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Authors: Grim, Tomáš, and Samaš, Peter

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Growth performance of nestling Cuckoos *Cuculus canorus* in cavity nesting hosts

Tomáš GRIM* & Peter SAMAŠ

Department of Zoology and Laboratory of Ornithology, Palacký University, 17. listopadu 50, Olomouc 77146, CZECH REPUBLIC

*Corresponding author, e-mail: tomas.grim@upol.cz

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Abstract. Generalist brood parasites, like Common Cuckoos *Cuculus canorus*, target many host species. Why other sympatric hosts are not used, or actively avoided, remains one of the main gaps in our understanding of parasite-host coevolution. Cavity nesting passerines always represented a text-book example of unsuitable hosts but recent evidence casts multiple doubts on this traditional view. In general, any species can become an unsuitable host for a parasite at laying, incubation, or nestling stages with the last one being much less studied than the others. Therefore we examined Cuckoo chick performance in five cavity nesting host species, including one regular Cuckoo host — the Common Redstart *Phoenicurus phoenicurus* and four non-hosts: the Pied Flycatcher *Ficedula hypoleuca*, Spotted Flycatcher *Muscicapa striata*, Great Tit *Parus major*, and Coal Tit *Periparus ater*. Natural nests of non-hosts, as opposed to artificial nest boxes with small entrance holes, are often placed in cavities that show both entrance and inner cavity sizes large enough for female Cuckoos to lay and Cuckoo chicks to fledge. We did not find any evidence for chick discrimination in non-hosts, i.e., no chicks were rejected, attacked, or neglected. Cuckoo chicks grew similarly in nests of all four species of non-hosts, similarly to chicks in host Redstart nests, and generally better than in nests of the most numerous Cuckoo host, the Reed Warbler *Acrocephalus scirpaceus*. Although Cuckoo chick fledging mass was highly host species-specific (i.e., showed high statistical repeatability across various host species), we did not find any evidence for the hypothesis that host body size (mass) positively affects parasite chick growth (fledging mass or age). These findings provide impetus to further study apparently unsuitable hosts and perhaps even reconsider traditional classifications of host suitability in the context of brood parasite-host coevolution.

Key words: brood parasitism, fledging, growth, host selection, hole nesting birds, metareplication

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INTRODUCTION

Some brood parasites are specialists at individual female level (typically, each female lays her eggs into the nests of only a single species) but generalists at the species level (different females parasitize different species). This pattern is especially pronounced in Common Cuckoos *Cuculus canorus* (hereafter: Cuckoos) where individual females only rarely lay in nests of other than their focal host (Davies 2000). This is supported by both observations (telemetry: Honza et al. 2002) and molecular analyses (Skjelseth et al. 2004). At the same time, the list of recorded Cuckoo hosts is longer than 100 species (Davies 2000). Generally, a typical Cuckoo host might be defined as a small passerine feeding its chicks with insects and building an open nest (Davies 2000). In contrast, birds feeding their chicks with non-insect diet (e.g., fruits) and building closed nests (e.g., tree or

ground holes) are considered unsuitable hosts (Davies 2000). Although these parameters are important on average (see, e.g., comparative studies: Soler et al. 1999), they cannot explain why some particular passerine species are used by Cuckoos, whereas others are not. Contrary to traditional classifications, some insectivorous passerines are unable to raise the young Cuckoo to fledging (Asian Verditer Flycatchers *Eumyias thalassinus*, Yang et al. 2013) while some non-insectivorous passerines are able to do so (Song Thrush *Turdus philomelos*, Grim 2006a). Some cavity-nesters are excellent Cuckoo hosts (Common Redstarts *Phoenicurus phoenicurus*, hereafter: Redstarts, Rutila et al. 2002) whereas some open-nesters are not (European Greenfinches *Carduelis chloris*, Samaš et al. 2012).

Are these particular examples exceptions to the rule or do they reflect more general patterns? This question cannot be answered via comparative

studies exactly because of the exceptions like Verditer Flycatchers, Song Thrush, Redstarts, or European Greenfinches. Further, comparative studies are correlative and therefore it is impossible to determine causality, e.g., whether a particular cavity-nester species is avoided by Cuckoos because it is a cavity nester or because it is, at the same time, a poor provider of parental care or feeds chicks with insects which are poorly digestible (and cavity-nesting is then simply a correlate of unsuitable diet; cf. Yang et al. 2013). To test these alternative views requires experimental field studies, especially cross-fostering of Cuckoo chicks into nests of apparently unsuitable hosts. This has so far been done only rarely (Grim 2006a, Grim et al. 2011, Yang et al. 2013, Li et al. 2016).

The best candidates for such experiments are cavity nesters, especially flycatchers (Muscicapidae) and tits (Paridae) (Grim 2016). Cavity nesting can prevent successful Cuckoo parasitism due to both entrance size (Lambrechts et al. 2010) and the inner size of the cavity itself (Avilés et al. 2006). As text-book examples of unsuitable hosts — if we accept the traditional view — they should not reject any foreign eggs (Davies 2000, see also Manna et al. 2016). Classical studies supported this view (Davies & Brooke 1989, Moksnes et al. 1991; see also recent data: Grim 2016). Also, cases of parasitism of cavity nesters are generally rare and mostly interpreted as mistaken layings by female Cuckoos that lacked active nests of suitable hosts (Moksnes & Røskaft 1995, Davies 2000). However, the rarity of natural Cuckoo parasitism and absence of egg discrimination in nest boxes might simply be an unavoidable result of small entrance sizes that do not allow Cuckoos to lay into flycatcher and tit nests in artificial nest boxes (Grim et al. 2014). In contrast, under natural conditions (i.e., not in artificial nest boxes) some cavity nesters breed also in cavities, woodpecker-made or natural (Wesołowski 1989), with entrances large enough (Maziarz et al. 2015) for female Cuckoos to lay (Grim et al. 2014). Cuckoo chicks should be easily able to fledge from such cavities because laying Cuckoo females enter cavities (our own video-recordings from nest boxes: $N = 63$, in prep.) and Cuckoo chicks have smaller body sizes than adult cuckoos (Mikulica et al. 2017). Therefore, interactions with Cuckoos in *natural* cavities would allow for coevolution between cavity-nesters and Cuckoos. This holds especially for species that consistently prefer holes with large entrances (Redstarts, Spotted Flycatchers *Muscicapa striata*).

Indeed, a recent study (Liang et al. 2016) showed that Great Tits *Parus major*, expected to accept any foreign eggs (just like any other unsuitable hosts), do in fact in some populations (mostly in Asia but also in Europe) show extremely high egg rejection rates of simulated Cuckoo parasitism (even up to 100% in some populations). This provided a clear evidence that Great Tits have been, contra traditional claims, involved in coevolutionary arms-races (Dawkins & Krebs 1979) with Cuckoos (importantly, egg rejection by Great Tits also could not be explained as a by-product of adaptations against conspecific parasitism, cf. Samaš et al. 2014). Preliminary data on Cuckoo chick growth in Great Tit nests suggested that Great Tits might in fact be one of the best Cuckoo hosts in terms of a host ability to raise the parasite chick (Grim et al. 2014). This exciting preliminary lines of evidence casted doubts on the traditional view that all hole-nesting passerines are unsuitable Cuckoo hosts. Clearly, more data on parasite-host interactions in apparently unsuitable or non-parasitized hosts are necessary to resolve these issues.

Although some cavity-nesters were studied as for their responses to foreign eggs (see above) we know virtually nothing about their responses to Cuckoo chicks (but see Grim et al. 2009a,b, 2014). Overall, chick stage has been (Grim 2007a, 2008) and remains the least studied breeding stage in the context of parasite-host coevolution. Therefore, the aims of the present study were threefold and specifically targeted at this poorly studied stage: (1) Chick discrimination: by cross-fostering Cuckoo chicks into nests of several supposedly unsuitable hosts we tested if these passerines possess chick discrimination abilities. According to “rarer enemy effect” hypothesis only pure acceptors of natural Cuckoo parasitism should evolve chick discrimination (Grim 2006b, 2011). Most populations (but not all: Liang et al. 2016) of cavity nesters seem to be pure acceptors of experimental parasitism and therefore good candidates to look for chick discrimination by hosts (which should result in chick death). Parasite chick death due to chick discrimination or unsuitable diet (including unsuitable insect diet: Yang et al. 2013) is one of potential viable explanations for rarity of parasitism in cavity hosts. Further, all (non-)host species tested by us show shorter nestling periods than the Cuckoo does; therefore, chick discrimination without recognition, when nests requiring too long period of host care are deserted by hosts, is a feasible defence mechanism in the cavity hosts

(Grim et al. 2003, Grim 2007b). This represents additional potential explanation for the Cuckoo avoidance of cavity nesters. However, this was not tested yet. (2) Host selection: by quantifying multiple Cuckoo growth and fledging parameters we examined whether hole-nesters other than Redstarts are avoided by Cuckoos because they are poor providers of parental/fosterer care (despite hole entrance size). Under this scenario, Cuckoo chicks can grow and fledge from cavity nests — i.e., in contrast to Chick discrimination situation, they do not die before fledging — but grow poorly due to insufficient host provisioning capacity. Thus, cavity nesters other than Redstarts might be suitable but inferior hosts. If this was true then parasite females should avoid them and parasite more suitable sympatric hosts (as found in another host-parasite system: de Mársico & Reboreda 2008). (3) Interspecific patterns: by using already published data (Anderson et al. 2009, Geltsch et al. 2012, Li et al. 2016; older studies reviewed in Grim 2006a) and our new data (this study) we re-examined a hypothesis of Kleven et al. (1999) that host body size is an important positive predictor of Cuckoo chick growth.

Most previous studies of these topics were based on comparison of two host species, which is methodologically problematic (Hurlbert 1984, Garland & Adolph 1994). To avoid a potential problem of biased general conclusions due to idiosyncratic (and therefore non-generalizable) traits of a particular host species, we studied a whole community of cavity nesting passerines in our Finnish and Czech study sites. We sampled all five sympatric and synchronously breeding (with Cuckoos) cavity nesting passerines that occupied nest boxes in our study locations. These included one regular Cuckoo host and four passerines that are currently classified as non-hosts or apparently unsuitable hosts.

MATERIALS AND METHODS

We collected data in two geographically distant nest box populations (Samaš et al. 2016). Finnish study site was located nearby Ruokolahti (61°24'N, 28°37'E) in south-eastern Finland and data were collected during 2012–2016. Czech study site was located nearby Bzenec (48°56'N, 17°15'E) in south-eastern Czech Republic and data were collected during 2016. We stress that our aim was not to compare the two sites — by doing so we would commit pseudoreplication (Hurlbert 1984,

Garland & Adolph 1994). Instead, the Czech study site was established in 2015 with an intent to create a spatial metareplicate (sensu Johnson 2002, Kelly 2006) of the Finnish site, i.e., we have chosen extensive pine forests of similar age and structure as those nearby Ruokolahti and nest box design and placement was identical to the Finnish site. Nest box inner dimensions were 10–16 × 9–13 cm × 25–32 cm (depth, width and height, respectively) with the entrance hole 6–8 cm wide, placed about 1.4–1.7 m above the ground and attached to the tree trunk by wire (see Grim et al. 2009b and Samaš et al. 2016 for additional details).

Study model species

The Common Redstart is the only known regular Cuckoo host that breeds in cavities (Ruttila et al. 2002, Thomson et al. 2016) and therefore was the only cavity host that could be studied in principle at any European study site. There is ample evidence from both the past (museum egg collections: Moksnes & Røskoft 1995) and present (field data: Thomson et al. 2016) that it is one of the major Cuckoo hosts in forest habitats (reviewed in Samaš et al. 2016). Redstarts are able to reject (by selective ejection or desertion) some experimental non-mimetic eggs (Davies & Brooke 1989, Moksnes et al. 1991, Hauber et al. 2014, Dinets et al. 2015). However, they accept majority of naturally laid Cuckoo eggs: plain blue Redstart-Cuckoo eggs show almost perfect chemical, spectral, and avian-perceived similarity to plain blue host Redstart eggs (Igic et al. 2012) thus preventing their recognition and rejection by hosts (Thomson et al. 2016).

Pied Flycatchers *Ficedula hypoleuca* were parasitized by Cuckoos in the past, as suggested by data from museum egg collections (Moksnes & Røskoft 1995), but are currently not victimized by Cuckoos (reviewed by Liang et al. 2016). Pied Flycatchers accept any foreign eggs (Davies & Brooke 1989, Moksnes et al. 1991). Interestingly, their eggs are apparently (for a human eye) identical to Redstart-Cuckoo eggs, but blue Cuckoo eggs are still chemically, spectrally and visually (assessed in avian visual space) more similar to blue eggs of Redstarts than to blue eggs of Pied Flycatchers (Igic et al. 2012).

Spotted Flycatchers are considered suitable Cuckoo hosts because they build nests not only in cavities but also in places accessible to laying Cuckoo females (Davies & Brooke 1989). They were often reported as Cuckoo hosts in the past (Moksnes & Røskoft 1995) but we could not find any published information on their recent parasitism

status (therefore, they are classified as “non-hosts”). Spotted Flycatchers selectively eject non-mimetic eggs but mostly accept mimetic model eggs (Davies & Brooke 1989, Moksnes et al. 1991).

Great Tits were recorded as hosts of the Common Cuckoo in various populations during the 20th century, based on both museum egg collections (reviewed in Moksnes & Røskaft 1995) and findings of hatched Cuckoo chicks (reviewed in Grim et al. 2014). In Europe, they seem to be pure acceptors of experimental parasitism: in most populations, they do not specifically eject even highly non-mimetic experimental eggs (Moksnes et al. 1991, Liang et al. 2016). Although Davies & Brooke (1989) reported low rates of egg rejection, all rejections were by desertion and there is no evidence that desertion is a specific response to parasitism in Great Tits (see Liang et al. 2016).

Coal Tits *Periparus ater* were not documented to be parasitized by Cuckoos based on data from museum egg collections (Moksnes & Røskaft 1995). Although some sources (reviewed in Grim et al. 2014) listed Coal Tits as Cuckoo hosts, they did not support such claims with any data. To our knowledge, no study has so far tested Coal Tit ability to recognize and reject foreign eggs.

In our study sites, other European cavity nesters either were not breeding in our nest boxes at all (e.g., Blue Tits *Cyanistes caeruleus*) or we did find a few of their nests but the birds finished their breeding before any Cuckoo chicks were available for cross-fostering (Crested Tit *Lophophanes cristatus* N = 1, Willow Tit *Poecile montanus* N = 1).

Thus, all these four non-host passerines currently suffer nil parasitism rates (in contrast to documented past parasitism in some of them). Also the Czech populations (of all study species) were not parasitized by Cuckoos (this study). In contrast, Redstarts were heavily parasitized in our Finnish study site (32.5%, n = 569 nests, Smaš et al. 2016).

Cross-fostering experiments

We found only limited numbers of nests of most non-hosts: 47 Pied Flycatchers, 4 Spotted Flycatchers, 291 Great Tits, and 2 Coal Tits (in contrast to 482 nests of Redstarts). Some of these nests were predated before we had a chance to cross-foster a Cuckoo chick from our source Redstart nests; in other cases non-host nests were poorly synchronized with host nests (i.e., no fresh Cuckoo hatchlings were available close to the expected date of hatching of a focal non-host nest). For example, many Great Tit clutches (36%)

have already started incubation (and were therefore too late for being parasitized by Cuckoo eggs — either naturally by Cuckoos or experimentally by us) even before the first Cuckoo egg appeared in a Redstart nest within the particular season (N = 264; sample size is smaller than above because some nests were already predated or deserted at the time when we found them, therefore it was impossible to estimate their age).

Therefore the numbers of Cuckoo chicks that were cross-fostered to non-host nests were lower: Pied Flycatchers, N = 3 (all in Finland); Spotted Flycatchers, N = 2 (both in Finland); Great Tits, N = 7 (six in Finland [including one natural parasitism case from Grim et al. 2014], one in the Czech Republic); Coal Tits, N = 1 (in the Czech Republic). Out of these 13 cross-fostered chicks some Cuckoos died due to inclement weather or grew poorly because of cohabitation with host chicks and died (Results), reducing the final sample size for Cuckoo chicks in non-host nests (N = 9). In Finland, all cross-fostered Cuckoo chicks hatched from eggs that were originally laid into nests of Redstarts (the only regular Cuckoo host available). In the Czech Republic, all cross-fostered Cuckoo chicks hatched from eggs that were originally laid into nests of Great Reed Warblers *Acrocephalus arundinaceus* (the currently most locally common Cuckoo host available: Jelínek et al. 2014). We could not cross-foster Cuckoos from Redstart nests in the Czech Republic because Redstarts are not currently parasitized by Cuckoos in the Czech Republic and surely not at our study site (Smaš et al. 2016, see above). Therefore, Cuckoos raised by Redstarts in the Czech Republic were cross-fostered from Great Reed Warbler nests (N = 4). All Cuckoos raised by Redstarts in Finland hatched from eggs that were naturally laid into Redstart nests (N = 14).

Because of these unavoidable natural constraints we adopted a paired experimental design to increase the power of our statistical tests (below). For cross-fostering we selected a Cuckoo hatchling that was best synchronized out of all available chicks in active nests. If more chicks of similar age were available, we selected the one that hatched at shortest distance from the recipient non-host nest.

We did not cross-foster eggs to avoid potential egg rejection by non-hosts. Indeed, our preliminary attempts to do so resulted in high rejection of natural Cuckoo eggs by Great Tits in both Finland (60%, N = 5) and Czech Republic (67%, N = 9; note that neither of our two study sites were

included in the study of Liang et al. 2016; our data thus provide an independent evidence that rejection ability of Great Tits is even more geographically prevalent than suggested by Liang et al. 2016, see Introduction). Just like in all previous studies, Cuckoo eggs in source nests (i.e., Redstart nests in Finland and Great Reed Warbler nests in the Czech Republic in the present study) and clutches in focal non-host nests did not hatch at exactly the same time; the Cuckoo egg typically hatched 1–3 days earlier than the clutch of focal non-host (see also Kleven et al. 1999, Grim 2006a, Li et al. 2016). From this reason and because of the risks of egg ejection by hosts (above) we cross-fostered all Cuckoo hatchlings at the hatching day (i.e., chick age = 0). We note that hatching asynchrony of 1–2 days is usual in non-manipulated naturally parasitized Redstart clutches (own data). We did not cross-foster Cuckoos between Redstart nests because previous studies consistently found no effect of such intraspecific cross-fostering in Great Reed Warblers (Kleven et al. 1999), and Reed Warblers *Acrocephalus scirpaceus* (Grim 2007b). We did not manipulate nest content in any of non-host recipient nests, i.e., Cuckoo chicks were left free to evict host nest content just like under natural non-manipulated conditions.

We weighed each Cuckoo chick every 1–4 days since hatching using digital scale with precision 0.1 g. We measured maximum tarsus length (see Fig. 4.5 in Sutherland et al. 2004) shortly before expected fledging time using digital calliper with precision 0.1 mm.

In some previous studies, hatching day was 1 (Kleven et al. 1999), in others it was 0 (Li et al. 2016). In the present study, hatching day was 0. Therefore, we detracted 1 day from reported fledging age from studies where hatching day was 1 to avoid biased interspecific analyses in the present study (our hypothesis 3, Introduction).

Statistical analyses

We estimated growth parameters of each Cuckoo using nonlinear regression with chick age as predictor and its body mass as a response. We used logistic function $W(t) = A/(1 + e^{(-K*(t-t_i)})}$ where $W(t)$ is mass at age t , A is the asymptotic mass, K is a measure of growth rate, and t_i is the inflection point on the growth curve (Starck & Ricklefs 1998). Some cross-fostered chicks died (inclement weather, competition with host chicks) before fledging and therefore could not be included in all analyses. Therefore sample sizes differ among analyses.

Because of naturally limited sample sizes we used paired comparative design and paired tests (which are more powerful than unpaired tests; for this approach see Grim et al. 2009b). For statistical analyses, each cross-fostered Cuckoo chick in a non-host nest was matched with two Cuckoo chicks in two separate Redstart nests that hatched (1) in the same breeding season, (2) as synchronously as possible and (3) as nearby as possible (within the same study site); one of the matched Redstart-Cuckoo chicks hatched shortly before and the other one shortly after the cross-fostered Cuckoo in a non-host nest. Following Grim et al. (2009b) we used two chicks (i.e., not only one) to improve the reliability of our comparisons, i.e., to make sure that our conclusions were not contingent on the particular pattern of chick pairing. The temporal difference in hatching dates between matched Cuckoos was usually only 3–4 days. Thus, we ensured that both chicks within each matched pair (before, after) experienced similar conditions (weather, food availability, predation risk, etc.). We then used paired t-test across all pairs ($N = 9$) to test for differences in all six growth and fledging parameters (K , A , t_i , fledging tarsus length, fledging mass and fledging age). Before running these paired tests, we performed a preliminary data exploration to assess how the growth parameters vary among Cuckoos reared by different species. We used K-means clustering to find potential patterns in data (Hartigan & Wong 1979). Since there were five (non-)host species involved, the algorithm grouped the data into five clusters. In K-means clustering, clusters overlapping with each other suggest similarity between compared groups (Romesburg 2004).

Some sample sizes were limited, e.g., single Cuckoo chick per some non-host species (Table 1). Samples were similarly limited in previous Cuckoo growth studies (see references in Grim 2006a and data in Grim 2006a, Grim et al. 2011). However, a small sample size does not automatically mean that estimated parameters are biased — if measurements are highly repeatable across individuals then even limited samples may be representative (Dingemanse & Dochtermann 2013, see also Samaš et al. 2011). Therefore we calculated repeatability of growth and fledging parameters in data sets from host and non-host species with larger sample sizes (at least three Cuckoo chicks per host species). We calculated repeatability using formula $r = V_B/(V_B + V_E)$, where V_B denotes between-host variance and V_E residual variance (following Nakagawa & Schielzeth 2010). Variance components were obtained from linear mixed

model with a growth or fledging parameter (at the individual chick level) as a response and species as a categorical random effect (Nakagawa & Schielzeth 2010). In the next step, we chose highly repeatable parameters (see Results) and calculated correlation between species sample sizes (number of Cuckoo chicks sampled per host species) and growth or fledging parameter values averaged per species.

Finally, we re-tested interspecific patterns (hypothesis 3, Introduction) that have been originally tested by Grim (2006a). We tested whether host body size (mass, in grams, data retrieved from Dunning 2008) covaried with Cuckoo chick measured fledging mass (cf. Fig. 2 in Grim 2006a) and fledging age (cf. Fig. 3 in Grim 2006a). Previously published Cuckoo growth data were retrieved from a review by Grim (2006a); although Grim (2006a) averaged data from multiple studies of the same host species we instead used original values (see references in Grim 2006a). Recently, additional two host species were studied as for Cuckoo growth in their nests by Li et al. (2016). We also included additional data for Cuckoos raised by Great Reed Warblers from Anderson et al. (2009) and Geltsch et al. (2012). We used GetData Graph Digitizer (<http://getdata-graph-digitizer.com/>) to extract values from graphs from these studies. Using these data sets and our new data (this study) we could use 23 estimates of growth parameters from 14 Cuckoo host species providing much more robust tests than the study of Grim (2006a) which used only 8 estimates from 8 host species. As additional improvements, we

weighed analyses by sample size and included host species as a random effect to control for potential covariation of estimates from the Cuckoos raised by the same host species.

We note that this “interspecific” comparison is in fact not an interspecific phylogenetic comparative study in the traditional sense. This is because the response variable is always measured in the same species (the Common Cuckoo). Therefore traditional phylogenetic comparative methods cannot be applied. There is also no need to control for within species phylogeny because separate Cuckoo genotypes cannot be differentiated genetically (Gibbs et al. 2000, Fossøy et al. 2016). Even if they could be, it would be impossible to employ such information because the majority of data on Cuckoo growth were collected without any genetic data (also note that many of the studies were published decades before modern genetic analyses were invented; for additional discussion see Grim 2006a, Grim et al. 2011).

All analyses were conducted in R 3.1.3 (R Core Team 2014). Results are reported as mean $\pm$ SE unless stated otherwise.

RESULTS

Chick discrimination

We did not detect any cases that might be interpreted as chick discrimination: all cross-fostered Cuckoo chicks ($N = 13$) originally grew normally (Table 1, Figs 1, 2). The exception were two Cuckoo chicks in Great Tit nests that did not succeed in

Table 1. Overview of growth parameters (mean $\pm$ SE) for Cuckoo chicks raised until fledging by host (Common Redstart) and non-host species that breed in cavities. Shown are both estimated parameters (K — growth rate, A — asymptotic mass, t_i — inflection point) and measured parameters (note that we measured tarsus only once and shortly before the estimated fledging, i.e., when chicks were 17 or 18 days old). Additionally to unpaired comparisons here (ANOVAs), see Table 2 for paired comparisons within matched pairs of chicks (Redstart vs. non-host). Sample sizes differ for tarsus measurements in some species: Common Redstart $N = 14$, Pied Flycatcher $N = 2$, Great Tit $N = 2$. For fledging age sample size differs for the Great Tit ($N = 3$) because one cuckoo chick was predated shortly before expected fledging (age = 17 days); the chick reached growth asymptote before predation therefore it was possible to reliably estimate growth and fledging parameters (except of age).

Parameter	Common Redstart ($N = 18$)	Pied Flycatcher ($N = 3$)	Non-host species Spotted Flycatcher ($N = 1$)	Great Tit ($N = 4$)	Coal Tit ($N = 1$)	F	p
Growth parameters							
K	0.379 $\pm$ 0.013	0.407 $\pm$ 0.048	0.329	0.370 $\pm$ 0.020	0.390	0.44	0.78
A	91.8 $\pm$ 3.3	101.7 $\pm$ 8.5	88.4	104.0 $\pm$ 5.5	87.3	1.01	0.42
t_i	8.1 $\pm$ 0.3	8.5 $\pm$ 1.7	8.6	8.9 $\pm$ 0.4	8.6	0.33	0.85
Fledging							
tarsus length	27.2 $\pm$ 0.5	26.5 $\pm$ 0.1	26.2	27.1 $\pm$ 0.8	—	0.22	0.88
body mass	90.2 $\pm$ 2.3	97.5 $\pm$ 9.2	81.4	99.6 $\pm$ 6.3	87.9	1.09	0.39
age	20.6 $\pm$ 0.4	20.7 $\pm$ 1.2	18.0	20.3 $\pm$ 1.2	20.0	0.58	0.68



Fig. 1. Cuckoo chicks raised by the Common Redstart (A), Pied Flycatcher (B), Spotted Flycatcher (C), Great Tit (D), and Coal Tit (E). Photographs (A) and (D) are natural parasitism cases, others are from experimental cross-fosterings (see Methods). Photo credits: T. Grim (A–D), P. Samaš (E).

evicting all host progeny and were raised together with host chicks (nine chicks in both cases). Cohabiting led to poor growth and consequent death of these Cuckoo chicks on day 9 and 12 post-hatch when they weighed only 11 and 12 g, respectively (normal mass of Cuckoo chicks raised alone in Great Tit nests is 53 and 78 g at these respective ages, Fig. 2D). Another two Cuckoo chicks died most likely due to inclement weather (intense rain, causing soaked nest cup material and chick hypothermia); these chicks died when 5

days old in a Great Tit nest and when 20 days old in a Spotted Flycatcher nest (both in Finland; both after they have evicted host offspring).

Host selection

All remaining Cuckoos ($N = 9$) grew well under normal circumstances (i.e., after successful eviction of host offspring). Cross-fostered Cuckoos did not differ among non-hosts in any of several growth or fledging parameters (K , A , t_f , fledging tarsus, fledging mass and fledging age; Table 1).

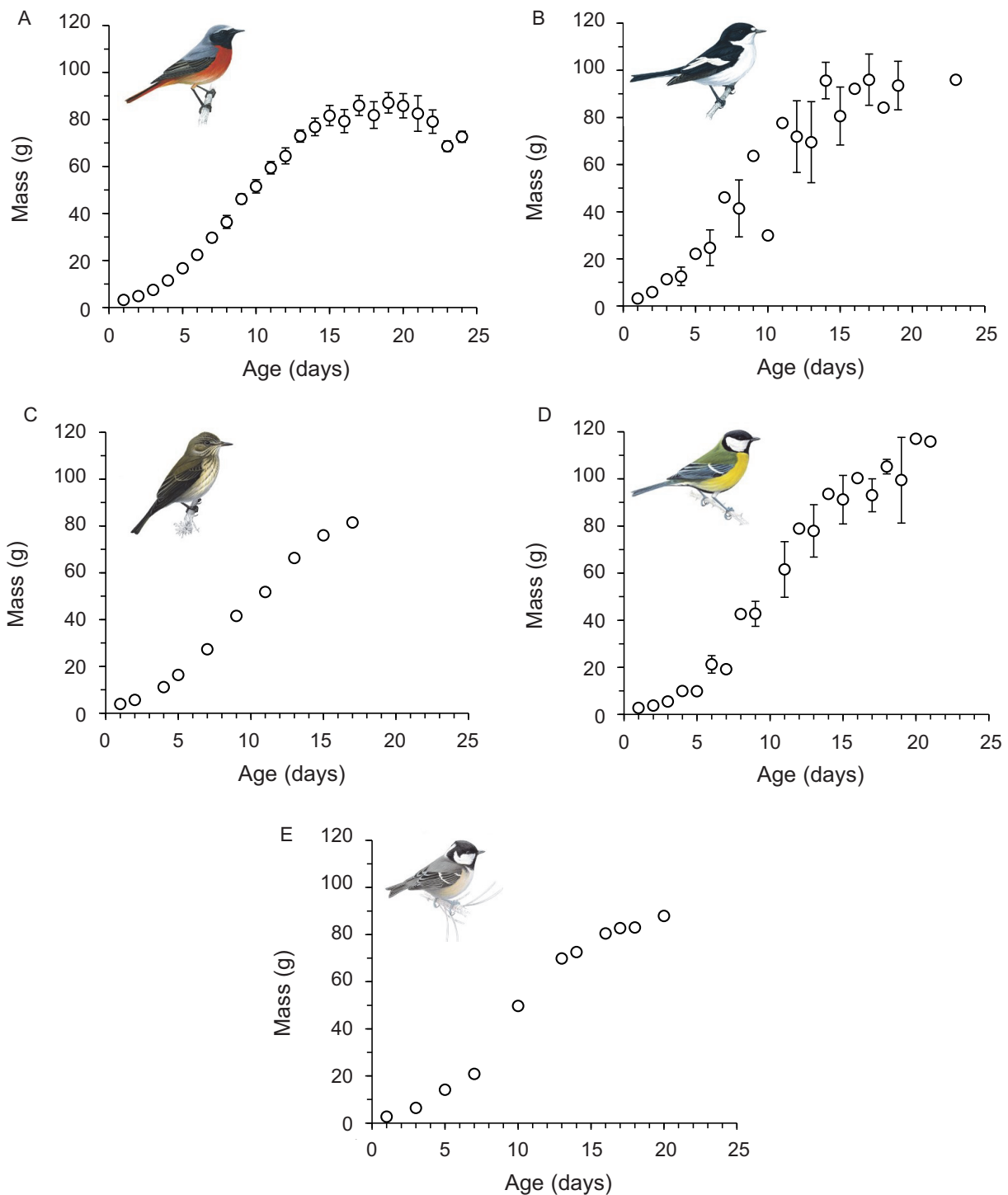


Fig. 2. Mass growth of Cuckoo chicks in nests of Common Redstarts (A), Pied Flycatchers (B), Spotted Flycatchers (C), Great Tits (D), and Coal Tits (E). Day 0 = day of hatching.

K-means clustering showed that all growth parameters of Cuckoos reared by non-host species overlapped with growth parameters of Cuckoos reared by Redstarts (i.e., clusters overlapped between all species). Therefore, it was statistically

reasonable to pool data from all four non-hosts into one comparative group. Paired comparisons between Cuckoos raised by Redstarts vs. those raised by non-hosts then showed that growth of cross-fostered Cuckoo chicks in non-host nests

Table 2. Paired t-test analyses of growth and fledging parameters between cross-fostered Cuckoos ($N = 9$) and matched Redstart Cuckoos that hatched shortly before ($N = 9$) or shortly after ($N = 9$) the cross-fostered ones in the same breeding season, as synchronously as possible and as nearby as possible (see Methods for details). Growth parameters: K — growth rate, A — asymptotic mass, t_i — inflection point.

Parameter	Non-host Cuckoos	Redstart Cuckoos		t		p	
		before	after	before	after	before	after
Growth parameters							
K	0.379 ± 0.018	0.370 ± 0.017	0.388 ± 0.019	0.76	0.52	0.47	0.62
A	99.7 ± 4.0	95.6 ± 5.4	88.1 ± 3.5	0.74	2.01	0.48	0.08
t_i	8.7 ± 0.5	8.4 ± 0.4	7.8 ± 0.3	0.84	1.73	0.43	0.12
Fledging							
tarsus length	26.7 ± 0.3	27.5 ± 0.7	27.0 ± 0.6	0.10	0.23	0.93	0.83
body mass	95.6 ± 0.3	93.2 ± 3.5	87.1 ± 2.8	0.34	1.65	0.74	0.14
age	20.1 ± 0.6	20.4 ± 0.5	20.7 ± 0.6	0.00	0.87	1.00	0.41

did not differ from spatio-temporally matched Redstart-Cuckoos in any of various growth or fledging parameters (Table 2).

Interspecific patterns

Repeatability of growth and fledging parameters K ($r = 0.00$), A ($r = 0.80$), t_i ($r = 0.10$), fledging mass ($r = 0.83$), fledging age ($r = 0.40$) varied considerably in Cuckoos reared by seven host species for which we had individual Cuckoo chick data (Table 3, excluding Cuckoos raised by Great Reed Warblers for which we had only species average data). Excluding hosts with only four or only three Cuckoo chicks did not change these estimates significantly. The repeatability of the highly repeatable parameters of asymptotic mass A and fledging mass did not correlate with sample size (Pearson's $r = 0.26$, $p = 0.58$ and $r = 0.21$, $p = 0.65$, respectively). This suggests that our analyses are not biased due to limited sample sizes for some species.

Cuckoo chick growth parameters of K and t_i were similar between non-host cavity nesters and all open nesting host species as seen from their overlapping 95% CIs (confidence intervals) (Table 3). Cuckoos in non-host cavity nesters reached higher fledging mass and asymptotic fledging mass (A) compared to Cuckoos in the nests of the most common Cuckoo host in Europe, the Reed Warbler (Table 3). Also compared to other open-nesting hosts, Cuckoos raised by cavity nesters grew better or at least similarly well (Table 3). Cuckoos in non-host cavity nesters had tendency to fledge later compared to all open nesting species (but see overlapping CIs: Table 3). All Cuckoo growth and fledging parameters were similar between non-host cavity nesters and Redstart, the only regular cavity nesting host species.

Host body size was not a statistically significant predictor of Cuckoo chick fledging mass ($F_{1,13.51} = 0.16$, $p = 0.70$; host body size slope estimate = 0.14 ± 0.34). Host body size also did not explain any significant variation in Cuckoo chick fledging age ($F_{1,13.48} = 0.00$, $p = 0.99$; host body size slope estimate = 0.00 ± 0.04).

DISCUSSION

All Cuckoo chicks cross-fostered by us into the nests of Pied Flycatchers, Spotted Flycatchers, Great Tits and Coal Tits were accepted by hosts and typically grew well until fledging or death due to competition with non-evicted host chicks or hypothermia. The latter happened due to heavy rains. Also Cuckoo chicks in Redstart nests often similarly died in such periods indicating that these deaths were not caused by host chick discrimination. Thus, absence of natural Cuckoo parasitism in these potential hosts cannot be explained via host chick discrimination (Grim 2006b, 2011). Cuckoo chicks in non-host nests often fledged at ages around 3 weeks, i.e., long after non-host own chicks would fledge (around 2 weeks). This suggests that these passerines do not show rigid rules regarding the timing of fledging (see Grim et al. 2003 and Grim 2007b for discussions).

Cuckoo chicks successfully evicted all host offspring in most nests, with only two unsuccessful Cuckoos in Great Tit nests. Cohabitation with Great Tit chicks resulted in death of both unsuccessful evictors before fledging. Cohabitation with Redstart chicks is similarly fatal to Cuckoos under both natural (Ruttila et al. 2002, Samaš et al. 2016, Thomson et al. 2016) and experimental conditions

Table 3. Cuckoo nestling growth performance (mean and 95% confidence intervals [CIs] in brackets) across selected host species. A — asymptotic mass, K — growth rate, and t_i — inflection point on the growth curve estimated from logistic function (Starck & Ricklefs 1998). We selected host species where $N > 1$ Cuckoo chick per host and where the source study provided parameters (means) with their 95% CIs or those could be estimated from SEs. We excluded experimental results where eviction effort was manipulated. Overlapping CIs suggest that Cuckoo chick growth parameters are not statistically significantly different between particular host species. Note that “Great Tit” includes data from Grim et al. (2014) from the same study population as our one.

Host species	N	K	A	t_i	Fledging mass	Fledging age	Host body mass	Source
Great Reed Warbler	11	0.368	91.1	8.7	88.3 (84.4–92.2)	18.0 (16.7–19.3)	30.0	Kleven et al. (1999)
	7	0.328	88.8	8.3	84.8 (81.04–88.56)	18.1 (17.23–18.99)	30.0	Anderson et al. (2009)
Reed Warbler	10	0.319	89.7	8.1	88.2 (84.8–91.6)	18.7 (15.3–22.1)	30.0	Geltsch et al. (2012)
	22	0.354	71.2	8.34	68.1 (65.1–71.1)	17.0 (15.8–18.2)	12.3	Kleven et al. (1999)
	27	0.372	71.6 (69.3–73.9)	9.0 (8.6–9.4)	69.3 (67.0–71.6)	17.7 (17.1–19.8)	12.3	Grim (2006a)
Song Thrush	3	0.357	97.1	9.6	95.2	18.3	67.8	Grim (2006a)
		(0.313–0.401)	(94.3–99.9)	(8.8–10.4)	(79.5–111.0)	(16.9–19.8)		
Oriental Reed Warbler	8	0.359	57.6	8.0	58.7	18.3	25.5	Li et al. (2016)
		(0.303–0.415)	(51.3–63.9)	(6.8–9.2)	(56.9–60.5)	(17.7–18.9)		
Reed Parrotbill	4	0.390	59.8	7.8	56.4	17.5	20.9	Li et al. (2016)
		(0.290–0.490)	(49.0–70.6)	(6.2–9.4)	(51.2–61.6)	(16.5–18.5)		
Redstart	18	0.379	91.8	8.1	90.2	20.6	14.6	this study
		(0.353–0.406)	(84.9–98.7)	(7.6–8.7)	(85.3–95.0)	(19.8–21.3)		
Pied Flycatcher	3	0.407	101.7	8.5	97.5	20.7	13.9	this study
		(0.201–0.612)	(65.4–138.1)	(1.4–15.6)	(58.1–136.9)	(15.5–25.8)		
Great Tit	4	0.370	104.0	8.9	99.6	20.3	18.3	this study
		(0.307–0.433)	(87.0–121.1)	(7.5–10.3)	(79.7–119.5)	(15.2–25.5)		

(Grim et al. 2009a). The quality of non-hosts in raising the Cuckoo chick was similar — there were no clear differences in any of the many measured or estimated growth and fledging parameters (Table 1) and the magnitude of differences was well within the range of variation detected in various other regular Cuckoo hosts (Table 3; see also Figs. 2 and 3 in Grim 2006a). Paired comparisons with Redstart-Cuckoo chicks (matched in time and space) revealed that non-hosts were similarly good at raising Cuckoo chicks as Redstarts. Finally, interspecific comparison, including our novel data and recently published data from other studies, did not support a hypothesis of Kleven et al. (1999) that larger body sized hosts are better at raising Cuckoo chicks (see also Grim 2006a).

Some previous studies (e.g., Kleven et al. 1999) tested a general hypothesis (e.g., host body size positively affects parasite chick growth) by comparison of two species only. This is methodologically problematic because two species always differ in multiple other factors than the focal one, e.g., not only in host body size but also in habitat selection, diet composition, mating system and many others. Therefore it is impossible to determine what caused the observed differences (e.g., body mass or any of the many other correlated traits?). Comparing two species represents pseudoreplication (Hurlbert 1984) and should be avoided (Garland & Adolph 1994) unless the tested question is not general but focuses specifically on a study systems that consists of only two species, i.e., no other sympatric host species are available (this happens rarely: Li et al. 2016). Even in such cases causality behind detected differences cannot be inferred in principle (Garland & Adolph 1994).

Indeed, already a limited analysis of Cuckoo chick growth in three hosts casted doubts on the conclusion that a larger body size host is able to raise Cuckoo chicks to higher fledging mass (Grim 2006a). Our results here provide a much more robust support for this conclusion (because our sample size is much larger than that of Grim 2006a, see above). We find especially revealing the comparison between two former subspecies of the Great Reed Warbler, which are nowadays generally accepted as two separate species. The fledging mass of Cuckoo chicks in the nests of the Great Reed Warbler (*sensu stricto*) is 88 g (Kleven et al. 1999) while it is only 59g in the nests of the Oriental Reed Warbler *A. orientalis* (Li et al. 2016). The body mass of the two hosts is very similar 28.5

g (Kleven et al. 1999) and 25.5 g (Dyrce & de Juana 2016), respectively. In fact, fledging mass of Cuckoo chicks raised by Oriental Reed Warblers is even lower than fledging mass (68 g) of Cuckoos raised by Reed Warblers that have much smaller body mass (12 g, Kleven et al. 1999). Thus, if Kleven et al. (1999) studied a different (Chinese) population of the Great Reed Warbler they would reach exactly opposite conclusions: host body size affects Cuckoo chick growth negatively. This highlights the risk of spurious conclusions when comparing only two species, each of them represented by only one population (Garland & Adolph 1994).

This comparison — and overall “interspecific” test (above) — provides clear evidence against a hypothesis that host body size positively affects Cuckoo chick growth. This raises a question which host traits are then responsible for a huge variation in Cuckoo chick growth and fledging parameters across various Cuckoo hosts. Because of multiple potential candidate life-history traits it will be necessary to estimate Cuckoo growth parameters in more Cuckoo hosts to avoid a statistical problem of low degrees of freedom in analyses where too many predictor variables are used to explain variation in too small data sets (i.e., the problem of model overfitting; Babyak 2004).

Future studies should focus on natural nests of apparent Cuckoo “non-hosts”. Our data and previous recent findings (Grim et al. 2014, Grim 2016, Liang et al. 2016) concur that we need to learn much more about Cuckoo-host interactions in cavity nesters before we can reach reliable conclusions (Grim 2016). For example, the traditional claim that the Great Tit is an unsuitable host has been clearly premature: Great Tits frequently reject experimental eggs (Liang et al. 2016), selectively eject natural Cuckoo eggs cross-fostered into their nests (this study) and are able to raise Cuckoo chicks better than most regular hosts (Grim et al. 2014, this study). Thus, Great Tit nests must at least locally experience a parasitism pressure from Cuckoos, or must have been parasitized regularly in the past, otherwise the existence of highly advanced egg discrimination abilities in Great Tits cannot be explained (see that egg rejection ability cannot be explained as a collateral damage to interspecific brood parasite from adaptations evolved in the context of conspecific parasitism: Samas et al. 2014, Grim 2016). In this context we suggest that the avoidance of larger nest entrances in some cavity nesters could have evolved not only due to predation (Wesołowski

1989, Maziarz et al. 2015), but also due to pressures from brood parasitic Cuckoos. Natural cavities of both Great Tits and other cavity passerines remain virtually unstudied (reviewed in Wesolowski 2007). Our results suggest that more focus on these so far neglected hosts in their *natural* cavity nests can bring exciting results and change our view of brood parasite-host coevolution.

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STRESZCZENIE

[Rozwój piskląt kukułki w gniazdach dziuplaków]

Pasożyty lęgowe klasyfikowane jako generaliści, takie jak kukułka, wykorzystują jako gospodarzy wiele gatunków ptaków. Lista gospodarzy kukułki obejmuje ponad 100 gatunków. Typowymi gospodarzami kukułki są niewielkie wróblaki dokarmiające pisklęta owadami oraz budujące otwarte gniazda. Dlaczego jednak wiele innych gatunków występujących sympatrycznie z kukułkami nie jest przez nie wykorzystywanych lub nawet są aktywnie unikane, pozostaje jedną z głównych luk w naszej wiedzy na temat koewolucji układu pasożyt lęgowy-gospodarz. Dziuplaki stanowią podręcznikowy przykład gatunków, które nie są odpowiednimi gospodarzami dla kukułek, co może wiązać się z rozmiarem otworu wejściowego do dziupli, jak i rozmiarem samej dziupli. Jednak ostatnie dane, szczególnie związane z usuwaniem przez dziuplaki eksperymentalnie podrzucanych jaj kukułki, rodzą poważne wątpliwości, co do takiego twierdzenia.

Każdy z gatunków może stać się nieodpowiednim gospodarzem dla pasożyta lęgowego na każdym z trzech etapów cyklu lęgowego — składania jaj, inkubacji oraz karmienia piskląt. Szczególnie temu ostatniemu etapowi poświęcono jak dotąd niewiele uwagi. Tymczasem w przypadku dziuplaków (i innych ptaków) może istnieć mechanizm rozpoznawania własnego potomstwa, a ponadto pokarm przynoszony pisklątom może być nieodpowiedni dla piskląt kukulek. Oba te mechanizmy mogą prowadzić do śmierci piskląt kukułki, co z kolei może powodować rzadkie obserwacje pasożytnictwa lęgowego w tej grupie ptaków.

W pracy zbadano rozwój piskląt kukulek w gniazdach pięciu gatunków dziuplaków — naturalnego gospodarza, jakim jest pleszka, dla której w ostatnich latach stwierdzono dość duży udział lęgów zapasożyconych przez kukułki, oraz gatunków niebędących jej gospodarzami — muchołówki żałobnej, muchołówki szarej, bogatki oraz sosnowki (Fig. 1). Naturalne miejsca gniazdowe tych dziuplaków w przeciwieństwie do standardowych skrzynek lęgowych, mają czasem na tyle duże otwory wejściowe, jak i same wnętrza dziupli, że umożliwiają samicom kukulek złożenie jaj oraz rozwój i opuszczenie gniazda przez ich pisklęta. W pracy badane dziuplaki gniazdowały w skrzynkach lęgowych o dużym otworze wlotowym (średnica 6–8 cm). Badania przeprowadzono na dwóch powierzchniach: w południowo-wschodniej Finlandii oraz w południowo-wschodnich Czechach. W przypadku gniazd pleszki badano pisklęta kukulek, które wykluły się z jaj złożonych bezpośrednio przez

samice kukułki (Finlandia) lub pisklęta, które pochodziły z gniazd trzcinaków (Czechy). W przypadku pozostałych dziuplaków do gniazd podrzucano pisklęta zabrane z gniazd pleszek (Finlandia) lub trzcinaków (Czechy). Podrzucanie piskląt do gniazd dziuplaków niebędących naturalnymi gospodarzami odbywało się w ten sposób, aby można było porównać uzyskane dla takiego pisklęcia wyniki z wynikami dla kukulek w gnieździe pleszek, które wykluły się w zbliżonym terminie. W ten sposób porównywano ptaki wyrastające w podobnych warunkach pogodowych, dostępności pokarmu i presji drapieżników.

Nie stwierdzono, aby podrzucone pisklęta kukulek w gniazdach gatunków niebędących naturalnymi gospodarzami zostały odrzucone lub były zaniedbywane. Wzrost piskląt kukulek w gniazdach wszystkich gatunków niebędących gospodarzami oraz w gniazdach pleszki nie różnił się (Tab. 1, 2, Fig. 2), a określone parametry wzrostu były nawet wyższe niż te stwierdzane dla piskląt wychowujących się w gniazdach trzcinaczka — najczęstszego gospodarza kukulek. Przeanalizowano również istniejące dane dotyczące tempa wzrostu i masy ciała piskląt opuszczających gniazda dla wielu różnych gospodarzy, ale nie stwierdzono, aby rozmiary ciała gospodarza pomyślnie wpływały na rozwój młodych kukulek (Tab. 3).

Badania te dostarczają impulsu do dalszych badań gatunków uznawanych do tej pory za nieodpowiednich gospodarzy dla kukułki, a także skłaniają do zakwestionowania tradycyjnej klasyfikacji cech gospodarza w kontekście koewolucji układu pasożyt lęgowy-gospodarz.