies three times lower than a host brood of equal mass (Samaš *et al.* 2018). Therefore, if both adult Redstarts

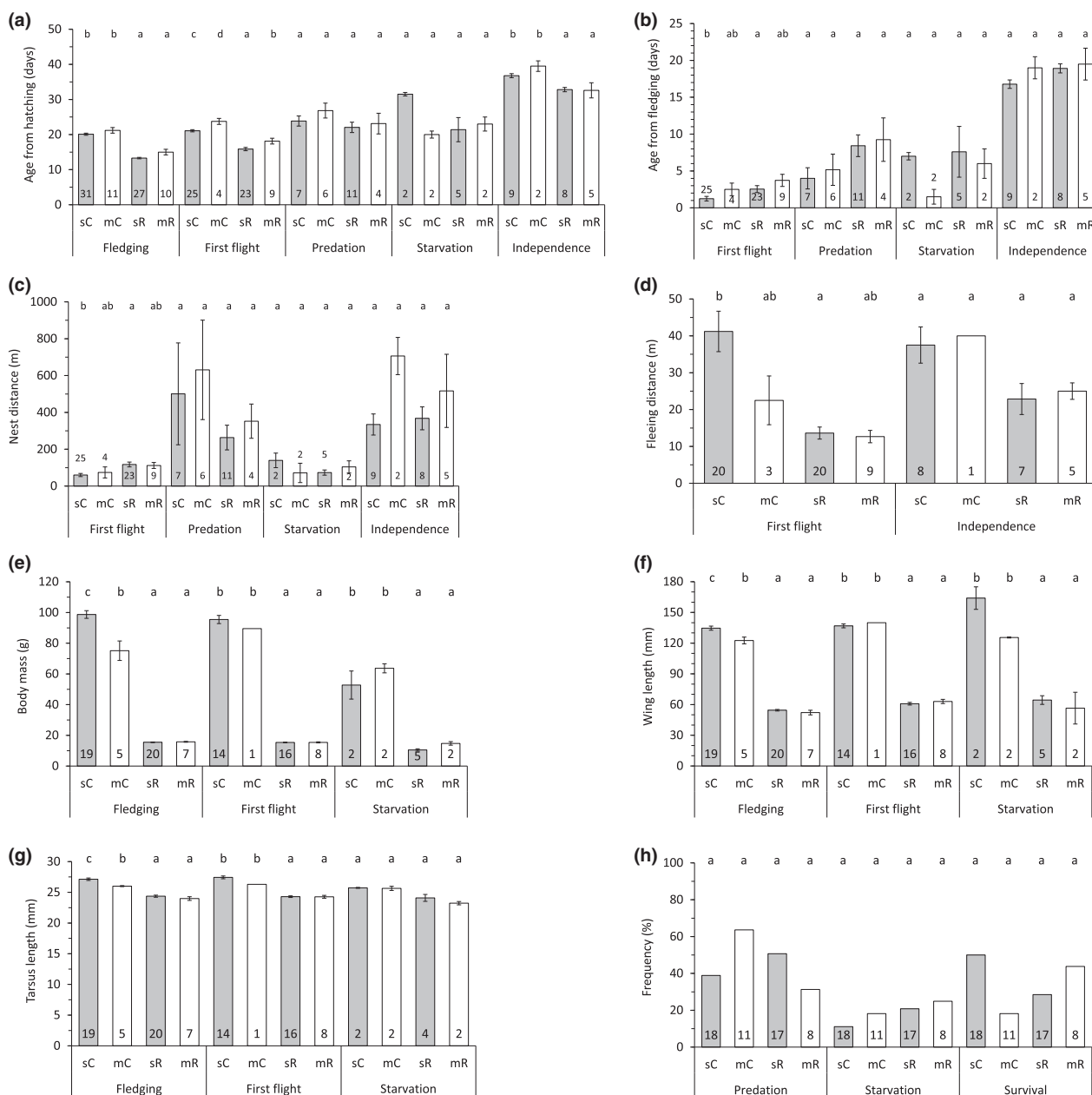


Figure 5. Fledging and post-fledging parameters (mean \pm se) among Cuckoos (C) and Redstarts (R) raised in solitary (s; grey bars) or in mixed broods (m; white bars) at pre-determined situations of biological interest (see Methods): (a) age from hatching, (b) age from fledging, (c) nest distance, (d) fleeing distance, (e) body mass, (f) wing length, (g) tarsus length and (h) outcome of the post-fledging period. Sample sizes are shown at the bottom of the bars and vary, e.g. because the fate of some fledglings was ‘unknown’ (see Methods). Results of between-group (sC, mC, sR, mR) post-hoc Tukey tests from linear models (Table S5) are denoted by letters above the bars: groups with different letters *within* each pre-determined situation are statistically significantly different. Not all potential combinations are included for various reasons (e.g. body measures cannot be taken from predated or independent fledglings).

feed all chicks in mixed broods almost equally (Grim *et al.* 2009a, 2017), then the absence of Redstart chicks is likely to result in an increase in

feeding rate for the Cuckoo even in the absence of one foster parent. As a result, Cuckoos from mixed broods may have received more food after

than before fledging of Redstart nest-mates, which thus may improve their condition during the post-fledging period (Cox *et al.* 2014).

Redstarts from mixed broods that survived a Cuckoo's eviction effort during the first days after hatching fledged at similar body mass to Redstarts from solitary broods. The Redstart chick accompanied by one weak Cuckoo competitor and one Redstart nest-mate (on average; see Methods) in a mixed brood probably experienced a similar or even higher provisioning rate as a Redstart chick reared with four other Redstart chicks (on average; see Methods) in a solitary Redstart brood (Samaš *et al.* 2018). In addition, the very large body size of the Cuckoo might affect heat loss rate in Redstart nest-mates, saving the energy required for thermoregulation in the sense that a large Cuckoo chick might in effect 'brood' the Redstart nest-mates (Grim *et al.* 2014). This cohabitation thus, paradoxically, may improve fledging condition of Redstarts in mixed broods, which is then maintained by continuous care by one parent during the post-fledging period.

Our results provide the first detailed and comprehensive insights based on reasonable sample sizes into the post-fledging period of any Cuckoo-host system. The only comparable study of Cuckoo post-fledging period (Wyllie 1981) found that Cuckoos in open-nesting Reed Warbler nests fledged on average 3–4 days earlier and first flew when they were 2–5 days younger than Redstart-Cuckoos. However, our mixed Cuckoos started to fly less than 1 day later and our solitary Cuckoos 1 day earlier after fledging than the Cuckoos raised by Reed Warblers (all numbers summarized from table 32 in Wyllie 1981). The relationship between higher fledging age and shorter time from fledging at first flight is consistent with prolonged nestling stage and flight capacity improvement in birds in general (Remeš & Matysioková 2016, Martin *et al.* 2018). In addition, both Cuckoo groups in our study reached independence older from hatching than those raised by Reed Warblers, but at similar age from fledging. Vega *et al.* (2016) assumed Cuckoos to be independent after they moved more than 20 km from the nest. Our observations show much lower nest distances at independence: 100–655 m in solitary Cuckoos and 605–807 m in Cuckoos from mixed broods (File S2).

Our results also showed about a week shorter nestling period in Redstarts than in young Cuckoos, but similar durations of post-fledging dependence.

The solitary Cuckoos achieved independence 2 days earlier after fledging compared with Redstarts from solitary broods. Thus, the prolonged nestling stage in cavity-nests and high predation risk of fledglings may be important factors driving the shortening of the Cuckoo post-fledging dependence period, in line with general patterns among birds (Remeš & Matysioková 2016). Another potential explanation to be tested in the future would be time-limited duration of parental care (as documented in a different Cuckoo host: Grim 2007b; see also Grim & Rutila 2017).

Predation, starvation and survival rates did not differ among fledgling groups. These results are not biased by the proportions of fledglings whose status we scored as unknown (see Methods) because proportions of 'unknown' fates did not differ among fledgling groups (File S2).

Only four (14%; two solitary and two mixed) of 29 Cuckoo fledglings died from starvation (see Methods), which confirmed Redstart as a suitable host for the Cuckoo in the sense of provisioning both before (Grim *et al.* 2017) and after fledging. Similarly, nine (17%) of 53 host fledglings starved during the post-fledging period (see Methods; Fisher's exact test $P = 1.00$). Thus, our findings are in line with the pattern that predation, but not starvation, is the primary source of fledgling mortality in passerines (Sullivan 1989, Yackel-Adams *et al.* 2006).

In the present study, 38% (11 of 29) of Cuckoo fledglings certainly survived until independence (see Methods). This estimate is very similar to the 42% (five of 12; Fisher's exact test $P = 1.00$) reported in a satellite telemetry study by Vega *et al.* (2016). Cuckoos raised by Reed Warblers in the study by Wyllie (1981) showed a survival rate of 22% (16 of 74) but this is not significantly different from the rate in this study (Fisher's exact test $P = 0.13$). The overall post-fledging survival rate to independence (36%) in Redstarts (19 out of 53; see Methods) was also statistically identical to that of our Cuckoos (Fisher's exact test $P = 1.00$).

Survival rate during the first 3 weeks after fledging ranged from 23 to 87% (mean \pm se = $59.0 \pm 0.03\%$, $n = 31$) in a review across passerine species (Cox *et al.* 2014). However, post-fledging survival rates of <40% combined with low overwinter survival may cause population declines (Cox *et al.* 2014). Vega *et al.* (2016) followed five Cuckoo fledglings raised alone in Redstart nests,

after achieving independence, and found a survival rate of 20% between independence and reaching the wintering grounds.

Finally, compensatory growth during the post-fledging period may itself influence development and survival of Cuckoos from mixed broods and may have long-term effects that are often not evident until much later in adult life (Metcalf & Monaghan 2001). To clarify these issues, further radio- and satellite-tracking studies of Cuckoos raised by Redstarts beyond the post-fledging dependence period are needed. The absence of similarly detailed studies prevents comparisons with other brood parasite–host systems, and this calls for more research on the virtually unknown post-fledging period in the context of avian co-evolutionary arms races.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

File S1: Table S1. Outputs of model for nest distances, i.e. dispersal distances from the natal nest (log-transformed to meet the assumptions of normality), in Cuckoo and Redstart fledglings raised in solitary or mixed broods.

File S1: Table S2. Outputs of full and final models for daily dispersal distances (log-transformed to meet the assumptions of normality), in Cuckoo and Redstart fledglings raised in solitary or mixed broods.

File S1: Table S3. Outputs of full and final marginal models (Poisson distribution, log link) for number of flights per hour in Cuckoo and Redstart fledglings raised in solitary or mixed broods.

File S1: Table S4. Outputs of full and final models for change in body mass in (a) Cuckoo and (b) Redstart fledglings raised in solitary or mixed broods.

File S1: Table S5. Comparison of fledging and post-fledging parameters among Cuckoos and Redstarts raised in solitary or in mixed broods at pre-determined situations of biological interest.

File S2. Raw dataset used in this study. (XLSX).