



NTNU – Trondheim
Norwegian University of
Science and Technology

Plaintive Cuckoo Nestling Adaptations and Development in Common Tailorbird Nests

- Costly Child Custody

Odd Helge Tunheim

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Supervisor: Eivin Røskoft, IBI

Co-supervisor: Frode Fossøy, IBI
Bård Gunnar Stokke, IBI
Wei Liang, Hainan Normal University

Norwegian University of Science and Technology
Department of Biology

Abstract

Avian brood parasitism represents a suitable system for studying coevolution, as parasite and host engage in an escalating arms race. The parasite develops adaptations to overcome host defences, and in addition develops traits that convince host parents to invest in the parasitic nestlings. A restricted number of study species have built much of the body of knowledge on brood parasitism, but as selection pressures vary between parasite-host systems, generalization between systems may vary in validity. This study aimed at investigating development, behaviour and adaptations of parasite nestlings in a poorly known parasite-host system consisting of the plaintive cuckoo *Cacomantis merulinus* and its common tailorbird *Orthotomus sutorius* host. Following the hypothesis that parasite nestlings solicit more parental care than host offspring, applying the derived understanding of the common cuckoo *Cuculus canorus* developmental characteristics and adaptations as a fundamental basis, three predictions were deduced: 1) the parasite nestlings would gain more weight than one tailorbird nestling, 2) the parasite nestlings would receive more provisioning than a host nestling, and 3) given that the previous predictions were met, the parasite nestlings would possess an extravagant begging display measured as begging intensity. The first prediction was redeemed, as the cuckoo nestlings gained more weight faster than host progeny. On the contrary to predictions 2 and 3, cuckoos did not solicit higher provisioning rates and they begged at rates equal to that of one host nestling during the first part of the nestling period. Differences in physiology between the two species where cuckoo nestlings allocate parental resources differently from host nestlings may provide an explanation as to why they gain more weight but fail to appropriate higher provisioning. Selection pressures may have favoured slower development during the first part of the nestling stage, where an intensification of the begging display during the latter half may convince parents to provide prolonged care to the cuckoo nestling and it may benefit from elevated feeding rates. The acquirement of a warning display may facilitate the exaggerated begging display. Cuckoo nestling mimicry of one tailorbird nestling's begging calls may be an adaptation that secures equal provisioning to one host nestling during the first period in the nest. The findings from this study are integrated in the body of knowledge on this parasite/host system, and coevolutionary adaptations of the system as a whole are discussed on the basis of previously attained knowledge of brood-parasitic systems.

Samandrag

Kullparasittisme hos fugl representerar velegna system for studium av samevolusjon, då parasitt og vert inngår i eit eskalerande våpenkapplau. Parasitten må trengje gjennom verten sitt forsvar og i tillegg utvikle tilpassingar til verten si livshistorie for å sikre tilfredsstillande omsorg frå fosterforeldra. Forståinga av kullparasittisme byggjer på studiar av få artar, og sidan seleksjonspress varierar mellom artar og kullparasittiske system, kan ukjende system avvike frå forventa funksjon. Dette studiet tek føre seg eit lite studert parasitt/vert system mellom klagegauk *Cacomantis merulinus* og langhaleskreddarfugl *Orthotomus sutorius*, kor reirunge-stadiet er ukjend for vitskapen. For å teste hypotesa om at reirparasittar tileignar seg meir foreldreomsorg enn vertsungar vart tre predikasjonar formulerte, kor forståinga av utvikling og tilpassing hos eurasiatisk gauk *Cuculus canorus* vart brukt som fundament: 1) gaukungen var forventa å tileigne seg høgare vekt samanlikna med ein vertsfuglunge, 2) gaukungen var forventa å motta høgare fôringsrate enn ein vertsunge, og 3) gitt at dei fyrste predikasjonane vart innfridde var gaukungen forventa å ha tileigna seg ein overdriven tigge-åtferd. Den fyrste predikasjonen vart innfridd, då gaukungen vaks raskare enn vertsungar. Predikasjonane 2 og 3 vart derimot ikkje nådd då gaukungen, gjennom den fyrste tida i vertsreiret, mottok like mykje mat og tigga like mykje som ein vertsunge. Fundamentale fysiologiske ulikheiter mellom artane, med blant anna arts-spesifikk fordeling av foreldreressursar, kan vere ei forklaring på kvifor gaukungen auka i vekt utan å tileigne seg meir mat enn vertsungane. Seleksjonspress kan ha lagt vilkår for ei låg utviklingsrate den fyrste delen av reirunge perioden, kor ei intensivering i tigging-åtferd den siste perioden kan påverke fosterforeldra til å gi gaukungen lengre foreldreomsorg enn til sine eigne ungar. Utviklinga av åtvaringsåtferd kan mogleggjere ei auka intensitet av tigge-åtferd. Strukturen på tiggelyden til gaukungen har mange fellestrekk med tiggelyden til ein vertsunge, noko som kan vere ei tilpassing for å sikre same fôringsfrekvens som ein vertsunge. Data frå dette studiet vart sett saman med kunnskap frå andre nivå av hekke-syklusen i dette systemet med drøfting av samevolusjon og system-funksjonar.

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Introduction

The main life-history trait that characterizes avian brood parasites is the apparent lack of parental care. Brood parasites deposit their eggs in nests of conspecifics (intraspecific brood parasitism) or in the nests of other species (interspecific brood parasitism), a reproductive strategy that is either obligate or facultative (Davies, 2000; Feeney, Welbergen, & Langmore, 2014). When a brood parasite successfully lays an egg in a host nest and the host accepts the parasitic egg, the host will care for the brood-parasitic progeny at the expense of own reproductive success. Thus, brood parasitism may act as a strong selective agent for hosts to develop a defence against parasitism, selecting for new adaptations by the parasite, again selecting for a counter-adaptation by the host, and so on, leading to a coevolutionary arms race (Davies, 2000; Davies & Brooke, 1988; Dawkins & Krebs, 1979; Rothstein, 1990).

This scenario has resulted in complex and varying parasite-host systems, where adaptations by the parasite and counter-adaptations by the host have been uncovered in most stages during the breeding cycle; frontline-, egg-, nestling- and fledgling stage (Brooke & Davies, 1988; De Mársico, Gantchoff, & Reboreda, 2012; Feeney et al., 2014; Langmore, Hunt, & Kilner, 2003; Welbergen & Davies, 2009). The focus of coevolutionary studies in brood-parasitic systems has traditionally mostly been on the egg stage (Davies, 2000; Moksnes & Røskaft, 1995; Rothstein, 1990). An alien egg can either be accepted or rejected by the host. Egg rejection follows two cognitive mechanisms; true recognition, in which the host compares the clutch to an internal template of expectations of its own egg morphology; and discordancy, in which the host rejects the egg that looks different from its own egg (Feeney et al., 2014; Rothstein, 1975). Hosts are known to be able to recognize alien eggs using morphological cues like colouration (e.g. Rothstein, 1982), shape (Mason & Rothstein, 1986), size (Marchetti, 2000), pattern (Stoddard & Stevens, 2010), the arrangement of eggs in the nest (Polačiková et al., 2013) and lastly a combination of the mentioned cues (Spottiswoode & Stevens, 2010). Support has been found for both mechanisms (true recognition; (Amundsen, Brobakken, Moksnes, & Røskaft, 2002; Lotem, Nakamura, & Zahavi, 1995), discordancy; (Marchetti, 2000) and for both in the same system (e.g. Moskat et al. (2010)). In order to ensure parasitism, selection on egg mimicry by the brood parasite is intensified (e.g. Rothstein, 1982). Acceptance of parasitic eggs is high if the perceived risk of being parasitized is low or if the cost of defence is high (Røskaft, Moksnes, Stokke, Bicik, & Moskat, 2002; Stokke, Honza, Moksnes, Røskaft, & Rudolfson, 2002). In some parasite-host

systems, defences (especially at the egg stage) have selected for specialization on one host by the brood parasite (as it participates in an arms race with the host), giving rise to genetically distinct parasite-races called *gentes* (Fossøy et al., 2011; Gibbs et al., 2000; Moksnes & Røskaft, 1995).

The appearance of brood parasitic nestlings is often very different from host nestlings. Given the acute ability to reject parasitic eggs, the apparent lack of alien nestling rejection by the host has puzzled scientists for decades (Davies, 2000), and nestling rejection or discrimination have so far only been found in a few systems (Grim, Kleven, & Mikulica, 2003; Langmore et al., 2003; Sato, Tokue, Noske, Mikami, & Ueda, 2010). Lotem (1993) neatly presented a model explaining that an adaptation by the host in learning to recognize brood parasitic eggs might be beneficial, while imprinting on nestlings might be maladaptive due to the cost of misimprinting if being parasitized during the first breeding attempt. In addition, physical and cognitive constraints, e.g. the change of morphology of nestlings throughout development and the hierarchical age structures in broods during the nestling period, may also halt brood-parasitic nestling recognition (Davies & Brooke, 1988; Grim, 2006a).

Various selection pressures, coevolutionary dynamics and local adaptations will alter spatially distinct populations leading to a greater diversity in phenotypes and genotypes. Encompassing this in a metapopulation perspective and associated evolutionary mechanisms (through gene flow, environmental stochasticity, various selection forces, extinctions and re-colonization), the presence of rejecters and acceptors in the same population can be explained by immigration of acceptors from non-parasitized populations (Røskaft, Takasu, Moksnes, & Stokke, 2006; Stokke, Moksnes, & Røskaft, 2005). Egg discrimination will be more beneficial to develop in terms of cognitive costs and costs of recognition errors, compared to nestling discrimination (Davies & Brooke, 1988; Planqué, Britton, Franks, & Peletier, 2002), making brood parasitic nestlings a “rarer enemy” (see rare enemy hypothesis; Dawkins and Krebs (1979)) and thus more difficult to develop a defence against (Grim, 2006a). The large inter-system variation in defence-portfolios might also be explained by the mechanisms of strategy-blocking (Britton, Planqué, & Franks, 2007) and strategy-facilitation (Kilner & Langmore, 2011). Strategy-facilitation suggests that for each line of host defence, evolution of another line of host defence might be promoted (e.g. recognizing adult brood parasite morphology might be followed by development of egg rejection (Feeney et al., 2014)) whereby strategy-blocking refers to how adaptation of one strategy may block the appearance of another strategy (e.g. in systems with nestling rejection, there is no egg-discrimination

(Britton et al., 2007)). If the benefit of strategy-facilitation outweighs strategy-blocking, hosts will develop complex defence portfolios (Kilner & Langmore, 2011). The ecology should always be considered in each system as strategy-blocking and strategy-facilitation might be conditional on the ecological parameters, with a general expectation of richer defence portfolios in richer environments (Britton et al., 2007).

Empirical evidence may provide indirect support to Lotem's (1993) model as hosts partly rely on "recognition-free" mechanisms (Feeney et al., 2014). Langmore et al. (2003) found that the primary cue superb fairy-wrens (*Malurus cyaneus*) used in discriminating against brood parasitic Horsfield bronze-cuckoo (*Chalcites basalis*) nestlings was the presence of a sole nestling in the nest. In addition, visual and vocal cues were applied in what might be a template-guided learning by hosts to avoid misimprinting on brood parasite nestlings if predated at the first breeding attempt, as older individuals were less likely to accept brood-parasitic nestlings (Langmore, Cockburn, Russell, & Kilner, 2009). As a probable response, Horsfield bronze-cuckoo nestlings have developed begging call mimicry, and visual host nestling mimicry in nestling down and colouration on the skin and flanges (Langmore, Maurer, Adcock, & Kilner, 2008; Langmore et al., 2011).

Some adaptations might not be developed as a consequence of the coevolutionary arms race, but rather as an adaptation by the parasite to tune in on the hosts life history (Davies, 2011; Rothstein, 1990). Examples may be the timing of parasitism in common cuckoo (*Cuculus canorus*) in which the female brood parasite surveys the laying progression of its hosts (Davies & Brooke, 1988), or during the act of parasitism where the brood parasite steals one or two host eggs, after depositing its own egg in the host nest (Davies, 2011; Rothstein, 1990). In addition, some parasite eggs have a relatively short incubation period providing an advantage of hatching earlier than host progeny. However, internal incubation may either be a consequence of protracted intervals between ovulation and laying, or may be refined as an adaptation given the likely advantages of this trait (Birkhead et al., 2010). Many parasite nestlings get rid of host eggs or nestlings from the nest, an adaptation which is energetically costly, but results in monopolization on parental provisioning by the brood parasitic nestling (Grim, Rutila, Cassey, & Hauber, 2009). In addition, to ensure that the brood parasitic nestling receives sufficient provisioning by the host, it has developed exaggerated begging signals, e.g. rapid and structurally similar begging calls (Davies, Kilner, & Noble, 1998; Kilner, Noble, & Davies, 1999), colourful gapes (Álvarez, 2004) or wing patches that simulate extra gapes in the nest (Tanaka & Ueda, 2005). In parasite-host systems where the brood parasitic nestlings match the begging call of host nestlings, the adaptation

may have developed as a result of reciprocal evolution driven by host discrimination (Langmore et al., 2003), to solicit increased provisioning (Davies et al., 1998) or solicit enhanced care over a prolonged period compared to host nestling, as host parents might reject progeny (brood parasite and own nestlings) that take too long to fledge compared with host progeny (Grim, 2007; Grim et al., 2003).

Non-evicting brood parasites must participate in food solicitation, which is normally higher as there are more begging gapes in the nest, and compete for the provisioning brought to the nest by the host parents (Kilner, Madden, & Hauber, 2004). As a result, brood-parasitic nestlings have tuned in on becoming a stronger competitor favoured in provisioning by hosts parents over own young (Soler, Martinez, Soler, & Møller, 1995). Such adaptations that invade mechanisms that host parents use as a measure of fitness of own nestlings are very difficult to counter (Redondo, 1993).

The cuckoo family, *Cuculidae*, is a phylogenetic group of birds renowned for its large amount of brood parasites (40 % of cuckoos) and the reproductive strategy has evolved independently three times in the lineage (Payne, 2005; Sorenson & Payne, 2005). Many cuckoo species are difficult to study, living in the tropics where the birds are difficult to see and nests are well hidden. Hence, in studies of brood parasitism the majority of accumulated knowledge is acquired from investigations on a few species (with emphasize on the common cuckoo) (Payne, 2005; Stevens, 2013). Recently focus has been broadened to a wider range of systems, which has strengthened some hypotheses derived from early studies and countered others (as presented above) (Stevens, 2013). In addition, different parasite-host systems are at different stages following various ecological selection pressures and hence various coevolutionary routes, which emphasizes the need of initiating studies on a broader range of systems (Britton et al., 2007; Stevens, 2013). Species in east and southeast Asia and New Guinea are especially under-studied, and could thus reveal novel deceptive traits that science has yet to uncover (Stevens, 2013).

The present study aims to bring insight into a poorly studied parasite-host system in south-western China between the plaintive cuckoo (*Cacomantis merulinus*) (hereafter referred to as cuckoo), a small Asian cuckoo and one of its hosts, the common tailorbird (*Orthotomus sutorius*) (hereafter referred to as tailorbird). In this system, attention has previously been given to studies of adaptations on the egg stage, revealing that the host has evolved dimorphic eggs that are mimicked by the cuckoo, and that mismatched cuckoo eggs are frequently rejected (Yang et al., in review). The nestling-stage in this parasite-host system is, however, completely unknown (Payne, 2005), with the exception of a few basic data on e.g. egg

incubation time. The plaintive cuckoo, being altricial, hatches naked and blind after 13.0 days (SD = ± 0.5 , $N = 5$) incubation, earlier than tailorbird nestlings that hatch after 13.7 days (SD = ± 0.7 , $N = 11$) (Wang, L. pers.comm.). The aim of this study is to disclose the coevolutionary relationship between the plaintive cuckoo and its tailorbird host at the nestling stage. In order to do so, the study was divided into two parts. Given the lack of knowledge about the plaintive cuckoo nestling, part a) is a descriptive study on the characteristics of cuckoo nestling growth and development. Such knowledge will be important as a fundament for further studies of this system and for a comparison with other host-parasite systems. The description of nestling development follows the procedures of Jonsomjit, Jones, Gardali, Geupel, and Gouse (2007). Part b) presents an experiment investigating cuckoo trickery and tuning on its tailorbird host, and the findings are discussed in relation to what is found in other parasite-host systems. Trickery refers to adaptations by the parasite developed to evade the defence lines of the host and are subjects of coevolution, whereas tuning is adaptations derived in brood parasitic progeny to adjust to the host life history, e.g. assuring sufficient provisioning and attuning to the incubation strategy of the host (Davies, 2011). In the common cuckoo and reed warbler (*Acrocephalus scirpaceus*) system, the host parents use the same provision rules, both visual and vocal cues, when feeding brood parasitic nestlings and their own young (Kilner et al., 1999). 6-7 days old common cuckoo nestlings deploy a begging call that mimic the begging call of a whole host brood (and at older ages far exceeds it) makes up for the deficit in gape area displayed at feedings and ensures that the single common cuckoo nestling receives sufficient provisioning – as much as a whole host brood (Davies et al., 1998; Kilner & Davies, 1999; Kilner et al., 1999). In addition, the begging call is relatively flexible enabling the parasitic nestling to tune in on different hosts based on experience of what call assimilates the highest provisioning (Madden & Davies, 2006), an adaptation that might be commonly applied by a range of brood parasites (Anderson, Ross, Brunton, & Hauber, 2009; Davies, 2011; Langmore et al., 2008; Mundy, 1973). Theory predicts that brood parasites will exploit hosts by demanding higher amounts of parental care given the lack of genetic relations to their hosts. This hypothesis was explored by formulating three predictions based on knowledge derived from studies on developmental and behavioural adaptations of the common cuckoo nestlings. The plaintive cuckoo nestlings were expected to: 1) be heavier and gain weight faster than one host nestling, 2) be provisioned at a higher rate and/or with better quality food than one host nestling and 3) given that the two other assumptions are met, possess a stimulus enabling it to attain the elevated provision rates.

Methods and materials

The study site and study species

The study site was in the vicinity of the village of Nonggang (22°30'N, 106°58'E), Guangxi Zhuang Autonomous Region in south-western China, close to the border with Vietnam. The landscape is a mosaic of steep limestone peaks covered in dense vegetation throughout cultivated flatlands. The area is considered to be situated on the margins of the tropics with an annual rainfall of 1.150-1.550 mm and a mean annual temperature of 20.8-22.4°C (Yang et al., in review). The fieldwork was performed during April-June in 2014 congruent with the breeding season for the common tailorbird and the plaintive cuckoo.

The common tailorbird, being an abundant bird species in the inhabited areas in the Nonggang vicinity, is a common host for the plaintive cuckoo (Payne, 2005; Yang et al., in review). It uses a variety of tree-species with sturdy leaves as the fundament for its nest, sewing one or two leaves together using organic material (Figure 1). The result is a dome-shaped fundament in which the tailorbird places its nest. Nonggang is on the northbound boundaries of the plaintive cuckoos distribution and it migrates from the Chinese breeding areas to spend the winter in more southern parts of its natural range (Payne, 2005; Yang et al., 2012). Even though some effort has been dedicated to studying the plaintive cuckoo, the co-evolutionary history amongst the two species is still largely unknown. Both species have two egg morphs, blue or white ground colour with brown/red spots. Within each tailorbird clutch only one egg type is found. A recent study has disclosed that the plaintive cuckoo egg deposition is not nest specific regarding matching host egg morph. The result is a 50% mismatching of the host egg morph by the cuckoo and will lead to host rejection of the cuckoo egg. In the Nonggang area 15-18% of tailorbird nests were parasitized (Yang et al., in review).

Implementation

The nests were found by systematically searching habitats suitable for nesting tailorbirds, whereby the nest location was plotted on a GPS (Oregon 450, Garmin International Inc., Kansas, USA) and nest details (egg morph, number of eggs, etc.) were noted. To reduce predation and host rejection of mismatched cuckoo eggs, eggs were moved to an incubator until hatched (Brinsea Mini EX, Brinsea Products Ltd, Sandford, UK), reared in temperature 37.5° C and a humidity level of 45%. Preferably nestlings would be returned to their natal nests, but due to high predation rates and unsuitable nest locations (in two situations for the

cuckoo nestlings), only the minority of the nestlings were reintroduced into their natal nests. For eggs from clutches that were not put in the incubator, a floating test (for details see Ackerman and Eagles-Smith (2010)) was used to determine the egg developmental stage, and when the expected hatching day emerged the nest was checked daily. Three experimental groups were assigned; 1) nests with one cuckoo nestling (“cuckoo group”), 2) nests manipulated to one tailorbird nestling (“one-host group”) and 3) nests holding a whole host brood (“brood”), where the brood size varied between four ($N = 11$) and five ($N = 2$) nestlings. The sampling methods were mostly not mutually exclusive for either part-studies of this thesis, so the methods of both part a) – that focus on cuckoo nestlings development and adaptations – and part b) – that investigate cuckoo nestlings adaptations to consolidate host provisioning, including experiments with tailorbird nestlings – are dealt with intermingled in this section. Data of the experimental groups was sampled following a three-day age-interval after hatching (day 1), where comparable data for all groups was acquired between day 3 and 9 (3 measurements in total). The brood was not monitored after day 9 in fear of provoking pre-fledging among asynchronously hatched nestlings (measurement on the brood group was initiated when all nestlings had hatched - resulting in within nest developmental variation). Cuckoo nestlings were followed from day 1 to day 18; the one-host group were followed from day 1 to day 12. Many of the plaintive cuckoo nestlings were monitored more frequently than the three-days intervals in order to document morphology development.

The manipulated nests varied in brooding stage and already present eggs were removed during day 2 and 3 for the one-host group to give the parent a gradual transition between brooding and hatching. For cuckoo nestlings, eggs were not removed unless the cuckoo failed to evict. Also, two plaintive cuckoo nestlings were found hatched in tailorbird nests and were aged after weight measurements and developmental traits and translocated to new nests because of inaccessible nest locations. When a tailorbird nest unexpectedly was found emptied of nest content, it was defined as predation. However, environmental factors such as heavy rainfall might also be a reason for nest content disappearing by flooding or nest destruction.

Nest activity was recorded with one sound recorder, Zoom H4N (Zoom Corporation, Tokyo, Japan), and four pen cameras, Hyundai model HYM-V808 (Hyundai Motor Group, Seoul, South Korea) on the specified days of age. The recorders were attached to a portable bamboo stick or natural vegetation around the nest, and they were concealed with leaves to make them as cryptic as possible. The tailorbird parents appeared to relatively quickly adjust to the nest surroundings after the setup, even though variation in vigilance and comfort after

equipment setup was registered within and between groups. These variations, following principles of random sampling, are assumed to be uniformly distributed among the experimental groups. Standardization of recorder-setup was stressed with the pen camera ideally capturing the nest entrance and a portion of the parental activity around the nest. Recording time at each nest varied between 90 and 105 minutes. Sound recordings were executed both out in the field ($N = 14$) and in the lab after one hour of starvation ($N = 16$) for cuckoo nestlings and one-host nestlings on day 3 and 6. Duration of field-recordings was approximately 2 hours and 1.5 minutes for lab recordings. For field recordings, the sound-recorder was optimally placed between 10 and 15cm from the nest entrance with the 2 microphones directed towards the nest opening and at the lab a bit closer (~10 cm from the begging nestling). In the lab, the nestling was placed in an artificial cardboard nest box filled with paper tissues. After one hour, knocking once at the cardboard box triggered begging and when the begging ceased, a new knock on the box followed. Recordings that were too noisy or did not capture begging calls were ignored in the analysis. A digitizer incorporated in the sound-recorder sampled the sound recordings at 44.1 kHz with 16 bits per sample. Analysis of the sound recordings was performed using RavenPro 1.5 (Cornell Lab of Ornithology, 2014, Ithaca, NY, USA). The settings used for the spectrogram analysis was 256 sample Hann window, 3dB filter bandwidth of 248Hz, time grid resolution of 128sample with 50% overlap and a discrete Fourier transformation size of 256 samples.

Measurements

Growth measurements of tarsus and weight were taken using a vernier calliper and an electronic balance. All measurements were taken by one person and after standardized methods (for tarsus length standards of Svensson (1992) were followed – consistent for both species). The electronic balance was calibrated between each weighing and measured to the nearest 0.01 gram and the tarsus length was measured with one electronic calliper and measured to nearest 0.01 mm.

From the video recordings, feeding rates and food item size were extracted. A feeding was defined as a parent observed to enter the nest with a food item in the beak and leaving the nest without the food item. On contrary, if the parents left with the food item, it was counted as a visit and not a feeding. Food item size was used as a measurement of food item quality. Data was acquired by assessing the size of the food item being brought to the nestling using bill length of the maintaining parent as the standard measurement. The food item was divided

into 5 different size-categories, where food items smaller than the length of the tailorbird bill were placed in category 1 or 2, food items of similar size to the parental bill being placed in category 3 and prey bigger than the length of the tailorbird bill length were placed in category 4 or 5. For each nest, a mean of prey item size was calculated to represent the prey size for that nest that day. Nests with less than 3 food item confirmations were excluded from the study.

To quantify begging, 10 second long sound-sequences with frequent begging were selected from the sound recordings and the number of begs were counted. For each nestling at least two sound samples and at most five samples were counted and the results were averaged. Three nestlings were sampled both in lab and in the field at the same day, and a mean was calculated between the two begging counts. No difference in begging intensity was found between the two different recording conditions for the one nestling groups (Mann-Whitney-Wilcoxon test: $W = 46$, $N1 = 10$, $N2 = 13$, $P = 0.26$), and there were no difference between begging intensity between lab and natural recordings for either cuckoo groups (Mann-Whitney-Wilcoxon test: $W = 17$, $N1 = N2 = 5$, $P = 0.42$) or one-host groups (Mann-Whitney-Wilcoxon test: $W = 21$, $N1 = 5$, $N2 = 8$, $P = 0.94$). Since there were no significant differences between lab recordings and field recordings, both were used in order to retain sample size and the mean counts were rounded off to nearest whole number.

Statistical analyses

Generalized Linear mixed effect models (GLMM) were used to handle the nested structure of this study where sampling and resampling of the same nests were conducted. Given the nature of developmental data, weight, food item size and feeding rate, most variables are expected to increase over days. Normalization of parameters, weight, weight increment, food item size and feeding rate, were tested for within age-intervals and confirmed. Justification for the statement can be made in that individuals are believed to have similar genetically predisposed growth patterns and physiological characters. The begging rate is assumed to follow Poisson distribution, as the measure of interest is the accumulated begs over a 10 seconds time interval. Focus was put on measurements in the age-interval of day 3 to day 9, where data on all groups was taken. Weight increment, being the weight gain between consecutive days had two measurements for the dataset, matched with downwarded feeding measurements; feeding rate and food item size observed on day 3 were used to explain the weight increment between day 3 and 6 and feeding measurements on day 6 was used to explain weight increment

between day 6 and day 9. Also, the weight of the brood group was summed up in order to get a clean comparison between the different experimental groups and different parameters. All statistical analysis was performed using the program R (R Core Team, 2013). The effect of each parameter was tested for experimental groups applying univariate analysis with linear regression models (LM), which was illustrated with the `sciplot` package (Morales, 2012). To include possible non-independence of parameters and pseudoreplication by sampling and re-sampling, generalized linear mixed effect models (GLMM) were used for feeding rate, food item size and weight increment. The `lmerTest` (Kuznetsova, Brockhoff, & Christensen, 2013) package were applied to gain p-values from the GLMM's, which is an extension of the `lme4` package (Bates, Maechler, Bolker, & Walker, 2014). Weight increment was explained by food item size, feeding rate, experimental groups and age of nestlings with nest identity as random variable. Factors selected to investigate trends for feeding rate and food item size were the other feeding measurement, age and the experimental groups, with nest identity as a random variable. Variables were arranged in a multiplicative relationship, enabling investigation of interactions. Then best model was selected by running the `dredge` function in the `MuMIn` package (Bartoń, 2014), rating the models after AICc values.

Results

General results

More than 80 common tailorbird nests were found within an area of 25km² (Figure 2). Due to high predation rate (~ 60 %) in the area and some unsuitable nests (remote location, nest discovered containing hatched nestlings, etc.), data was acquired from 38 nests. After experimental manipulation, 13 of the nests contained one cuckoo nestling, 12 nests contained one host nestling and 13 nests contained a whole brood (4/5 host nestlings). Within the brood group there were no statistical differences in feeding rates between the nests containing 4 hosts ($N = 11$) and 5 hosts ($N = 2$) (Welch's two-tailed t-test: $t_{2,4,24} = -0.07$, $P = 0.95$) or food item size (Welch's two-tailed t-test: $t_{2,3,47} = 0.19$, $P = 0.86$). Even though these statistical results may not justify merging the two groups (given low values on degrees of freedom), merging will increase further statistical power (as sample size increases) in analyses and it may not make much difference biologically. They were thus fused as the "brood group". Out of the 38 nests, nestlings fledged in 24 nests (brood: $N = 10$, cuckoo: $N = 5$ and one-host: $N = 9$). The nestlings had still not fledged in 6 nests when the study ended, and the last 8 nests were predated during the study period. Tailorbird parents deserted one nest with an introduced cuckoo nestling (the same day the nestling was introduced to the nest, and the cuckoo nestling was reassigned to a new nest), but no nest containing own nestlings was deserted.

a) Descriptive data on nestling development

Morphology development

Development of characteristic traits of cuckoo nestlings is described in detail in Table 1 and photos visualizing the development for both tailorbird and cuckoo are presented in Figure 3. At hatching, the plaintive cuckoos were the same colour as host nestlings: pinkish with a pale yellow colour on extremities, but marginally larger and heavier ((weight \pm SD in grams) cuckoo hatchlings: 1.15 ± 0.06 , $N = 8$; tailorbird hatchlings: 0.79 ± 0.06 , $N = 6$). Cuckoo nestlings gained weight faster than tailorbird nestlings (Figure 4), and the growth patterns followed a sigmoidal growth curve. Cuckoo nestlings also had a stronger weight increment over the three-day interval than tailorbird nestlings (Figure 5). Contrary to the weight trends, tarsus length grew slower in cuckoo nestlings but almost reached the same length as tarsus length for tailorbird nestlings as fledglings (Figure 6). The gape colour of cuckoo nestlings was red without any markings, but turned deeper red as the cuckoo aged. On the contrary, tailorbird nestlings had a yellow gape with two black tongue markings. The cuckoo bill was pale yellow, but darkened with age with only the tip remaining yellow by the time the nestling

fledged. The pinkish skin colour started to darken after 3 days of age, and the emergence of feathers strengthened this impression. The eyes started opening around day 6. Cuckoo nestlings fledged just after 18 days of age ($N = 5$), and the fledglings possessed a juvenile plumage similar to the female plaintive cuckoo hepatic morph. Tailorbirds experienced a faster development and hence a shorter nestling period than cuckoo nestlings. Feathers appeared and started unsheathing at an earlier point yet the eyes opened at around the same time as for cuckoo nestlings. Tailorbird nestlings fledged between day 12 and 13 ($N = 4$), however, two individuals fledged at day 15 after abnormally slow growth-development in one and louse infestation in the other.

Eviction

Cuckoo nestlings were translocated to nests of different brooding stages, depending on nest availability. Hence most cuckoos experienced the presence of tailorbird nestlings, $N = 9$ (that were always evicted), where one individual evicted a sole nestling but none of the eggs and another did not experience the presence of eggs. Cuckoo nestling eviction behaviour was observed to be initiated at the earliest on day 2 ($N = 4$) and the behaviour apparently ceased by day 5 ($N = 3$). Eviction was observed in 9 of the 13 nests. The three individuals where eviction was not captured had in common that all were reared in nests with eggs and never experienced the presence of nestlings. One of them was observed to possess eviction behaviour, but failed to heave the eggs over the nest rim. The last nestling was found post-hatching and aged to be 6 days old when eviction behaviours are relaxed (but was found alone in the nest without control of nest content).

Warning display

Cuckoo nestlings developed a defence trait at 11 or 12 days of age whereby they, if approached by a potential threat, made themselves bigger by raising up in the nest, puffing out their feathers, lifting their heads, displaying their wings and red gape and striking intimidatingly at the threat. If the nestling was removed from the nest, it liberated sticky and mild smelling faeces. The behaviour was retained throughout the nesting stage and after the trait was acquired, no cuckoo nestlings were predated ($N = 6$).

Begging display

Plaintive cuckoo nestlings possessed exaggerated begging displays, evident during the second half of the nestling period (after the warning display was attained); whenever host parents appeared in nest surroundings, nestlings shook their heads intensively, often while displaying their big, red gapes. Even after being fed, the begging display continued. Furthermore,

parasite nestlings emitted strong begging calls that were similar in structure to those produced by tailorbird nestlings (Figure 7). Seemingly, during these first days, the pitch of the call varied between the two species; cuckoo nestling calls were most frequently observed at 3 - 4 kHz whereas the tailorbird calls were most often around 5 - 6 kHz, but both species produced partials (several tones produced simultaneously) over a wide tone-range. Between day 6 and day 9 the pitch of the partials often overlapped between the species calls, which may indicate that cuckoo nestlings were tuning in on hosts begging calls. After day 9, the begging calls of the two species started to diverge. Where the tailorbirds gave a drawn-out, noisy or toneless “pccchh”-call, the cuckoo begging calls remained more structured on “purer” frequencies with several partials of varying energy. Interestingly the loudest partial had changed from being the fundamental partial at day 3 and 6 to the secondary or tertiary partial from day 9 in the cuckoo begging calls. Given the tonal complexity of the cuckoos begging call, it may not differ substantially in “sound output” compared to the more noisy tailorbird nestling begging calls.

b) Experiment on cuckoo nestling exploitation of host parents

From the predictions stated in the experimental setup, prediction 1 was met, as cuckoo nestling mass was larger than the mass of one-host nestlings (growth rate; Figure 4 and weight increment; Figure 5) on all distinct days, over the comparable age interval between day 3 and day 9. The mass differences between the one-nestling groups were significant on day 6 and 9 for growth rates (Table 2 a) and significant for all days for weight increment (Table 2 b) in the univariate analyses. In addition, cuckoo nestlings were sligher and gained less weight over day-intervals than what would be accumulated by a whole brood, differences being significant for all days (Table 2 a and b). The average weight of one host nestling was insignificantly lower than for the mean weight of one host nestling in a brood in a multivariate analysis (GLMM: $F_{3,95} = -0.44$, $P = 0.661$).

A wide variety of insects were fed to the nestlings, but frequent prey included the lychee giant shield bug (*Tessaratoma papillosa*) nymph, a large variety of larvae/caterpillars and different species of butterflies and grasshoppers. Food items delivered to cuckoo nestlings and one-host nestlings were of similar size (Table 2c and Figure 8). However, the whole brood was fed with insignificantly larger food items than the one-nestling groups. Only one model was presented within the delta AICc model selection value interval (Table 3 b), which included experimental group and age. Age was highly significant, and the effect over days

stated that a whole brood was fed with significantly larger food items than the two comparable groups (Table 4 b).

The whole brood was provisioned at a higher rate than cuckoo nestlings and one-host nestlings, whereas no significant difference was found between cuckoo nestlings and one-host nestlings between day 3 and day 9 (Figure 9 and Table 2 d). However, at day 12 cuckoo nestlings were provisioned at a higher rate than the one-host nestlings (LM: $t_{2,9} = 2.19$, $P < 0.05$). Model selection presented two models within delta AICc = 2 (Table 3 c); feeding rate explained by 1) experimental groups and age or 2) experimental groups, age and food item size. Model 1 was preferred after following parsimony principles, a decision strengthened by little differences in variation (R^2 -values) explained between models. Age was highly significant in explaining group variation in feeding rates, as provisioning was positively correlated with age, which was expected as growth is associated with increase in needs. The univariate analyses indicated similar trends, where the whole brood was fed at a higher rate compared to one-nestling groups, the effect being significant over days (Table 4 c). However, no significant difference between cuckoo and one host nestling was confirmed. Even though the one-nestling groups were fed at a lower frequency than what was distributed to a brood, the nestlings were fed at a higher rate than independent nestlings in a whole brood (cuckoo nestling: GLMM: $F_{3,31.71} = 2.903$, $P < 0.01$, one-host nestling: GLMM: $F_{3, 30.93} = 3.813$, $P < 0.001$).

Feeding measurements and age were selected as fixed variables for analysis of weight increment, with nest identity set as the random effect to account for non-independence and pseudoreplication, and through model selection five models were found to be within the AICc range (Table 3 a). The simplest model included only the experimental groups, whereas other models in addition comprised feeding rate, food item size, and the interaction between experimental groups and food item size, as explanatory variables. Staying faithful to maximum parsimony rules, the simplest model, including experimental groups alone, was selected as the best model explaining weight increment. Thus, feeding rate and food item size did not have a significant effect on weight increment.

For begging intensity on days 3 and 6, there were no significant differences between one-host nestlings and cuckoo nestlings (GLMM: $z = -0.129$, $P = 0.897$) (Figure 10). Symptomatically, cuckoo nestlings begged less than the whole brood of host nestlings (GLMM: $z = 6.685$, $P < 0.001$).

Discussion

Applying knowledge accumulated from work conducted on common cuckoo nestlings (e.g. Davies et al., 1998; Kilner & Davies, 1999) on the system under study raised predictions that the plaintive cuckoo nestling would solicit higher provisioning rates than host nestlings as a result of extravagant begging display and consequently reach greater mass than host nestlings. Indeed, the plaintive cuckoo nestling gained greater mass and remained larger throughout the nestling period as compared to host nestlings, but the study failed to find support for cuckoo nestlings being provisioned at a higher rate. Consequently, the study failed to find evidence for any supernormal traits exploiting parental provisioning. In accordance with the feeding rate observed solicited by the parasite nestling, it signalled the same need as one host nestling applying a begging call that resembled the begging call of a single host nestling during the first period of the nestling stage.

The process of eliminating host progeny may incur antagonistic effects for parasite nestlings; the act of eviction may in itself be costly in terms of energy expenditure and the annihilation of the host brood may reduce the signalling capability of cuckoo nestlings. Plaintive cuckoo nestlings were observed to be more responsive at evicting host nestlings than host eggs, as some individuals either were hampered at evicting eggs or failed to recognize egg presence altogether. Plaintive cuckoo nestlings were also found to initiate eviction behaviour on the second day post-hatching, which is similar to common cuckoo nestlings that evicted the first offspring after just above 40 hours post-hatching (Honza, Voslajerova, & Moskat, 2007). This finding is contradictory as nestling eviction is expected to be energetically costlier than egg eviction (Grim et al., 2009). Plausible mechanisms explaining this observation may lie within physiological constraints and ecological conditions; developmental constraints on an early initiation of eviction behaviour (i.e. nestlings need to exceed a developmental threshold before they can bear the costs of eviction), deep and variable nest-shapes (Grim, 2006b; Kleven, Moksnes, Røskaf, & Honza, 1999) and/or a less pronounced effect of internal incubation (as plaintive cuckoos hatch around 17 hours before host hatchlings (Wang, L. pers.comm.) compared with the common cuckoo nestlings that hatches 31 hours earlier than their respective host progeny (Birkhead et al., 2010)).

Parent-offspring conflict theory predicts that parents are selected to allocate resources evenly between reproductive events throughout their lifetime, whereas offspring should demand more provisioning than parents are willing/able to give, yet offspring selfishness is constrained by inclusive fitness costs incurred on future siblings by demanding too much resources (Harper, 1986). Brood parasites on the other hand are unrestrained by kinship with

their host parents and in addition, their parental care demands are thus expected to exceed those of the host nestlings. The theory has received some support from studies on the common cuckoo, where parasitic nestlings during the first half of the nestling stage begs informatively, but exaggerate the begging display during the latter part (Kilner & Davies, 1999). Since the cuckoo nestlings are of larger size than host progeny, and are the sole occupants of the nest, selection favours nestlings that have developed traits invading their hosts' provisioning rules and acquire a substantial increase in feeding rates. The common cuckoo nestling makes up for a subnormal visual stimulus (few gapes in the nest) by a supernormal vocal stimulus that equals the begging call of a whole brood around 6 - 7 days of age, but thereafter exceeding it (Kilner & Davies, 1999). The plaintive cuckoo nestlings have a size advantage over host nestlings, but on the contrary to common cuckoo nestlings, they produced a begging call of similar structure and intensity as one host nestling. Consequently, the cuckoo nestlings were fed equally much and with the same food quality as one host nestling. This finding was valid for all comparable data except for day 12, where the brood parasitic nestling was provisioned more than one host nestling. This difference may partly be explained by parents encouraging host nestlings to fledge by enticing nestlings with food items from outside the nest (pers.obs.). Alternatively, the increased investment in exaggerated begging displays in cuckoo nestlings during this age-interval may ensure the increased provisioning rate. The provisioning rate for the cuckoo nestling was kept at a high rate after day 12 (Figure 9), and given the prolonged care yielded by host parents, the cuckoo nestling indeed receives an overall higher accumulated amount of provisioning compared to host nestlings.

As prediction 2 and 3 were not met, the first stage troubleshooting the deviations would be to discuss plausible flaws and biases concerning the experimental design applied in this study. And indeed there are a few factors that can affect the detection of a biased proportion of parental provisioning in favour of the parasite nestling. The definitions of the feeding rate may allow misinterpretation of feeding events (i.e. when nestling digestive capacity is reached and parents instead eat the food item themselves). The sample size may be small, and since no genetic analyses of kinship were performed, nestling relationships may be confounded. The assumptions of adjustment time to recording setups may be insufficient for tailorbirds and recording time (1.5 hours) may be too brief, in addition to variable environmental conditions, where data was collected as categorical variables that, if included in any models, would limit the statistical power substantially. Though biases may exist, the concentrated variation within experimental groups and the appearance of the statistical

models produced appears fairly clean and may, in concordance with several other explanations (outlined below), support the dismissal of prediction 2 and 3.

One obvious, yet proximate, explanation exists in fundamental physiological characteristics of the study species; at fledging, after around 19 days in the nest, the plaintive cuckoo nestlings are approximately four times the sizes of their foster-siblings. This weight-ratio difference was less extreme than for the common cuckoo nestlings raised by reed warblers that were eight times larger when they fledged around day 17 (Kilner et al., 1999). Nestlings are expected to grow at a maximum rate allowable by the trade-off between resources available for growth and maturation of tissue function, following tissue level constraints (Jonsomjit et al., 2007; Ricklefs, Starck, & Konarzewski, 1998), suggesting that the cuckoo nestlings and the tailorbird nestlings allocating parental resources differently and thus follow separate developmental trajectories. This realization sows doubt over the use of weight as a proxy for provisioning in brood parasitic experiments per se, as the link between provisioning and mass gain is not necessarily linear. Kilner and Davies (1999) showed that common cuckoo nestlings grew more slowly than a similar sized blackbird (*Turdus merula*) nestling, but equivalent to a whole brood of reed warbler nestlings, and therefore might have less needs than blackbirds. Similar developmental characteristics can be at play in the scenario under study where the plaintive cuckoo ultimately needs more time to mature than host nestlings and where need increases with time. Additionally, there is a strong selection for optimization of digestive efficiency that is limited by digestive capacity (Caviedes-Vidal & Karasov, 2001; Soler, de Neve, Pérez-Contreras, & Rubio, 2014), and bird species differ in their ability to assimilate nutrients (Levey & Rio, 2001). Soler et al. (2014) found that brood-parasitic great spotted cuckoo nestlings (*Clamator glandarius*) possessed a more efficient digestion system than their co-reared magpie nestlings (*Pica pica*), which might be considered an adaptation or a feature that differs between phylogenetic lineages (Soler et al., 2014). Intriguingly as this explanation is, it may not be directly applicable for the plaintive cuckoo without further studies, given that there might be a stronger selection for digestion efficiency in the great spotted cuckoo nestlings as they are raised sympatrically with host nestlings.

Tuning in on host begging call structure might be a widely spread adaptation for brood parasites (Davies, 2011), where the parasitic nestling uses host provisioning as cues for developing a begging call to consolidate sufficient provisioning that often is a mimic of host begging calls (Langmore et al., 2008; Madden & Davies, 2006). During the first 6 days in the nest, the plaintive cuckoo nestlings begged as frequently as one host nestling and hence much

less frequently than the sound output from a whole brood (Figure 10). In addition, the cuckoo nestlings apparently mimic the begging calls of the tailorbird nestlings up to day 9, whereby begging call structure followed different trajectories with the tailorbird nestlings producing toneless calls, and the cuckoos preserving the thrilling partials on distinct tones. This complexity in tones of the cuckoo begging call becomes more obscure and noisy over time. Qualitatively, the begging calls signalled by the parasite indeed seems like mimicry of host begging calls, but the validity of this statement needs to be further addressed with a control begging sound of a suitable species.

In accordance with increased intensity of vocal signalling, the visual stimuli intensified with age, whereby the increasingly larger nestlings puffed their feathers up, displayed their red gape and shook their heads during feedings. Congruently, the obtained warning display, believed to combat predation, could facilitate the development of the elaborated begging display. As predation rates were high, this selection-pressure constitutes a potent force for adaptation by being cryptic during the first period of development whereby after surpassing a developmental threshold, inducing the development of dishonest begging traits (which is consistent with development of common cuckoo (Kilner & Davies, 1999)).

When provisioning their young, parents follow integration rules composed of both visual and vocal stimuli that signal nestling needs (Kilner et al., 1999). The cuckoo nestlings' larger sizes were predicted to act as an enhancer on food solicitation. On the other hand, the vocal components would predict a provisioning rate equal to one host nestling, as cuckoo nestlings both beg as much as one host nestling (during the first 6 days in the nest) and apparently have tuned in on host nestlings' begging calls. Kilner and Davies (1999) found that common cuckoo nestlings begged informatively as intensity varied with need. Observations of plaintive cuckoo nestlings reaching their digestion capacity being incapable of accepting food items during the first 6 days in the nest may give reasons to assume that plaintive cuckoo nestlings begged as a consequence of need. This indicates that cuckoo nestlings are satisfactorily fed during the first period of the nestling stage and successfully signal need to host parents. Contradictorily, theory predicts that selection would favour exploitation of host parents by brood-parasite nestlings (this is of course under the assumption that there are no other antagonistically selective forces at work – i.e. predation pressure, which could hamper the development of elaborated signalling), which totally lacks genetic stake in foster parents. Thus, the cuckoo nestlings may benefit from increased provisioning, but may be restricted in communicating needs to host parents. One plausible explanation (given the apparent lack of knowledge on tailorbirds rule-of-thumbs for provisioning) is that tailorbirds may apply

different provisioning rules than what is expected (as larger nestlings are not receiving a majority share) or discriminating against cuckoo nestlings that may be incapable or physically restricted in infiltrating host signalling. Considering the apparent obtainment of similarly structured begging calls, it seems reasonable to assume that cuckoo nestlings have been under selection for developing a vocal signal that foster parents respond to, as such derived begging calls may be costly to produce and in particular costly to exploit to the parasite nestlings provisional advantage. The development of provisioning rules may facilitate a line of defence at the nestling stage (i.e. having well developed provisioning rules will be beneficial under brood reduction events), which may enable host parents to discriminate against alien nestlings. Though controversial to suggest, failure of acquiring a biased proportion of the provisioning may also make sense in light of discrimination or rejection of parasite nestling by tailorbird parents. This is obviously dependent on the relative age of the coevolutionary relationship between the plaintive cuckoo and the common tailorbird, the virulence (i.e. fitness costs) the parasitism incur on the tailorbirds and the parasitism rate over time. It may also be plausible that an arms race over selection for supernormal traits (i.e. traits that persuade host parents to invest more in parasite nestling) have reached a stable state, where the parasite has to settle for less than optimal feeding rates (as it is provisioned equally to one host nestling) being a subject of several other selection forces. Rejection has only been determined on parents deserting parasite nestlings that take an abnormal time to fledge (Grim et al., 2003), or by rejecting alien chicks following cost free and learnt cues (Langmore et al., 2003; Sato et al., 2010). Mimicry of host nestlings begging calls have been pointed out as an adaptation to combat host recognition of parasitic nestling and thereby discrimination (Langmore et al., 2003). And even though no desertions by tailorbird hosts were interpreted as host rejection of parasitic nestling, an additional experiment with four red-whiskered bulbul (*Pycnonotus jocosus*) nestlings assigned to separate tailorbird nests showed interesting results. One of the nestlings presumably fledged around day 12 after gaining high provisioning and mass, whereas three never fledged; two disappeared (noted as predation) and one was deserted (between day 3 and day 6). These observations only indicate that tailorbirds may be able to reject highly demanding nestlings or even reject alien offspring.

The validity of the discrimination statement needs to be addressed with an understanding of the brood-parasitic system as a whole, and the observations and discussions derived from this study can be added to the body of knowledge on the coevolutionary relationship between common tailorbirds and plaintive cuckoos. Following the model of strategy blocking, an efficient defence line built on an early stage during the breeding cycle

will obstruct the facilitation of further defence lines. However, frequency-dependent selection on the dimorphic eggs possessed by both tailorbirds and cuckoos have favoured the two morphs being equally common (as matched eggs are normally accepted, whereas mismatched are rejected – and hence a low scope for recognition errors), which indicates that half of the cuckoo eggs deposited in tailorbird nests were accepted (since the cuckoos are not egg-morph selective when placing their eggs) (Yang et al., in review). The seriousness of this breach and the selection pressures facilitating new lines of defence depends on the virulence of the parasite and the age of the system (as older systems are predicted to contain a more complex defence-portfolio (Kilner & Langmore, 2011)). Compared to the costs the common cuckoos inflict on their host parents, plaintive cuckoo nestlings may be slightly more benign as they demand less provisioning (as much as one host nestling during early nestling development), but on the contrary, plaintive cuckoo nestlings are able to arrest care for a slightly longer period. Tailorbirds may also be able to re-nest, as the breeding season is longer than for e.g. reed warblers. Whether the virulence of the parasite is strong enough to direct selection towards more refined defence lines or whether the defence is sufficiently strong to tolerate the parasite, needs to be addressed through further studies.

Conclusion

Plaintive cuckoo nestlings eliminated host progeny by eviction but failed to consolidate higher provisioning rates than one young hatchling, although they received a higher feeding rate than one host offspring in a full brood. Cuckoo nestlings gain weight faster and develop more slowly than host nestlings, findings that could be explained by the two species following different developmental pathways. Indeed, need changes with time, as older cuckoo nestlings received elevated provisioning rates compared to younger cuckoo nestlings and host nestlings during the second half of the nestling stage. As cuckoo nestlings are able to arrest care for another 7 days after host nestlings fledge, the accumulated amount of food will be greater and they may be fed at a higher rate during the last half of the nestling stage. Facilitated by the development of the warning display, a more complex and intensified begging display could be allowed. In addition, the apparent changes of the begging call to higher complexity and intensity (and high similarity to host begging call structure) may be an indication that the cuckoo nestlings are altering their begging sound in tune with host provisioning or to invoke host acceptance of prolonged nestling period (Davies, 2011). Parents would benefit from revealing a nestling cheat as early as possible, as time spent rearing and caring would be less. Thus, late development of an intense begging display would benefit the cuckoo if discrimination occurs and with regards to predation.

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“It’s a magical world... Lets go exploring”

- Bill Watterson

Ethical note

The experiments executed in this study comply with the current laws of China, where they were performed. Fieldwork was carried out under the permission of Nonggang National Nature Reserves, China. Experimental procedures were in agreement with the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University.

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Tables

Table 1. Cuckoo nestling development characteristics following three-day intervals.

Age (days)	Indicator characteristics
1-3	Hatched with pinkish-coloured skin that turned yellow towards the extremities. Eyelids had grey colouration. No neossoptiles present. No pins were visible. A cavity on the lower back was prominent for eviction purposes. The gape colour was diffuse red/orange without any conspicuous markings. The bill was pale yellow and the rectal flanges were of a more saturated yellow colour. This appearance lasted to day 3, when alar pins started emerging in the subcutaneous layer and skin darkened. $N = 12$.
4-6	Skin darkened, appearing more red/purple/brown. Darker colouration over emerging teleoptiles. The remiges emerged and had pierced the skin on the alar tract. Rectrices on the caudal tract emerged and pierced the skin. The contour feathers emerged and pierced the skin on the capital- and the ventral tracts. Feather-pins on the femoral- and crural tracts appeared. Eye started opening (earliest on day 5). The base of bill darkened, whereas the bill tip remained pale yellow and the rectal flanges brighter yellow. The gape turned deeper reddish. $N = 12$.
7-9	Feather-pins on the lower part of the dorsal tract emerged and together with the crural- and femoral tract pierced the skin. All teleoptiles were under rapid growth. The alar remiges pins turned paler in the outer end and started erupting. Eyes continued opening. The gape turned deep red. $N = 7$.
10-12	Ventral-, femoral-, capital and caudal tracts erupted. Alar tract continued unsheathing. Eyes were open. $N = 6$.
13-15	Dorsal tract started erupting. Extensive unsheathing on all teleoptiles. Exposed feathers covered a large amount of hidden pin sheaths. $N = 6$.
16-18	The plumage appeared buffy and completed, mostly true for contour feathers. However, primaries and secondaries, as well as rectrices, were unsheathed a bit over half the way. Still possible to see pin sheaths on dorsal tract. $N = 5$.

Table 2. Overview over estimates (\pm standard errors (SE)), degrees of freedom (d.f), t -values and P values of the different parameters; weight (a), weight increment (b), food item size (c) and feeding rate (d). The parameters were estimated for the experimental groups (Exp.gr) over comparable days by an univariate analysis approach applying linear regression models (LM). For the experimental groups “1c” denotes cuckoo nestlings, “1h” denotes one-host nestlings and “4h” denotes the brood. The cuckoo nestling was selected as the intercept; hence the P value on the cuckoo variable should be ignored.

Variable	Exp. gr	day 3				day 6				day 9			
		estimates (SE)	d.f	$t=$	$P\leq$	estimates (SE)	d.f	$t=$	$P\leq$	estimates (SE)	d.f	$t=$	$P\leq$
a) Weight	1c	2.68 (± 0.43)	34	6.29	0.001	6.47 (± 0.55)	29	11.84	0.001	12.57 (± 0.90)	21	13.92	0.001
	1h	1.93 (± 0.43)	34	-1.25	0.221	4.01 (± 0.60)	29	-3.03	0.01	6.20 (± 0.80)	21	-5.29	0.001
	4h	8.37 (± 0.41)	34	9.61	0.001	19.02 (± 0.60)	29	15.47	0.001	26.40 (± 0.85)	21	11.18	0.001
b) Weight increment	1c	NA	NA	NA	NA	3.66 (± 0.40)	28	9.08	0.001	5.93 (± 0.60)	21	9.90	0.001
	1h	NA	NA	NA	NA	2.04 (± 0.42)	28	-2.77	0.01	2.16 (± 0.53)	21	-4.72	0.001
	4h	NA	NA	NA	NA	10.14 (± 0.42)	28	11.10	0.001	8.39 (± 0.56)	21	3.01	0.01
c) Food item size	1c	2.59 (± 0.18)	19	14.20	0.001	3.38 (± 0.20)	20	17.38	0.001	3.48 (± 0.21)	16	16.48	0.001
	1h	2.48 (± 0.29)	19	-0.32	0.754	3.31 (± 0.21)	20	-0.233	0.818	3.45 (± 0.17)	16	-0.08	0.936
	4h	2.99 (± 0.20)	19	1.44	0.165	3.80 (± 0.20)	20	1.532	0.141	3.85 (± 0.19)	16	1.29	0.214
d) Feeding rate	1c	5.58 (± 0.98)	23	5.71	0.001	5.84 (± 1.30)	22	4.49	0.001	8.65 (± 2.14)	18	4.03	0.001
	1h	3.53 (± 1.32)	23	-1.25	0.223	7.40 (± 1.56)	22	0.77	0.451	9.77 (± 1.75)	18	0.41	0.690
	4h	9.96 (± 1.08)	23	3.01	0.01	14.40 (± 1.46)	22	4.38	0.001	19.77 (± 2.14)	18	3.67	0.01

Table 3. Model selection by the dredge function in the MuMIn package of R for three parameters: weight increment (a), food item size (b) and feeding rate (c). Parameters included in the GLMMs as fixed factors were age, experimental groups, food item size and feeding rates and nest identity were set as the random variable. All model parameters were set with multiplicative relationships allowing interactions between parameters, and all models had nest identity as random effect accounting for pseudoreplication. Model output included AICc values (with $\Delta AICc$ with an upper limit of 2 presents the best models – which are recognized by low $\Delta AICc$ values), coefficient of determination R^2 and degrees of freedom (d.f.). The symbol + denotes the inclusion of a categorical variable, empty spaces denotes exclusions in the model and NA symbolizes the parameter under investigation.

Parameters included	(Int)	Age	Exp.gr	FI	FR	Exp.gr.:FI	R^2	d.f.	AICc	$\Delta AICc$
a) Weight increment	4.34		+				0.80	5	146.4	0.00
	2.66		+	0.81	-0.13		0.83	7	146.7	0.31
	2.58		+	0.57			0.81	6	147.1	0.74
	-0.47		+	1.57		+	0.84	8	147.7	1.33
	4.88		+		-0.09		0.81	6	147.7	1.36
b) Food item size	2.24	0.15	+	NA			0.38	6	113.2	0.00
c) Feeding rate	1.58	0.10	+		NA		0.57	6	366.5	0.00
	3.30	1.10	+	-0.76	NA		0.57	7	368.2	1.68

Table 4. Estimates (\pm SE), degrees of freedom, t -values and P values for the experimental groups after running the best GLMM models (outcome of model selection as presented in Table 3) for three parameters; weight increment (a), food item size (b) and feeding rate (c). The only variable selected in the best model to explain weight increment was experimental groups. For both food item size and feeding rate, the best model included age together with the experimental groups. All models had nest identity as a random effect. Estimates presented are the actual estimates for each group.

Parameter	Variables	estimates (SE)	d.f.	$t=$	$P \leq$
a) Weight increment	cuckoo	4.52 (\pm 0.40)	33.72	11.424	0.001
	one host	2.10 (\pm 0.40)	29.49	-4.361	0.001
	brood	9.38 (\pm 0.40)	30.27	8.646	0.001
b) Food item size	cuckoo	2.24 (\pm 0.19)	60	11.61	0.001
	one host	2.18 (\pm 0.23)	60	-0.33	0.743
	brood	2.64 (\pm 0.20)	60	2.46	0.05
	age	0.15 (\pm 0.03)	60	5.26	0.001
c) Feeding rate	cuckoo	0.99 (\pm 1.34)	63.1	0.74	0.46
	one host	1.03 (\pm 1.57)	63.2	0.02	0.98
	brood	8.31 (\pm 1.43)	61.3	4.89	0.001
	age	1.01 (\pm 0.17)	47.6	6.01	0.001

Figures



Figure 1. A typical tailorbird nest neatly placed in a leaf-fundament created by sewing one or two leaves together. The tailorbird egg clutch morph is blue, and has been parasitized by a plaintive cuckoo of the white egg morph.

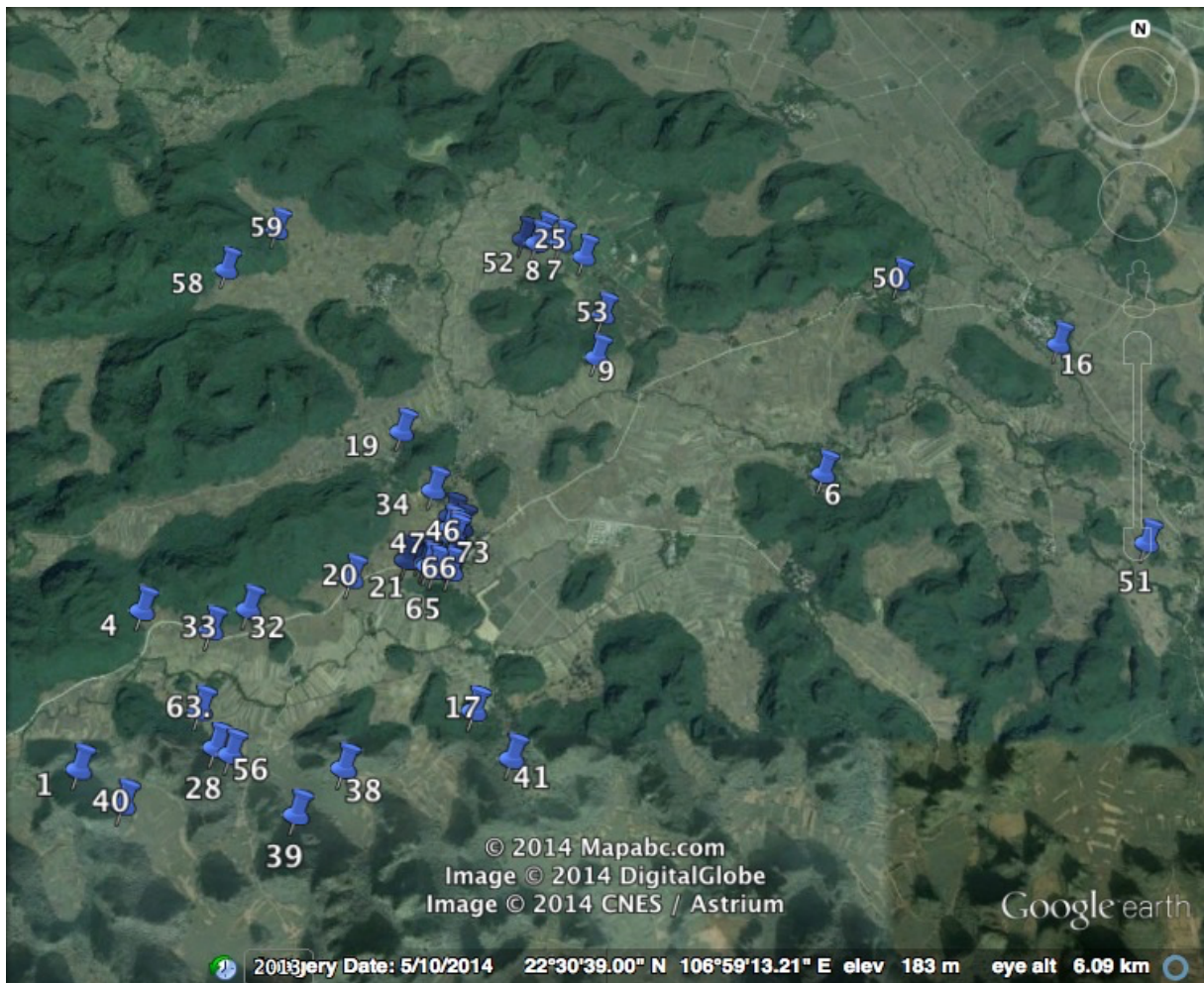


Figure 2. The 25 km² large study area showing the 38 uniquely numbered nests supplying data to the study. Most nests were found in the Nonggang village proximity, that can be viewed on the map as an accumulation of nests almost in the center at coordinates 22°30'N, 106°58'E. Coordinates were retrieved with GPS and are displayed illustratively through Google Earth (Google, 2013).



Figure 3. Cuckoo nestling (left panel) and tailorbird nestling (right panel) developmental stages documented with 3 days intervals, from hatching on day 1 to just before fledging on day 18 (cuckoo) and day 12 (tailorbird).

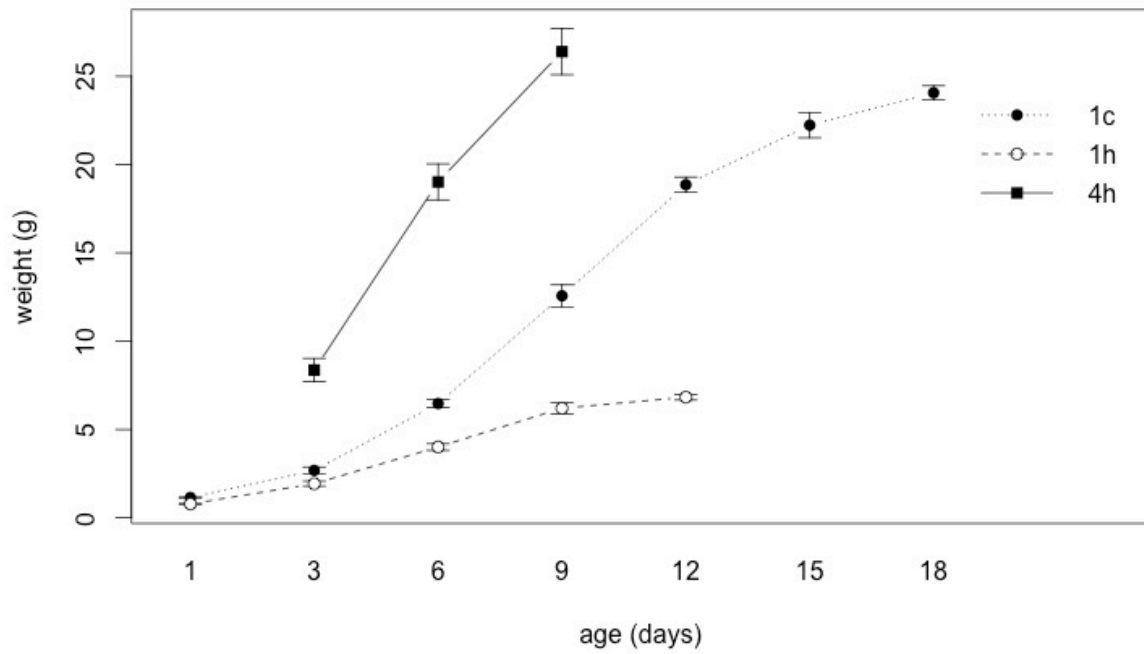


Figure 4. Growth rates of cuckoo nestlings (solid circles), one-host nestlings (open circles) and a whole brood (solid squares). Age is presented by days on the x-axis and weight is shown in grams on the y-axis.

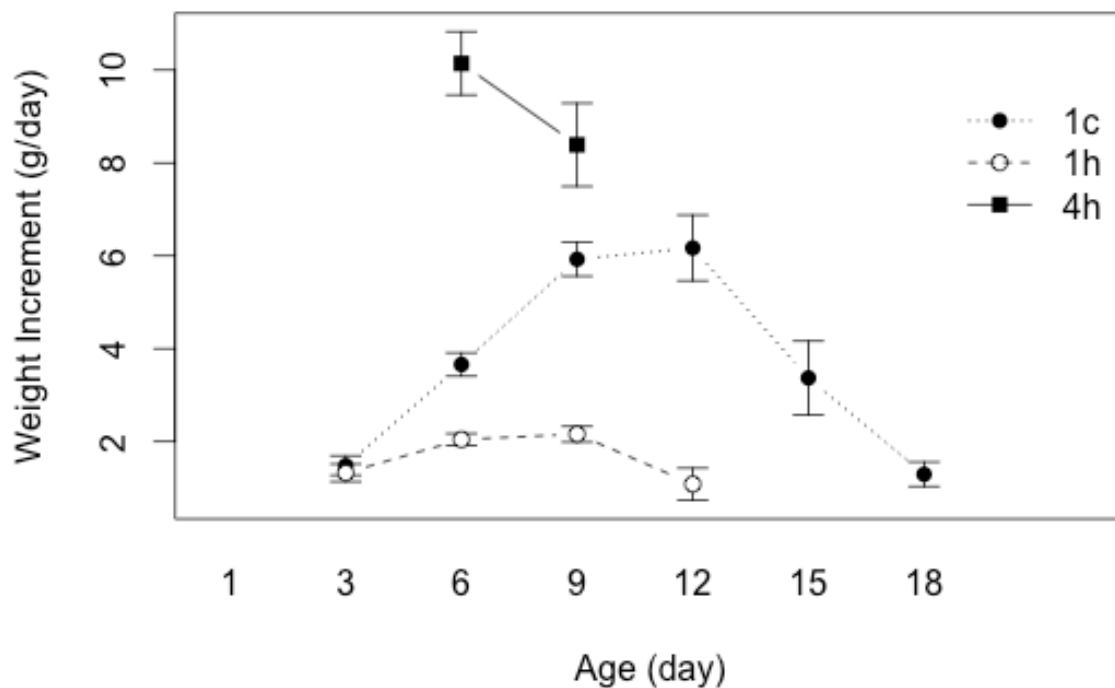


Figure 5. Weight increment, mass gained between two day-intervals, of cuckoo nestlings (solid circles), one-host nestlings (open circles) and a whole brood (solid squares). Age, presented in days, is shown on the x-axis and weight increment, which is presented as grams gained from the previous day of measure, on the y-axis. Cuckoo nestlings gain more weight over days than one host nestling, but less than a whole brood.

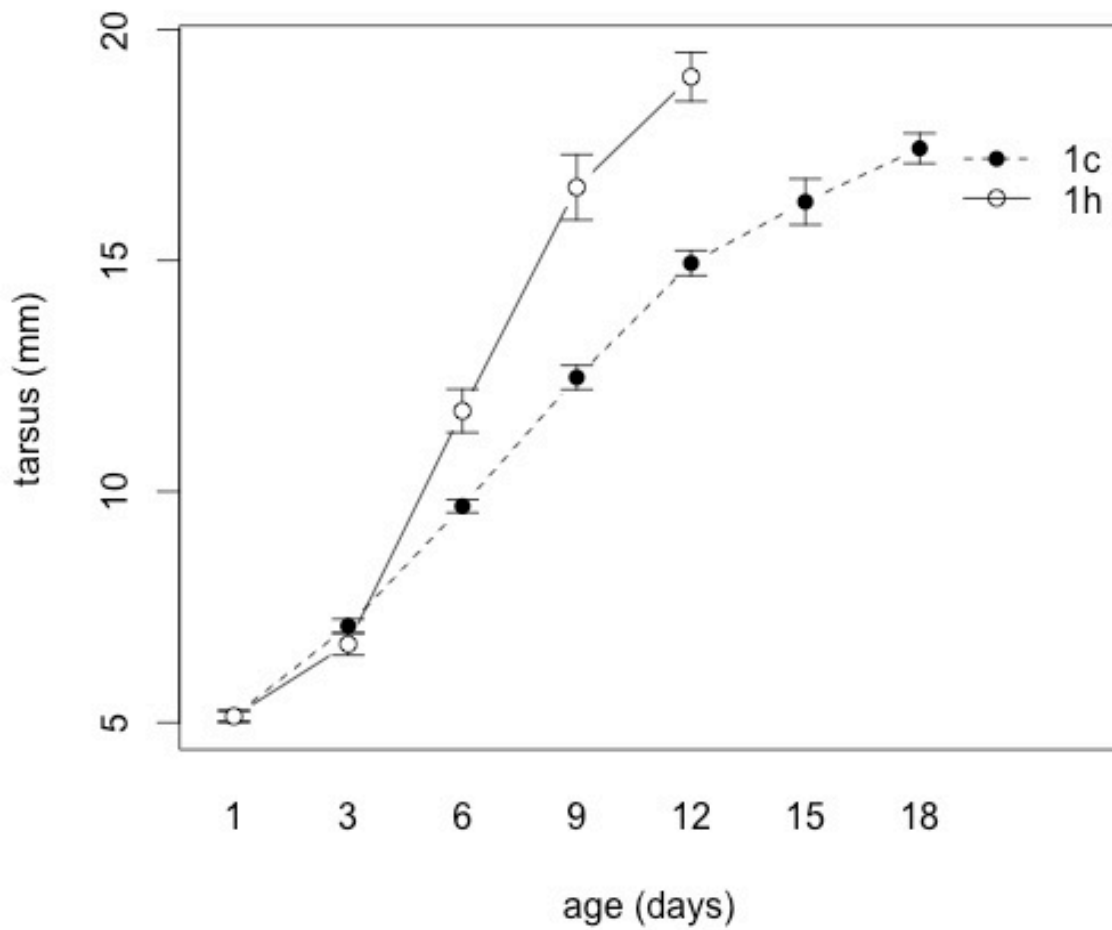


Figure 6. Tarsus growth rate follow a sigmoidal growth curve with age displayed as three-days intervals on the x-axis and tarsus length in mm on the y-axis. For cuckoo nestlings, solid circles (“1c”), the growth of tarsus length is slower when compared to tailorbird nestlings, open circles (“1h”), and the max tarsus length is longer for tailorbirds than cuckoos.

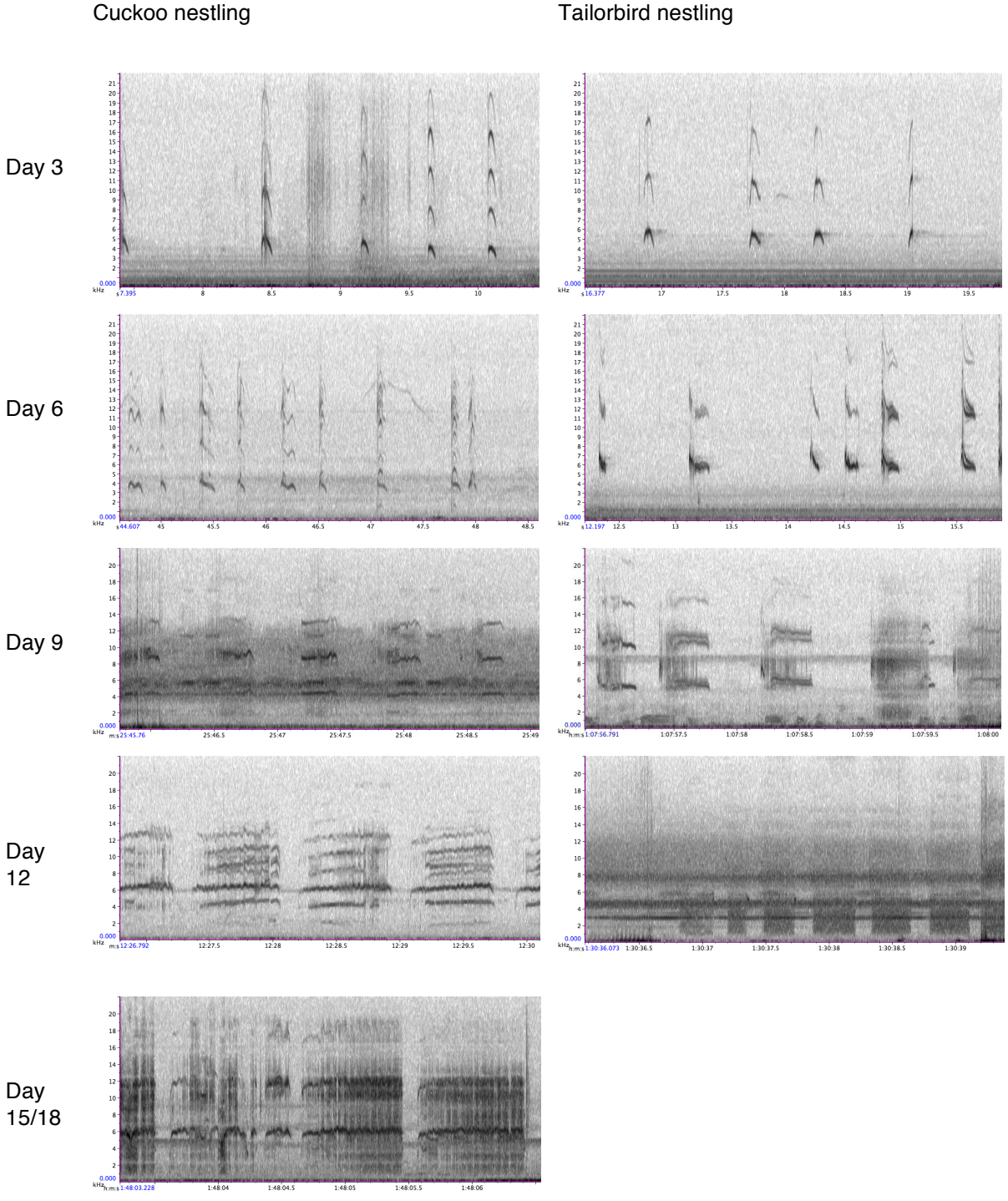


Figure 7. Spectrogram displaying begging calls of cuckoo nestlings (left panel) and tailorbird nestlings (right panel) over age-intervals (the very left panel). Time is shown on the x-axis (similar time-capture of all spectrograms) and frequency on the y-axis (from 0 to 21 kHz). Between day 1 and day 6 begging calls of the two species were structurally similar, however, a difference in pitch was observed with cuckoo nestlings begging call initially lower pitched

than tailorbird nestling calls. An alteration of the begging calls occurred between days 6 and 9, where the output of both species were intriguingly similar in structure and energy. After day 9, a structural divergence of the begging calls between the species occurred, where tailorbird nestlings produced an intense, toneless “pcccchhhh” sound, viewed as noise in the spectrogram. On contrary, the cuckoo nestling preserved pure tones and produced long-lasting trills. As the begging calls of cuckoo nestlings were tonally complex (consists of several tones produced simultaneously) with several partials of varying energy, the complete sound output might not differ too substantially between the species. An interesting observation regarding the cuckoo nestling begging call is the apparent change of pitch emphasize from being put on the fundamental partial, to the secondary or tertiary after day 6.

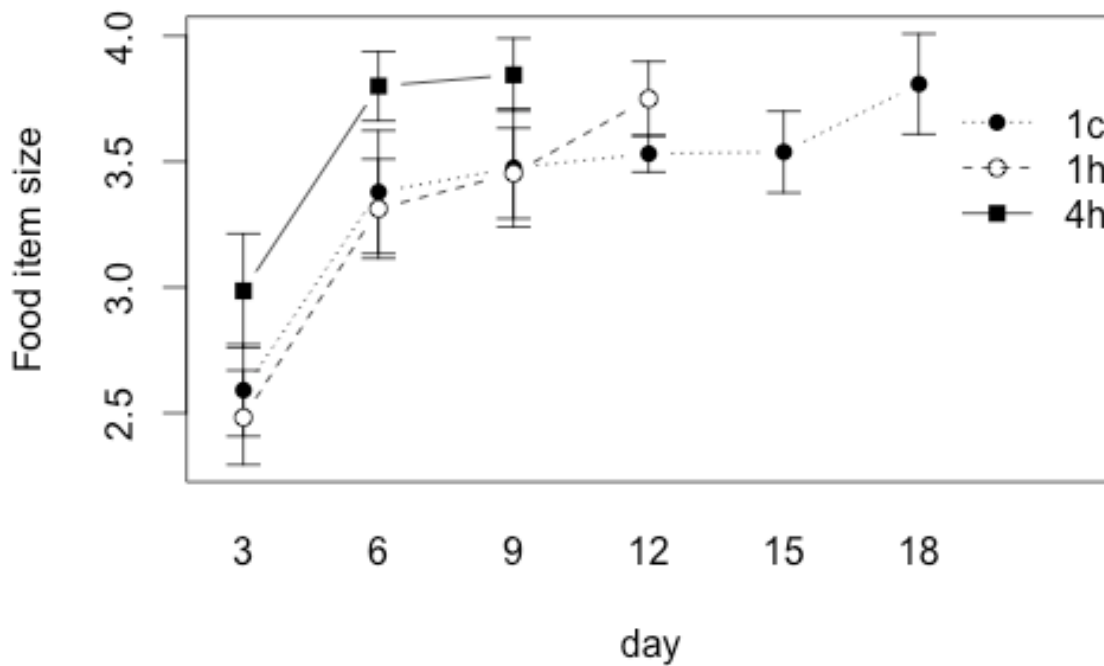


Figure 8. The whole brood (solid squares, “4h”) were fed with larger food items than cuckoo nestlings (solid circles, “1c”) and one-host nestlings, (open circles “1h”), throughout the nestling stage. Age is displayed on the x-axis and food item size on the y-axis. Food item size is calculated as a mean of all food items provisioned to a nestling, where each food item were placed in a size category ranging from 1-5, with 1 being small to 5 being large.

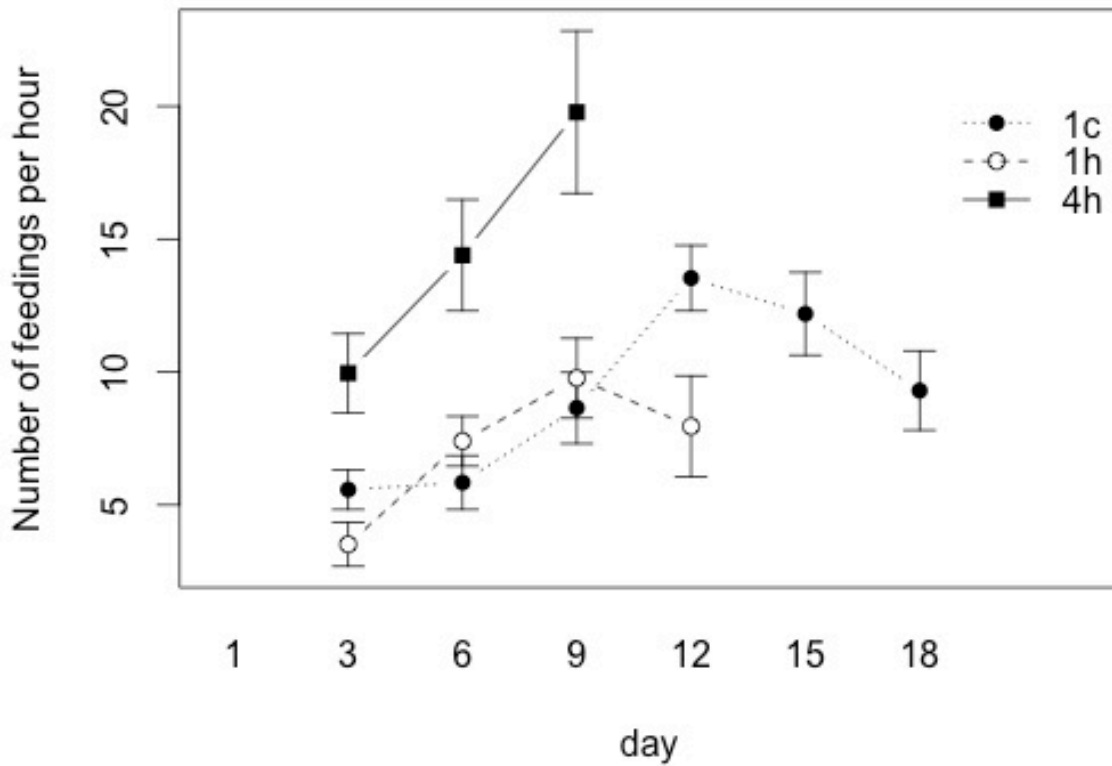


Figure 9. A whole brood (solid squares, “4h”) was fed at a higher frequency than the cuckoo nestlings (solid circles, “1c”) and the one-host group (open circles “1h”). Provisioning rates were insignificantly different between cuckoo nestlings and one-host nestlings over the comparable days, except for day 12 when the cuckoo nestlings were fed at higher rates. Age is presented on the x-axis and feeding rate (number of feedings per hour) is showed on the y-axis.

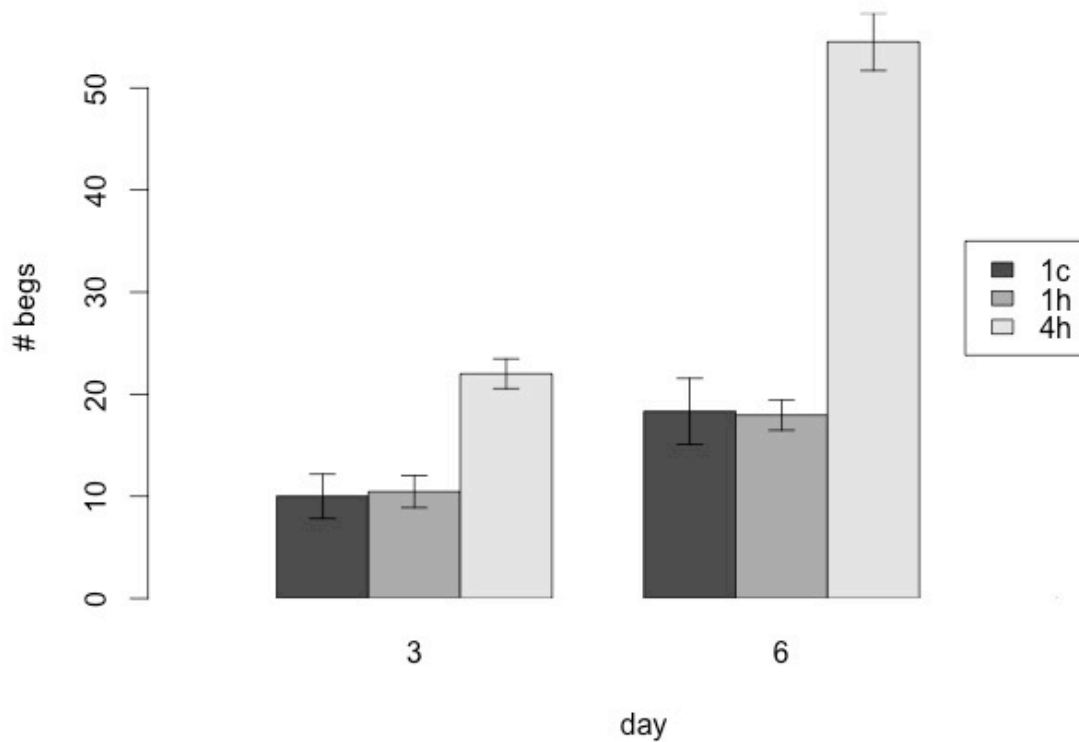


Figure 10. Begging intensity was measured as number of begs during a 10 seconds interval of intense begging (normally when a parent is provisioning the young – or alternatively for half of the one-host and cuckoo nestling groups by a mechanical trigger in the lab), which was sampled several times for each individual and a mean number of begs were extracted. Begging intensity was recorded on day 3 and day 6 for all groups. On day three the whole brood (“4h”, $N = 4$), displayed with the light-grey bars, begged at a higher intensity than the one host nestling group (“1h”, $N = 4$), medium-gray bars, and the cuckoo nestling (“1c”, $N = 5$), dark-grey bars. The same outcome was found on day six between the brood (“4h”, $N = 6$) and the one-host nestlings (“1h”, $N = 9$) and the cuckoo nestlings (“1c”, $N = 6$). The one-nestling groups begged at a similar rate.