

Cuckoos do not select redstart hosts of better quality despite potential growth consequences for nestlings

Teresa M. Abaurrea ^{a, b, *}, Angela Moreras ^{c, d}, Jere Tolvanen ^e,
Robert L. Thomson ^{c, f}, Rose Thorogood ^{a, b}

^a Helsinki Institute of Life Sciences, University of Helsinki, Helsinki, Finland

^b Research Programme in Organismal and Evolutionary Biology, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

^c Fitzpatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa

^d Faculté de foresterie, de géographie et de géomatique, Laval University, Quebec, Canada

^e Ecology and Genetics Research Unit, University of Oulu, Oulu, Finland

^f Section of Ecology, Department of Biology, University of Turku, Turku, Finland

ARTICLE INFO

Article history:

Received 22 February 2025

Initial acceptance 11 April 2025

Final acceptance 10 June 2025

Available online 16 September 2025

MS. number 25-00136R

Keywords:

brood parasitism

common cuckoo

common redstart

cuckoo activity

Cuculus canorus

host choice

individual quality

nest availability

Phoenicurus phoenicurus

Common cuckoo, *Cuculus canorus*, females rely on host species to raise their young and therefore should benefit from targeting high-quality individuals that maximize their fitness. Empirical evidence for individual host selection is, however, mixed with some studies suggesting random choice. Nevertheless, it is possible that the lack of consistent evidence for host selection may be because spatio-temporal variation in host availability has rarely been accounted for, or because the implications of host choice on fitness outcomes have not been tested experimentally. Here, we combined long-term monitoring data with an experiment to examine whether cuckoo females parasitising common redstarts, *Phoenicurus phoenicurus*, target individual hosts of higher quality to optimize their nestlings' growth. We first explored the scope for cuckoos to choose, finding spatial and temporal variation in host nest availability and host quality (using completed clutch size as a proxy). Cuckoos may choose hosts at different spatial scales (i.e. near neighbours versus habitat patches), so we next investigated whether parasitism varied with host quality (1) across the study area and (2) among nests within putative breeding areas. However, we found no evidence that redstarts laying larger clutches were more likely to be parasitized. Finally, we conducted a crossfostering experiment to disrupt the cuckoo's choice of nest. Moving cuckoo eggs to nonparasitized nests and between parasitized nests had no effect on morphometric growth of nestlings (mass, tarsus and wing length). Nestlings raised by foster parents differing in quality (i.e. smaller/larger clutch size) from the original nest tended to grow faster but smaller in asymptotic mass and tarsus length. Together these results suggest that the potential fitness benefits of choosing high-quality hosts do not compensate possible costs of searching for hosts in this system, although using different proxies for individual quality could help resolve the complexities inherent to host choice.

© 2025 The Author(s). Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Across animal taxa, oviposition decisions have fundamental implications for fitness as they determine the developmental environment and availability of resources needed for successful reproduction (Refsnider & Janzen, 2010). Most bird species also invest in parental care beyond oviposition (Cockburn, 2006), with intraspecific variation in how they incubate eggs and provision young (Westneat et al., 2013). For example, high-quality parents select territories with higher abundance (Decker et al., 2012)

and/or quality of food resources (Wilkin et al., 2009). This results in provisioning more food of better quality to nestlings (Pagani-Núñez & Senar, 2014) and measurable improvements in nestling growth and survival (Schwagmeyer & Mock, 2008; Silva et al., 2007). Avian brood parasites, however, avoid the cost of caring for their young by relying on the parental care abilities of their hosts (Davies, 2000). As the brood parasite's parental investment ends at oviposition, parasitic females may therefore gain an adaptive benefit from being choosy about laying their eggs in the nests of high-quality host parents and ensuring optimal conditions for offspring growth (Louders et al., 2015).

* Corresponding author.

E-mail address: teresa.abaurrea@helsinki.fi (T. M. Abaurrea).

Despite studies testing this hypothesis across different host species, there is only mixed empirical support that brood parasites assess individual differences and adjust their oviposition decisions accordingly. In some cases, host females in better body condition (e.g. great reed warbler, *Acrocephalus arundinaceus*, hosts of common cuckoos, *Cuculus canorus*; Poláčiková et al., 2009), those that lay larger eggs (e.g. rufous bush chat, *Cercotrichas galactotes*, hosts of common cuckoos; Alvarez, 2000) or those building larger nests (e.g. common redstarts, *Phoenicurus phoenicurus*, hosts of common cuckoos, Moreras et al., 2025; magpie, *Pica pica*, hosts of great spotted cuckoos, *Clamator glandarius*, Soler et al., 1995) are more likely to be parasitized. Common cuckoos can make selective oviposition decisions to match the appearance of the host's eggs (e.g. to reduce egg rejection by daurian redstarts, *Phoenicurus aureus*; Zhang et al., 2023). However, while some of these host traits could indicate differences in parental quality (e.g. Ardia & Clotfelter, 2007; Møller et al., 2014; Silva et al., 2007), the majority of studies suggesting evidence for individual host selection have been largely correlational and several other studies have found no evidence to support the hypothesis, either by common cuckoos (Wang & Liang, 2023) or other avian brood parasites (e.g. in shiny cowbirds, *Molothrus bonariensis* (Kattan, 1997) or brown-headed cowbirds, *Molothrus ater* (Orrians et al., 1989)). Instead, these studies support the alternative hypothesis that brood parasites follow a 'shotgun' strategy (Kattan, 1997) and lay their eggs in whatever suitable nest they can find.

A possible explanation for this mixed evidence for host selection may be because spatio-temporal variation in host nest availability and host quality is rarely accounted for (Kattan, 1997; Marton et al., 2019; Poláčiková et al., 2009; but see Soler et al., 2020). To choose high-quality individuals, brood parasite females require multiple host nests to be available at the right time and place (Jelínek et al., 2014). Brood parasitism is usually most successful if it coincides with when the host is laying her own eggs (Davies, 2000; Soler et al., 2020). Thus, each potential host nest detected by the cuckoo only has a short temporal window of suitability. In addition, if cuckoos compete for access to host nests then the spatial scope for choice could be constrained to local 'breeding areas' or territories (Moskát et al., 2020), which may or may not overlap (Koleček et al., 2021). Common cuckoo females, for example, can show aggressive responses towards each other (e.g. Moskát et al., 2020) and typically lay eggs within an area (Koleček et al., 2021) that they patrol to facilitate parasitism while the host is still egg-laying (Davies, 2000; Davies & Brooke, 1988; Koleček et al., 2021). If competition for host nests is high then it may be more challenging for cuckoos to be selective (e.g. magpies building larger nests are more likely to be parasitized in years when great spotted cuckoo activity is low; Molina-Morales et al., 2016). Therefore, to detect nonrandom oviposition depending on host quality, the extent of spatial and temporal choice available to cuckoos needs to be considered (Lyon, 1993).

Finding a relationship between host quality and parasitism is, however, insufficient evidence that host selection is adaptive for brood parasites. Showing a maternal effect like nest-site selection requires evidence that it has a consequence for fitness (Marshall & Uller, 2007), but unfortunately it is logistically very challenging to track individual cuckoo females and assess their lifetime reproductive success. Few studies have described their individual breeding success even within a season (e.g. Kleven et al., 2004; Koleček et al., 2021; Nakamura & Miyazawa, 1997; Vogl et al., 2004) or the factors associated with survival and recruitment of offspring (e.g. Koleček et al., 2020). Nestling growth and asymptotic body size are instead often used as

proxies of fitness in studies of wild birds as they correlate with juvenile survival (e.g. Beauchamp, 2023; Bryant, 1978; Naef-Daenzer & Gruebler, 2016). While there are no studies yet available on the relationship between cuckoo nestling size and survival or breeding success, brood parasite growth varies among different host species (Grim, 2006; Grim et al., 2014; Winnicki et al., 2021) even if they have similar breeding ecologies (Grim & Samaš, 2016). Furthermore, the growth of brood parasitic nestlings can also vary depending on whether the parasite grows up alone or among host nestlings (Geltsch et al., 2012; Grim et al., 2009a), depending on eviction effort (Anderson et al., 2009; Grim et al., 2009b, 2011), nest architecture (Grim et al., 2009b, 2011), diet (Grim et al., 2017) or even depending on the social mating status of its host (Trnka et al., 2012). Therefore, it is likely that common cuckoo nestling growth varies according to differences in host quality, and if experimentally disrupted, would provide stronger evidence that cuckoo host selection is adaptive, and thus, expected to evolve.

Here, we used a nestbox breeding study population of common redstarts, *Phoenicurus phoenicurus*, (redstarts hereafter) to test whether common cuckoo females (cuckoos hereafter) target host nests according to parental quality, while taking spatio-temporal variation of nest availability into account. Cuckoo females are host-specific brood parasites (Fossøy et al., 2016), and those that use redstarts lay immaculate blue eggs, which mimic the host's phenotype (Stoddard & Stevens, 2011) and are rarely found in the nests of other species (Moksnes et al., 1995; see Methods). This local high host-specificity and the ease of monitoring alternative redstart nests available for parasitism (that is, because of nestboxes) therefore provides a unique opportunity to assess individual host selection in space and time. First, to evaluate whether choice is possible for cuckoos we used a georeferenced breeding monitoring data set collected over 9 years to describe spatio-temporal variation in host availability and quality. Second, we tested whether redstarts were more likely to be parasitized if they were of higher quality than other redstarts nesting nearby. We used completed clutch size as a proxy for individual redstart host quality because it is a reliable indicator of parental investment (Garamszegi et al., 2004; Houston et al., 1983) and individual quality in other avian species (Slagsvold & Lifjeld, 1988, 1990; Winder et al., 2023) and is readily available data that allow for replication in other host species. Moreover, common redstarts, our host species, select breeding areas depending on vegetation structure (Martínez et al., 2010), and this vegetation affects completed clutch size in this species (N. Martínez, 2012). This could indicate that high-quality individuals that lay larger clutches may get the better territories compared with low-quality individuals that lay smaller clutches. We do not yet know which individual host traits cuckoos may pay attention to, so we chose to use a proxy for quality to first establish whether nonrandom choice occurs (laying cuckoos cannot use clutch size as a cue as parasitism occurs before clutch completion). We predicted that female redstarts who laid larger clutches should be more likely to be parasitized during laying. As it is unclear, however, at what spatial scale female cuckoos select areas to breed (that is, larger-scale habitat selection or imprinting (Koleček et al., 2020; Teuschl et al., 1998) versus attraction to quality of territorial cuckoo males defending a smaller area of host nests (Ciaralli et al., 2024), we tested our prediction both at the scale of the study area and within putative breeding territories while accounting for temporal variation of nest availability. Third, we conducted a crossfostering experiment to test whether disrupting individual host nest choice affects the growth of cuckoo nestlings. We predicted that cuckoo nestlings raised in the host nest chosen by their

mother would grow larger and/or faster than cuckoo nestlings moved to nonparasitized redstart nests.

METHODS

Study Site and Nest Monitoring

Fieldwork was conducted in Scots pine, *Pinus sylvestris*, forests near Oulu, Finland (64°60'N, 25°42'E) that have a ground cover of lingonberry, *Vaccinium vitis-idaea*; bilberry, *Vaccinium myrtillus*; heather, *Calluna vulgaris*; mosses, *Pleurozium schreberi* and *Dicranum spp.*; and lichens, *Cladonia spp.* Since 2002, commercially available wooden nestboxes (Linnunpönttö Oy) have been placed approximately 1.5 m above the ground, 100 to 250 m apart, in an area of approximately 60 km² (Thomson et al., 2016). The boxes measure 17.5 × 17.5 × 28 cm (external width × depth × height) with a 7 cm diameter entrance hole and were emptied of old nest material each spring before the first redstarts and cuckoos arrived after their migration from sub-Saharan Africa to breed at the study area in early May (Grim & Rutila, 2017; Moreras, 2023; Samaš et al., 2016; Thomson et al., 2016). The number of nestboxes increased in the study area from 271 to 374 during the years of this study, and all were georeferenced using a hand-held Global Positioning System device (± 5 m accuracy).

Nestboxes were monitored for breeding activity at least once a week throughout breeding seasons (2013–2022, excluding 2020 because of coronavirus disease (COVID)-19 pandemic restrictions) and we identified the occupying species through visual inspection of nest materials, egg colour and pattern and nearby adult birds (Fig. S1). While five other species were observed using the nestboxes (great tits, *Parus major*, average *N* nestboxes per year ± SD = 47 ± 16, range 10–62, average box occupancy = 19 ± 6 % per year; pied flycatchers, *Ficedula hypoleuca*, average *N* nestboxes per year ± SD = 20 ± 9, range 12–41, average box occupancy = 9 ± 4 % per year; crested tits, *Lophophanes cristatus*, four nests occurring in 3 years; blue tits, *Cyanistes caeruleus*, one nest; willow tits, *Poecile montanus*, one nest), almost all parasitism events occurred in redstart nests (2 great tit nests were parasitized in the 9-year study period).

Once a nestbox was occupied by redstarts, it was monitored approximately every 3–5 days to record laying date of the first egg (hereafter laying date), clutch size, incubation status and presence of cuckoo eggs (see Fig. S2 for a map of location of parasitized nests). Nestboxes occupied by species other than redstarts were monitored in a similar way but less frequently. Redstarts lay clutches of seven eggs on average, which they incubate for approximately 13 days (Rutilla et al., 2002; Samaš et al., 2016). If the laying of the first redstart egg was missed, then the date of clutch initiation was back-calculated assuming that redstart females lay one egg per day during the laying period (Thomson et al., 2016). The expected hatching date for cuckoo eggs was estimated by calculating 12 days from the onset of incubation. Nests were monitored until predation, until abandonment occurred, or until day 12 or 13 when nestlings were close to fledging (redstart nestlings: 15 days, cuckoo nestlings: 21 days). Whenever a nestbox was visited, we checked for any mislaid cuckoo eggs outside the box (i.e. eggs on the ground) to avoid underestimating parasitism. Redstarts very rarely eject naturally laid cuckoo eggs (Avilés et al., 2005; Rutilla et al., 2002; Thomson et al., 2016).

Crossfostering Experimental Design and Protocol

To test whether a cuckoo's choice of host nest may be adaptive, we conducted a crossfostering experiment with cuckoo eggs laid in 2014–2019. We randomly assigned cuckoo eggs to one of three

treatments based on whether the nest where the cuckoo egg hatches is the same where the cuckoo female laid it, and the parasitism status of the final nest of the cuckoo egg: (1) 'chosen', the cuckoo egg was handled while measurements were taken for a different study but left to hatch in the redstart nest as intended by the cuckoo female; (2) 'crossfostered', after measuring, the cuckoo egg of a parasitized redstart nest was relocated to a different parasitized nest, which cuckoo egg was, in turn, taken to a third nest, either parasitized or not; and (3) 'nonchosen', the cuckoo egg of a parasitized nest was relocated to a nonparasitized nest (for a map of locations of manipulated nests, see Fig. S3). In our cuckoo–redstart study system, cuckoo females do not remove a host egg when laying their own (Grim & Rutila, 2017) and so we acted in a similar manner when either parasitizing 'nonchosen' nests or moving cuckoo eggs among 'chosen' nests. Therefore, our experimental manipulation followed what happens naturally. To reduce risk of hatching failure, cuckoo eggs were moved prior to initiation of incubation and therefore the assignment of the receiving nests in the nonchosen treatment was blind to differences in the redstarts' complete clutch size. After hatching (hatching date is day 0), cuckoo nestlings were measured every 3 days until 18 days of age to record their weight (to the nearest 0.01 g), tarsus length (to the nearest 0.01 mm) and wing length (to the nearest mm), which is a reduced frequency of measurements compared with other studies available on cuckoo nestling growth (e.g. Grim, 2006). For logistical reasons, some nestlings were not measured at all ages. In our system, 15%–20% of cuckoos fail to reject host nestlings and are therefore raised in mixed broods (Samaš et al., 2016; Thomson et al., 2016); however, all cuckoo nestlings in our crossfostering experiment were raised alone. Nests were not checked again until after the estimated fledging date to avoid force-fledging the nestlings. Thus, we did not have an exact fledging date, so we assumed that a nestling fledged if it survived until 18 days of age.

Data Analysis Methods

Our initial data set included only nestboxes occupied by redstarts with complete information available for laying date, clutch size, latitude and longitude, and where we were confident that our monitoring did not miss any possible parasitism events (*N* = 961). This filtering removed nests that were abandoned before or during laying (redstarts usually start building several nests before completing one, personal observation), or depredated before clutch completion. The data set was then truncated to remove nests that were active only when cuckoos were not present in the study area (that is, parasitism was impossible; according to the date on which the first and last cuckoo egg of the season was laid, *N* = 9), and we excluded any nests with clutches larger than eight eggs (*N* = 7) because these were most likely laid by multiple females (personal observation; when females take over an occupied nest they start egg laying without building a new nest cup). Lastly, we excluded nests with no information on cuckoo egg-laying date (*N* = 5). Our available data set therefore included 940 nests, and all data analyses detailed below were conducted in R version 4.3.2 (2023-10-31 ucrt, R Core Team, 2023).

Spatio-temporal variation in nestbox occupancy and host quality

We first investigated whether cuckoos had scope to choose among host nests by testing for spatiotemporal variation in nestbox redstart occupancy relative to other bird species and host quality. Therefore, we built generalized additive mixed models (GAMMs, which allow the inclusion of nonlinear effects of predictive variables in the model) describing nestbox occupancy and clutch size as a function of laying date and location of nests. We

built these models using package *mgcv* (version 1.9.0, Wood, 2017) with laying date included as a spline-based smooth term with default dimensions of the basis and a two-dimensional full tensor product smoother for geographic coordinates (recommended for covariates at different scales, such as latitude and longitude, Wood, 2006; Zuur et al., 2014). We used a full tensor product smoother rather than a tensor product interaction (that is, smooth main effects and smooth interaction) because we were interested in variation throughout our study area rather than variation with latitude and longitude separately (Wood, 2017). Year was included as a random intercept to account for annual variation (e.g. in environmental conditions and sample sizes). Nestbox occupancy was modelled using a binomial distribution and logit link function, and variation in clutch size was modelled using a Gaussian distribution with an identity link function. Although clutch size is a discrete count variable and often modelled using a Poisson distribution, in this case the model residuals conformed best to a normal distribution.

Parasitism occurrence according to individual host quality

A nest may be parasitized for two reasons: because it is the only nest available in the area or because a cuckoo chooses it from alternative nests. Similarly, a nest may be left unparasitized

because a cuckoo chooses an alternative nest, or because there are no cuckoos laying eggs in the area. To analyse the potential for parasitism occurrence (i.e. choice) according to host quality using clutch size as a proxy rather than a cue for cuckoo females, we therefore filtered the data set to only include host nests that were likely to be within the breeding range of an active female cuckoo and in areas where she had a choice of nests to parasitize. It was not possible to estimate the breeding area of individual female cuckoos in our study by for example, phenotyping or genotyping to assign maternity (Koleček et al., 2021). Instead, we extrapolated a biologically informed estimate of breeding area from the most comprehensive published descriptions available (65 ha for cuckoos parasitizing great reed warbler hosts, Koleček et al., 2021) and adjusted it according to the density of nests in our study area (median = 0.09 nests/ha versus median = 0.29 nests/ha for great reed warbler in Koleček et al., 2021). This generated an estimate (195 ha) that corresponded to an 800 m radius circle, which we then centred on each nest (nestboxes are distributed regularly throughout the forest, Fig. S1) to determine whether a choice for parasitism was possible. These focal nests could be parasitized or unparasitized but were only retained in the data set if there was at least one other host nest available (that is, an alternative choice for parasitized focal nests) and at least one parasitized nest (that is,

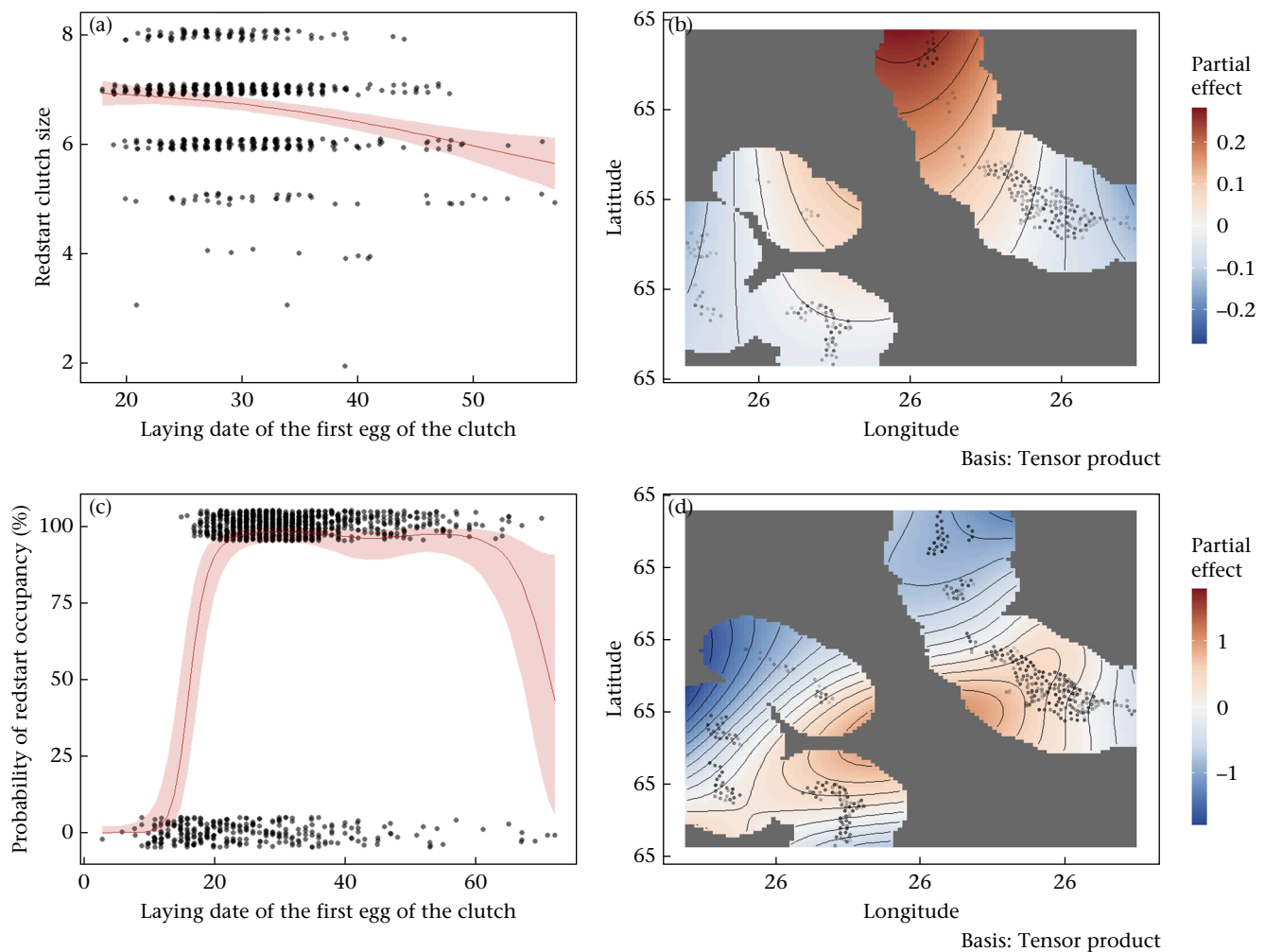


Figure 1. Spatiotemporal variation of nestbox occupancy and clutch size. Output of models describing (a, b) clutch size and (c, d) nestbox occupancy as a function of (a, c) laying date and (b, d) location. Variation among years was accounted for with a random intercept effect, and the relationship to the variable of interest (i.e. partial effect) is shown either by plotting the line of best fit (red solid line) with the 95% CI (red shading, a, c) or by a colour ramp (b, d). For a map showing the distribution of parasitized nests in a sample year, see Fig. S2. Nests and data points are indicated by black jittered dots with transparency indicating overlapping points.

indicating an active cuckoo in the area for unparasitized focal nests) located within the cluster (i.e. the 800 m radius circle). Nests within clusters were considered available for choice by cuckoos if (1) the egg-laying period overlapped with that of the focal nest and (2) the alternative nest/s was not parasitized before clutch initiation of the focal nest (that is, it was still available for the cuckoo to choose). The final data set included 685 focal nests where cuckoos had potential to make a choice among a cluster of alternative nests.

To investigate evidence for choice based on host quality, we used GAMMs with a binomial distribution and logit link to test whether hosts with larger complete clutches were more likely to be parasitized. Separate models were built to analyse choice at different spatial scales (see Introduction for rationale): (1) across the entire study area (i.e. all redstart nests available, Fig. 1a) and (2) within a local putative breeding area (i.e. nests available within clusters, Fig. S4). To account for variation in clutch size during the season and across the study area, (1) we included the following: a three-way tensor product interaction among clutch size, latitude and longitude; a three-way tensor product interaction among laying date, latitude and longitude; a two-way tensor product interaction between clutch size and laying date; and all underlying two-way tensor product interactions and main effects as predictors. As main effects, we included clutch size with restrained basis dimensions ($k = 7$, range of clutch sizes was 2–8 eggs), laying date, latitude and longitude as cubic regression splines. Cubic regression splines were used in this analysis and the following (that is, choice within a local putative breeding area) because these splines do not need reparameterization to be interpretable and thus allow defining of main effects that mimic the tensor product interaction fit (Wood, 2017). Finally, we accounted for annual variation in parasitism occurrence with a random intercept for year.

We calculated a rank clutch size score for each focal nest compared with the clutch size of all alternative nests available within its cluster (2) using the rank function (base R package, R Core Team, 2023); larger clutch sizes were ranked with higher numbers, and ties were assigned a mean rank (see Fig. S5 for variation in clutch sizes within clusters). As the number of nests available within clusters varied (Fig. S4), we penalized the rank of the focal nest (that is, by dividing rank by number of available nests per cluster) so that those with more alternatives for parasitism were weighted more heavily than clusters where fewer choices were available. Each nest and its associated attributes were represented only once in the data set used for these analyses. Nests within each cluster were accounted for in the penalized clutch size rank described above. The full model testing the relationship of clutch size and parasitism status of the focal nests therefore included the penalized rank as cubic regression spline, a tensor product interaction containing latitude and longitude and the main effects of this interaction as cubic regression splines. To account for variation in local cuckoo activity, we included the number of parasitized nests within the 800 m radius circle (excluding the focal nest if it was parasitized) before and during the cluster's focal redstart egg-laying period as another cubic regression spline. Cuckoo females lay eggs for up to 51 days per season (Koleček et al., 2021); thus, including nests parasitized from the beginning of the breeding season until the end of the egg-laying period of the focal nest in our cuckoo activity estimate allowed us to capture the activity of each female within its putative laying area. Finally, we included year as a random intercept. We then conducted model selection on the full models for the two spatial scales using the 'dredge' function from the MuMIn package (version 1.47.5, Bartoń, 2023). We first constructed a confidence set of models, ordered by ascending AIC values. From this set, we

excluded models that were more complex versions of those with lower AIC values (Richards et al., 2011).

Effect of host nest choice on cuckoo nestling growth

We estimated the asymptote and growth rate (k) for weight (g), tarsus length (mm) and wing length (mm) by fitting a standard logistic growth model (Ricklefs, 1968) using the 'SSlogis' function in a nonlinear least squares framework implemented with the 'nls' function in R (stats package, R Core Team, 2023). To our knowledge there is no study analysing the best fit growth model for Cuculiformes, but the logistic growth model is flexible enough to fit well across multiple avian orders (Passeriformes, Starck & Ricklefs, 1998; Galliformes, Aggrey, 2002; Columbiformes, Gao et al., 2016). We calculated these growth parameters for 47 cuckoo nestlings but removed two nestlings that died before 18 days of age (from two different treatments, and both in 2014). It was not possible to investigate survival further because of this small number of losses. Additionally, one nestling's wing length was measured only twice, which did not provide enough timepoints to fit a growth model. Thus, wing models included data from 44 nestlings only.

We used the asymptote and growth rate of weight, tarsus length and wing length as response variables and built GAMMs with Gaussian distribution and identity link function to include hatching date as a nonlinear predictive variable. These models included the type of nest as a categorical predictor with three levels, i.e. chosen, crossfostered and nonchosen (20 nestlings in chosen nests, 7 in crossfostered nests, and 18 in nonchosen nests in weight and tarsus length, and 20, 7 and 17, respectively, in wing length). We incorporated hatching date as a smoothing function with default dimensions of basis and year as random intercept to control for variation among years. As these models were investigating the consequences of perturbing a cuckoo female's choice, we used a weight term to give more importance in the model fit to nestlings that originated from parasitized nests in areas where there were relatively more alternative nests to choose among (that is, available nests/mean(available nests)). We used a similar procedure as described above and defined a nest as available if it was within 800 m radius of the parasitized nest, if the host egg-laying period overlapped with that of the nest where the experimental cuckoo egg was laid and if the alternative nest was not parasitized before the laying period of the focal nest. We then compared these models' Akaike's information criteria corrected for small sample size (AICc) with two models containing only the covariates of year or hatching date and year.

Since cuckoo eggs were moved for this experiment as soon as possible after laying, the complete clutch size (i.e. parental quality) was not yet known, so we could not control for this source of variation during crossfostering. Therefore, we also conducted an exploratory analysis to investigate the effects of moving nestlings to foster nests with smaller, similar or larger clutch sizes than the ones originally 'chosen' by the cuckoo female. Here, we only included nestlings that hatched from eggs moved to crossfostered and nonchosen nests ($N = 25$ for weight and tarsus length and 24 for wing length) and built linear models with clutch size difference (that is, the numeric difference between the redstart clutch size where the cuckoo nestling hatched and the clutch size in the cuckoo's original nest) as a quadratic explanatory variable. Whenever the quadratic term was not significant, it was removed from the model.

Ethical Note

This study was conducted following the current laws and recommendations for animal welfare of Finland. Permits to place

nestboxes in our study area were granted by the City of Oulu (564-2017-8 and 564-2020-4), and nest monitoring and experiments throughout the study years were conducted under research permits POPELY/136/07.01/2014 and VARELY/921/2017 granted by Elinkeino-, liikenne- ja ympäristökeskus (Centre for Economic Development, Transport, and the Environment of Finland). Additionally, animal welfare approval (ESAVI/12343/2020) was granted by Etelä-Suomen aluehallintovirasto (Regional State Administrative Agency of Southern Finland). During nestbox monitoring, we approached cautiously to avoid stepping on mislaid cuckoo eggs and to minimize disturbances to birds inside and around the nestboxes. Monitoring was conducted at intervals no shorter than 2 days, and nestboxes were opened slowly to reduce stress. For the crossfostering experiment, we took advantage of the high proportion of cuckoo eggs laid inside the nestbox but outside the nest cup (Thomson et al., 2016). Such eggs are usually left unincubated, so our experimental manipulation increased their likelihood of hatching. Cuckoo eggs found in redstart nests were carefully collected, placed in a small box lined with soft cotton, and promptly transported to another nest at the egg-laying stage. Only 2 out of 47 manipulated cuckoo nestlings died. These two nestlings belonged to different treatment groups but the same year (2014), suggesting that their mortality was likely caused by particularly harsh environmental conditions that year rather than by our experimental manipulation, which included less frequent growth measurements than other studies on cuckoo nestling growth (Grim, 2006).

RESULTS

Spatiotemporal Variation in Nestbox Occupancy, Host Quality and Host Nest Availability

Redstarts occupied over half of the nestboxes we provided each year (average N per year \pm SD = 163 ± 33 , range 120–219, which represents 67 ± 5 % per year), with occupancy varying in both space and time (Table S1, Fig. 1c and d). A nestbox was more likely to be occupied by redstarts than by other species in the central areas of the study site, and during the central days of the breeding season (Table S1, Fig. 1c and d). There was also spatial and temporal variation in clutch size, our proxy for individual host quality, with larger clutches being laid earlier in the season and towards the north of the study area (Table S1, Fig. 1a and b). At the scale of a cuckoo's likely breeding area, or 'cluster' around each focal host nest, most often there were at least two nests available for a cuckoo to choose from (851 clusters, that is, 90.5 %, contained the focal nest plus at least one other available nest), and the range of clutch sizes within clusters varied from 1 to 5 (median 3, Fig. S5). In our final data set, there were between 2 and 24 available nests, with four nests as the most frequent situation (Fig. S4).

Parasitism Occurrence according to Individual Host Quality

On average, there were 30 (\pm SD 16) cuckoo eggs laid per year in our study area (range 8–59 eggs, total: 266 cuckoo eggs across 9 years) resulting in 34 % of redstart nests being parasitized each year (241 nests parasitized in total, average \pm SD parasitized nests per year = 27 ± 14 , range 8–51 nests). There were 23 cases of multiple parasitism (21 nests parasitized twice, and 2 nests parasitized three times); however, these nests were not included in the analysis.

There was no strong evidence to accept or reject the hypothesis that clutch size may affect the occurrence of parasitism. The highest ranked model describing parasitism probability at the spatial scale of the study area included clutch size with a

marginally nonsignificant negative and linear effect (Table 1, Fig. 2A), but the second highest ranked model (Δ AIC = 1.61) did not include clutch size (Table S2). We explored this further with a post hoc G-test of independence to test whether the proportion of nests parasitized varied among redstart clutch sizes and found that while most clutches had 6 or 7 eggs (79.2 % of 685 nests), clutches with 3–5 eggs were parasitized more often (Fig. 2a, G-test: $G = 56.45$, χ^2 $df = 12$, $P < 0.001$). Results from the top-ranked model also suggested that nests from later in the season (i.e. date) or those towards the east of our study area (longitude) were more likely to be parasitized (Table 1, Fig. S6a and b).

At the local scale of a putative cuckoo breeding area (i.e. within clusters), the final model set included only one model, which featured the number of parasitized nests per cluster and longitude (Table 1). The highest-ranking model that also included the penalized clutch size rank variable (i.e. number of parasitized nests per cluster, longitude and penalized clutch size rank) had a higher AIC (Δ AIC = 1.72, Table S2, Fig. 2b) than the top-ranking model and would have been excluded based on model selection criteria (Richards et al., 2011). This indicates that the penalized clutch size rank variable was not supported in explaining parasitism risk. However, as this variable is central to our research question, we report its parameter estimates in Table 1. The estimates for the number of parasitized nests per cluster and longitude were qualitatively identical between the top-ranked model and the highest-ranking model that included penalized clutch size rank. In both models, focal nests within clusters with higher cuckoo activity (i.e. more parasitized nests) were significantly more likely to be parasitized (Table 1), as were those located further east (longitude; Table 1), mirroring the patterns observed at the broader study-area scale.

Effect of Host Nest Choice on Cuckoo Nestling Growth

Models including the type of nest showed no significant effects on weight, tarsus length or wing length growth parameters (asymptote and growth rate; Table 2, Fig. 3a–c, e), and all full models were >2 AICc larger than models containing only the covariates (Table S3). For growth curves of all analysed cuckoo nestlings, see Fig. S7. However, when we investigated the effect of moving cuckoo nestlings to nests with differing complete clutch sizes, we found that those who were moved to a nest with a clutch size similar to their original nest tended to be heavier (Fig. 3bi) and obtained weight more slowly (Fig. 3bii) than nestlings moved to nests with a clutch size very different from the original nest where their mother had laid her egg (Table 3). Nestlings that were raised by parents with similar sized clutches also grew longer tarsi (Fig. 3di) but not wings (Fig. 3fi), and there were no differences in the growth rates of these two morphometrics (Fig. 3dii, fii). However, these results were from a relatively small sample size (24–25 nestlings moved to nonchosen nests) and were influenced by two cuckoo nestlings with a large difference in clutch size (clutch size increased or decreased by three eggs, Table S4). Once these two nestlings were removed, the relationship between growth parameters and clutch size difference became linear and nonsignificant. Therefore, these results should be interpreted with caution.

DISCUSSION

In theory, brood parasite females should be under selection to maximize the quality of host parental care and choose among individual hosts accordingly (Louders et al., 2015). There however is currently mixed support for this hypothesis, in part because host nest availability has rarely been accounted for (e.g. Kattan, 1997

Table 1
Parasitism occurrence according to variation in clutch size at different spatial scales

	Parameter estimate	SE	z value	edf	χ^2	P
Study scale area						
Intercept	-0.669	0.139	-4.799			<0.001***
s(Clutch size, bs='cr')				1.001	3.437	0.064
s(Laying date, bs='cr')				2.821	16.501	0.002**
s(Longitude, bs='cr')				1.49	14.167	0.002**
s(Year, bs='re')				4.855	12.606	0.008**
Local breeding scale area						
Top-ranked model						
Intercept	-0.678	0.086	-7.901			<0.001***
s(No. of parasitized nests per cluster, bs='cr')				3.404	49.047	<0.001***
s(Longitude, bs='cr')				4.351	25.46	<0.001***
Highest ranked model including penalized clutch size rank						
Intercept	-0.678	0.086	-7.901			<0.001***
s(Penalized rank, bs='cr')				1.001	0.280	0.597
s(No. of parasitized nests per cluster, bs='cr')				3.359	48.890	<0.001***
s(Longitude, bs='cr')				4.389	25.797	<0.001***

Results of generalized additive mixed effect models of parasitism occurrence ($N = 685$ nests). Clutch size, laying date, longitude and number of parasitized nests per cluster (bs='cr') were included in models as cubic regression splines, and year (bs='re') was included as a random intercept. Local breeding area estimated as nests within 800 m radius of focal nests. Variables are described using mgcv package syntax. edf: effective degrees of freedom. Significant P values (according to alpha 0.05) in bold (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$).

versus Poláčiková et al., 2009), and it is not known whether being choosy is adaptive for the cuckoo in the first place. Here, we expected that common cuckoo females would select nests of high-quality redstart hosts (using completed clutch size as a proxy) if we accounted for their scope to make a choice (that is, spatial and temporal variation in host availability, quality and cuckoo activity). Furthermore, we predicted that disrupting these choices experimentally would lead to cuckoo nestlings growing smaller and/or slower in nests not chosen by cuckoos for parasitism, suggesting that choosiness could be adaptive. However, we found no evidence that cuckoos chose higher-quality redstarts, either at the scale of a cuckoo's putative breeding area, or across the study site. In fact, we found weak nonsignificant evidence in the opposite direction: across the study site, cuckoos tended to be less likely to parasitize redstarts laying larger clutch sizes. We also found only weak

evidence that the growth of cuckoo nestlings was poorer when raised in a nest with a different clutch size from where they had been laid. Why, despite utilizing data from across multiple years to provide scope to detect patterns even with environmental variation, were we unable to detect clear evidence for, or against, host selection?

Is There Scope for the Cuckoo Female to Choose?

The first criteria to detect evidence for host selection by cuckoos is that there is sufficient variation in hosts to choose from. We found spatial variation in the number of host nests available at any given time for parasitism, both across the study site and at the scale of putative cuckoo breeding areas, and variation in clutch size with redstarts laying larger clutches earlier in the season and in

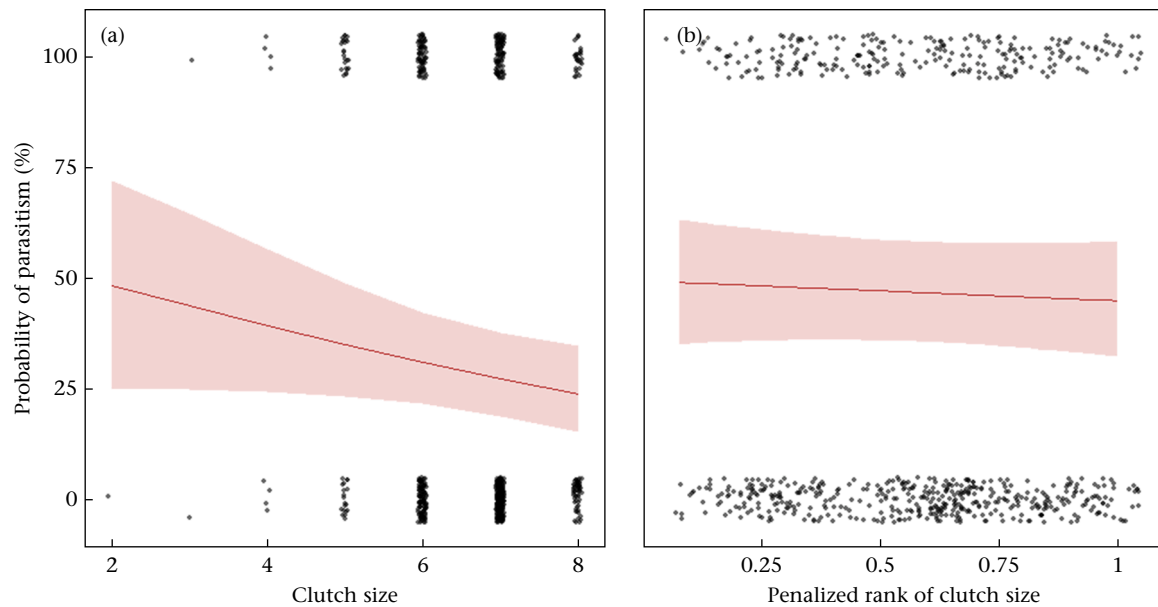


Figure 2. Parasitism occurrence according to clutch size, a common proxy for host quality, at (a) scale of the study area and (b) relative to other nests within the putative laying area of a cuckoo (ranked then penalized by available nests). The mean clutch size (± 1 SD) in (a) is 6.65 ± 0.87 eggs and (b) shows the best fitting model including penalized clutch size rank ($\Delta AIC = 1.72$ from the top-ranked model). In both plots, points represent raw data from nests ($N = 685$; jittered to improve visibility), red lines indicate line of best fit from generalized additive mixed models (see Table 1), and the shaded areas indicate 95% CIs.

Table 2
Summary statistics of generalized additive mixed models (Gaussian distribution with identity link) explaining the different cuckoo nestling morphometrics

		Estimate	SE	t value	edf	F	P
Weight (N = 45)							
Asymptote	Intercept	97.489	2.746	35.503			<0.001***
	Type of nest (crossfostered nest)	8.144	7.255	1.123			0.268
	Type of nest (nonchosen nest)	2.031	5.084	0.4			0.692
Growth rate	s (hatching date)				1.874	0.761	0.025*
	Intercept	0.373	0.009	40.376			<0.001***
	Type of nest (crossfostered nest)	-0.02	0.026	-0.757			0.453
	Type of nest (nonchosen nest)	0.003	0.018	0.144			0.886
	s (hatching date)				0.00001	0	0.741
Tarsus length (N = 45)							
Asymptote	Intercept	28.236	0.354	79.832			<0.001***
	Type of nest (crossfostered nest)	1.189	0.802	1.482			0.146
	Type of nest (nonchosen nest)	-0.232	0.562	-0.412			0.682
Growth rate	s (hatching date)				0.443	0.096	0.188
	Intercept	0.266	0.01	25.372			<0.001***
	Type of nest (crossfostered nest)	-0.003	0.024	-0.127			0.899
	Type of nest (nonchosen nest)	0.005	0.017	0.3			0.766
	s (hatching date)				0	0	0.649
Wing length (N = 44)							
Asymptote	Intercept	148.102	4.001	37.014			<0.001***
	Type of nest (crossfostered nest)	3.312	7.333	0.452			0.654
	Type of nest (nonchosen nest)	2.646	5.215	0.507			0.615
Growth rate	s (hatching date)				0	0	0.882
	Intercept	0.235	0.01	23.945			<0.001***
	Type of nest (crossfostered nest)	-0.002	0.01	-0.216			0.830
	Type of nest (nonchosen nest)	0.000	0.007	0.018			0.986
	s (hatching date)				0	0	0.706

Full models include type of nest as categorical predictive variable, hatching date as smoothing function with default dimensions of basis and year as random intercept. Variables are described using *mgcv* package syntax. t value, T statistic; edf, effective degrees of freedom; F, F statistic. Significant P values (according to alpha 0.05) in bold (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$).

the northern parts of our study area. Clutch sizes are variable in redstarts (e.g. Fig. 2a) and there is considerable variation in reproductive success (e.g. 63.2 % nests fledge at least one chick; Moreras et al., 2022) and body condition (Moreras et al. unpublished data) among birds at our study site. Furthermore, we detected sizeable variation in e.g. asymptotic mass and wing length of the cuckoo chicks they raised. This suggests that there is variation in host quality for cuckoos to select from. Indeed, we did find some evidence to suggest that choice was possible, but in the opposite direction (that is, a nonsignificant weak trend for smaller clutches to be parasitized). Furthermore, because we analysed potential relationships with clutch size variation at two temporal scales (that is, across the season and within the laying period of the host), we were able to control for potential bias because of seasonal patterns as well as the most relevant temporal window (host egg-laying period) for cuckoo host choice (Samaš et al., 2016).

While it is unlikely that we missed many parasitism events as we rarely observe redstarts without active nests in our boxes (Moreras et al., 2021, personal observation), it is possible that we under- or overestimated availability of host nests at the scale of a cuckoo's breeding area. Most previous studies have estimated the laying areas of female cuckoos based on tracking their movements (e.g. Koleček et al., 2021; Nakamura et al., 2005; Vogl et al., 2004) or variation in egg phenotype (e.g. Šulc et al., 2022). The genetic line of female cuckoos that parasitizes redstarts (redstart cuckoo gens) lays immaculate blue eggs with relatively little variation (Stoddard & Stevens, 2011), and we were not able to use either radio frequency identification or the Global Positioning System to track cuckoos' activity, or molecular methods to assign parentage, within or across years of the study. Therefore, we based our analyses for choice among neighbouring host nests using the most accurate estimate available for the size of cuckoo laying areas. This was based on cuckoos parasitising *Acrocephalus* warbler nests in reed beds (Koleček et al., 2021). Cuckoo female breeding areas vary

within and between studies using different hosts (Moskát et al., 2019; Nakamura et al., 2005; Vogl et al., 2004; Williams et al., 2016), albeit using less accurate methods to determine maternal identity (Koleček et al., 2021), and it is possible that laying areas do not scale with differences in host density as we assumed. To investigate this possibility, we repeated our analyses using different sized radii to estimate cuckoo breeding areas, but the results were very similar and are not shown here. Nevertheless, to rule out this possibility it would be crucial in future to use more sophisticated methods to improve the resolution of individual cuckoo female laying decisions, at least at the scale of putative breeding territories.

Do Cuckoo Females Choose Higher-Quality Hosts?

Given that it was likely that there was scope for cuckoos to choose, there are several nonmutually exclusive explanations for why we failed to detect evidence for cuckoos selecting higher-quality hosts. First, it could indicate that cuckoo females do not choose specific nests for parasitism but rather use a shotgun strategy among the nests they find at a suitable host breeding stage (i.e. during laying). However, we found that smaller clutch sizes were parasitized more frequently, even though they were not the most commonly available nests. This supports the possibility of nonrandom host choice (e.g. Soler et al., 1995; Wang et al., 2020), although the pattern could also be explained by seasonal variation in redstart breeding behaviour. Nests with small clutches (2–5 eggs) are less abundant (54 out of 685) than those with more eggs. Thus, even if cuckoos parasitize these small clutch size nests by chance, this could create a weak pattern in our parasitism likelihood results that would be hard to disentangle from real choice.

Second, it is possible that clutch size is an inappropriate proxy for individual host quality in redstarts. Clutch size has traditionally

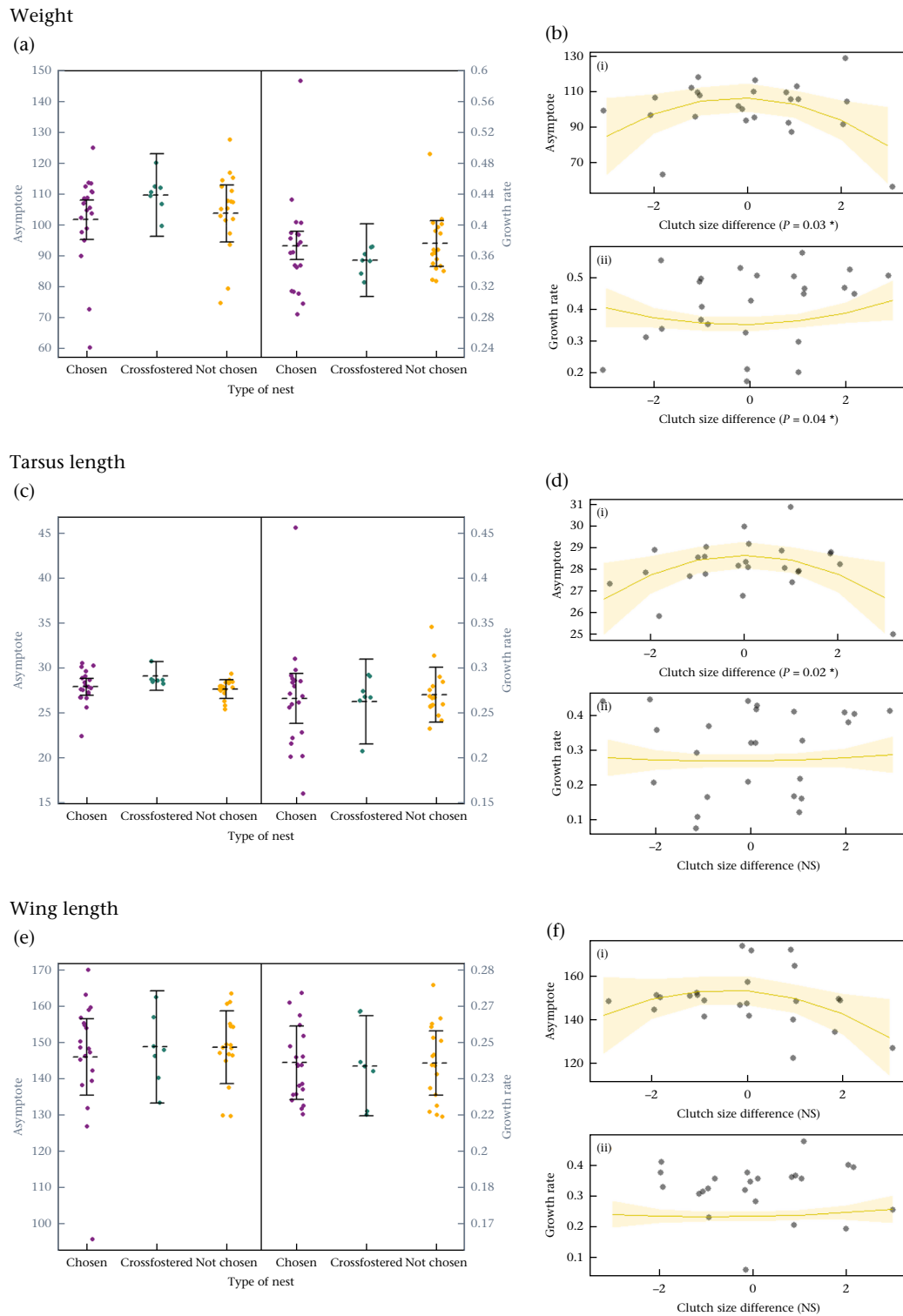


Figure 3. Model plots for weight (g), tarsus length (mm) and wing length (mm) results. (a, c, e) Models with response variables (asymptote and growth rate for all nestlings, $N = 45$ for weight and tarsus length, $N = 44$ for wing length) as a function of two covariates (type of nest, hatching date) and one random effect (year). In purple, nestlings that hatched in the nest originally chosen by their mothers, in green, nestlings crossfostered to nests already parasitized, and in orange, nestlings moved to nests that were not chosen by any cuckoo female. (b, d, f) Models for the asymptote (i) and growth rate (ii) as a function of clutch size difference (only data of nestlings crossfostered to parasitized nests, and those that hatched in nonchosen nests, in light green, $N = 25$ for weight and tarsus length, $N = 24$ for wing length).

been described to be a good proxy for quality in other passerines (Garamszegi et al., 2004; Houston et al., 1983) because theory and experiments demonstrate that the optimal clutch size for individuals varies depending on their ability to rear offspring and

survive to breed again (e.g. Davies et al., 2012; Visser & Lessells, 2001). However, with rapidly changing climates, it is possible that redstarts are not tracking environmental changes adequately and there may now be a mismatch in parental ability and the hosts'

Table 3
Summary statistics of the LMs explaining the different cuckoo nestling growth parameters, including clutch size difference as a predictive variable

		Estimate	SE	t value	P
Weight (N = 25)					
Asymptote	Intercept	100.736	2.917	34.529	<0.001***
	Clutch size difference	-5.944	14.587	-0.408	0.688
	Clutch size difference ²	-33.794	14.587	-2.317	0.03*
Growth rate	Intercept	0.368	0.008	44.842	<0.001***
	Clutch size difference	0.027	0.041	0.653	0.521
	Clutch size difference ²	0.089	0.041	2.176	0.041*
Tarsus length (N = 25)					
Asymptote	Intercept	28.178	0.223	126.378	<0.001***
	Clutch size difference	0.091	1.115	0.081	0.936
	Clutch size difference ²	-2.778	1.115	-2.492	0.021*
Growth rate	Intercept	0.271	0.007	39.118	<0.001***
	Clutch size difference	0.002	0.005	0.316	0.755
Wing length (N = 24)					
Asymptote	Intercept	149.053	2.524	59.065	<0.001***
	Clutch size difference	-1.672	1.714	-0.975	0.34
Growth rate	Intercept	0.238	0.006	40.564	<0.001***
	Clutch size difference	0.003	0.004	0.700	0.491

Clutch size difference was included as a quadratic predictive term, but if not significant was removed from the model. Significant *P* values (according to alpha 0.05) in bold (***, *P* < 0.001; **, *P* < 0.01; *, *P* < 0.05). t value, T statistic.

behavioural cues indicative of quality that were previously reliable for eavesdropping cuckoos (Szymkowiak & Schmidt, 2022; White et al., 2022). Alternatively, higher-quality parents may not necessarily be the ones laying the largest clutch sizes if redstarts are adjusting their clutch sizes to match local conditions. For example, birds at high risk of predation (Dillon & Conway, 2018; Zanette et al., 2011) or ectoparasitism (O'Brien & Dawson, 2005) reduce their clutch sizes. Brood parasite activity could also elicit a similar response (Soler et al., 2001), making our proxy less meaningful. Nevertheless, there is no evidence that redstarts adjust either their nest site choice or clutch size to experimentally induced cues of parasitism risk (tested at our study site using playbacks of cuckoo calls, Tolvanen et al., 2017). Therefore, it could be beneficial to conduct our study using an alternative proxy for individual quality, such as body condition, if sufficient data were available.

Third, it may be that higher-quality parents for cuckoos are not those that go on to lay the largest clutches, if other life history traits are taken into account (e.g. Both & Visser, 2005). Cuckoo nestlings eject nest mates within hours of hatching, which is energetically costly (Grim et al., 2009b) and not always successful in redstart nests. For example, in 15%–20% of cases cuckoo nestlings fail to remove all of the redstart's own eggs or newly hatched young from the nest (potentially affected by the use of nestboxes, Samaš et al., 2016; Thomson et al., 2016) and those raised in mixed broods tend to fledge less frequently than cuckoo nestlings raised alone by redstarts (Rutila et al., 2002; Samaš et al., 2016; Thomson et al., 2016). The energetic costs of eviction may be recoverable (Grim et al., 2009b), although experimentally reducing this cost by removing host eggs shows that eviction affects the cuckoo nestling's growth trajectory since, they take longer to reach a similar asymptotic mass than nestlings that do not pay this cost (Grim et al., 2009b). It is unknown whether this has consequences for a fledgling's survival or the mother's fitness, but catch-up growth decreases direct fitness across a range of taxa (Hector & Nakagawa, 2012). It is possible, therefore, that the cuckoo female must balance choosing high-quality parents against the costs of eviction experienced by her nestling to maximize her fitness, especially when parasitising nest box breeding redstarts. This may result in the optimum clutch size for cuckoo chicks being intermediate—those more frequently parasitized according to our results. This 'just right' intermediate size has also been observed in

a nest-sharing parasite, the brown-headed cowbird (Antonson et al., 2022), though the mechanism differs from cuckoos. Cowbird nestlings passively reduce the host brood to an intermediate number, trading off between stimulating provisioning and competing with host nestlings to optimize their growth and survival (Antonson et al., 2022). To disentangle these potential explanations, further research using alternative quality indicators is needed, as well as to determine which redstart traits are directly or indirectly linked to individual quality.

Does Disrupting the Cuckoo Female's Choice Affect Nestling Growth?

If cuckoos choose specific host nests to maximize their offspring's growth and survival, we expected that disrupting this choice experimentally would lead to measurable differences. Instead, when comparing growth between nestlings that remained in their original nests to those moved to a different nest (either parasitized or not), we found that cuckoo nestlings maintained growth at a similar rate and obtained a similar asymptotic size. This could support suggestions that cuckoo nestlings have adaptations to manipulate any individual host to meet their demands (e.g. Kilner et al., 1999; M. Soler & Soler, 1999). However, when we took the difference in clutch size into account among nests where we moved eggs, we found some tentative evidence that modifying the growth environment according to parental quality might have an effect. Cuckoo nestlings raised in nests with a completed clutch size similar to where it was initially laid grew larger in terms of mass and tarsus length than nestlings that hatched in nests with either fewer or additional host eggs than expected. This 'average is good, extremes are bad' pattern is often reported for nestlings in disadvantaged growth environments (e.g. Zárybnická et al., 2015); however, it was largely driven here by two nestlings that experienced the most extreme change in complete clutch size (smaller/larger by three eggs). Despite conducting our experiment over 6 years with approximately 300 nestboxes per year, our sample size for this analysis was small (*N* = 25 for weight and tarsus length and 24 for wing length) and unbalanced since we moved eggs before clutches were complete (i.e. blind to completed clutch size). Nevertheless, together these results suggest that benefits gained by selecting specific hosts may be minimal compared with the

energetic costs involved in paying close attention to available hosts and potential cues of parental quality. Furthermore, host choice could be contextual and vary depending on availability of hosts (Martínez et al., 1996; Stokke et al., 2007), on yearly average host quality (e.g. linked to food availability, Korpimäki & Hakkarainen, 1991; Korpimäki & Wiehn, 1998), or on brood parasite density (Molina-Morales et al., 2016; Soler et al., 2020). It is therefore possible that host choice strategies differ depending on local conditions, and such local conditions could even render host choice not worthwhile in this system.

Conclusion

In conclusion, while we expected that taking spatial and temporal variation in host nest availability and quality into account would reveal evidence for targeted oviposition decisions by cuckoos, our study has not provided strong evidence either for or against this hypothesis. At the scale of a putative breeding area, cuckoos did not show any preferences to parasitize hosts that went on to lay larger clutches. However, across the study site there was some hint that cuckoos may 'choose' to parasitize some hosts over others, albeit in the opposite direction to what we predicted. Specifically, nests we presumed to be of lower quality parents (i.e. smaller clutches) were parasitized more often than expected. While simply moving cuckoo eggs to nonparasitized (i.e. not chosen) nests did not affect nestling growth trajectories, moving cuckoo eggs to nests laid by parents investing in larger or smaller clutch sizes resulted in somewhat altered growth (although our sample size was small and influenced strongly by two cuckoo nestlings). Whether these differences would affect fitness of individual cuckoos, however, remains both unknown and difficult to study. Resolving whether cuckoos benefit from making selective oviposition decisions as many other parasites do (Soler et al., 1995; Tomás et al., 2017; Wang et al., 2020) is therefore likely to require more sophisticated quantitative and statistical tools to track cuckoo activity and assessment of variation in host quality.

Author Contribution

Teresa M. Abaurrea: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Angela Morales:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Jere Tolvanen:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Robert L. Thomson:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Rose Thorogood:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Conceptualization.

Data Availability

All data are deposited at FigShare. Parasitism data set is available at <https://figshare.com/s/ee8ffccbdca863ed7d55>. Growth data set is available at <https://figshare.com/s/255f8792e348d3b10346>.

Declaration of Interest

The authors have no relevant conflict of interest to disclose.

Acknowledgments

We thank all the field assistants for their help during fieldwork: Claire Buchan, Felicitas Pamatat, Guilia Masoero, Selengemurun Dembereldagva, Verity Bridger, Carles Durà, Victoria Pritchard, Mikko Karjalainen, Ryan Miller, Mira Sassi, Joshua Weiss, Tapani Neuvonen, Keanu Meyer, Ronja Saarinen and Justine Loof. We also thank Jesús Abaurrea and Jesús Asín (University of Zaragoza, Spain) and the Biodata Analytics Unit (University of Helsinki, Finland) for statistical advice. Finally, we thank Tomás Grim, Deryk Tolman and two anonymous reviewers for helpful comments on the manuscript. This study was supported by the Societas pro Fauna et Flora Fennica, the Finnish Cultural Foundation (grant code: 00200147 Central Fund) and by a doctoral school salary position from the University of Helsinki, all granted to T.A., in addition to several other funding institutions throughout the years (Societas pro Fauna et Flora Fennica and Oskar Öflunds Stiftelse to J.T.). None of the funders had any influence on the content of the submitted or published manuscript.

Supplementary Material

Supplementary material associated with this article is available at <https://doi.org/10.1016/j.anbehav.2025.123319>.

References

- Aggrey, S. (2002). Comparison of three nonlinear and spline regression models for describing chicken growth curves. *Poultry Science*, 81(12), 1782–1788. <https://doi.org/10.1093/ps/81.12.1782>
- Alvarez, F. (2000). Clutches of rufous bush chats *Cercotrichas galactotes* parasitised by cuckoos *Cuculus canorus* contain larger eggs. *Ardea*, 88(1), 109–112.
- Anderson, M. G., Moskát, C., Bán, M., Grim, T., Cassey, P., & Hauber, M. E. (2009). Egg eviction imposes a recoverable cost of virulence in chicks of a brood parasite. *PLoS One*, 4(11), Article e7725. <https://doi.org/10.1371/journal.pone.0007725>
- Antonson, N. D., Schelsky, W. M., Tolman, D., Kilner, R. M., & Hauber, M. E. (2022). Niche construction through a Goldilocks principle maximizes fitness for a nest-sharing brood parasite. *Proceedings of the Royal Society B: Biological Sciences*, 289(1982), Article 20221223. <https://doi.org/10.1098/rspb.2022.1223>
- Ardia, D. R., & Clotfelter, E. D. (2007). Individual quality and age affect responses to an energetic constraint in a cavity-nesting bird. *Behavioral Ecology*, 18(1), 259–266. <https://doi.org/10.1093/beheco/arl078>
- Avilés, J. M., Rutila, J., & Møller, A. P. (2005). Should the redstart *Phoenicurus phoenicurus* accept or reject cuckoo *Cuculus canorus* eggs? *Behavioral Ecology and Sociobiology*, 58(6), 608–617. <https://doi.org/10.1007/s00265-005-0941-7>
- Bartoń, K. (2023). MuMIn: Multi-model inference. <https://CRAN.R-project.org/package=MuMIn> (Version 1.47.5) [Computer software].
- Beauchamp, G. (2023). Annual apparent survival across species is lower in juvenile than adult birds but has similar ecological correlates. *Ibis*, 165(2), 448–457. <https://doi.org/10.1111/ibi.13167>
- Both, C., & Visser, M. E. (2005). The effect of climate change on the correlation between avian life-history traits. *Global Change Biology*, 11(10), 1606–1613. <https://doi.org/10.1111/j.1365-2486.2005.01038.x>
- Bryant, D. M. (1978). Environmental influences on growth and survival of nestling house martins *Delichon Urbica*. *Ibis*, 120(3), 271–283. <https://doi.org/10.1111/j.1474-919X.1978.tb06788.x>
- Ciaralli, S., Esposito, M., Francesconi, S., Muzzicato, D., Gamba, M., Dal Zotto, M., & Campobello, D. (2024). Ritual displays by a parasitic cuckoo: Nuptial gifts or territorial warnings? *Animal Behaviour*, 207, 147–156. <https://doi.org/10.1016/j.anbehav.2023.11.003>
- Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B: Biological Sciences*, 273(1592), 1375–1383. <https://doi.org/10.1098/rspb.2005.3458>
- Davies, N. B. (2000). Cuckoos, Cowbirds and Other Cheats. *T. & A.D. Poyser*.
- Davies, N. B., & Brooke, M. de L. (1988). Cuckoos versus reed warblers: Adaptations and counteradaptations. *Animal Behaviour*, 36(1), 262–284. [https://doi.org/10.1016/S0003-3472\(88\)80269-0](https://doi.org/10.1016/S0003-3472(88)80269-0)
- Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An Introduction to Behavioural Ecology*. John Wiley & Sons.
- Decker, K. L., Conway, C. J., & Fontaine, J. J. (2012). Nest predation, food, and female age explain seasonal declines in clutch size. *Evolutionary Ecology*, 26(3), 683–699. <https://doi.org/10.1007/s10682-011-9521-7>
- Dillon, K. G., & Conway, C. J. (2018). Nest predation risk explains variation in avian clutch size. *Behavioral Ecology*, 29(2), 301–311. <https://doi.org/10.1093/beheco/axr130>

- Fossøy, F., Sorenson, M. D., Liang, W., Ekrem, T., Moksnes, A., Møller, A. P., Rutila, J., Røskaft, E., Takasu, F., Yang, C., & Stokke, B. G. (2016). Ancient origin and maternal inheritance of blue cuckoo eggs. *Nature Communications*, 7, Article 10272. <https://doi.org/10.1038/ncomms10272>
- Gao, C. Q., Yang, J. X., Chen, M. X., Yan, H. C., & Wang, X. Q. (2016). Growth curves and age-related changes in carcass characteristics, organs, serum parameters, and intestinal transporter gene expression in domestic pigeon (*Columba livia*). *Poultry Science*, 95(4), 867–877. <https://doi.org/10.3382/ps/pev443>
- Garamszegi, L. Z., Török, J., Tóth, L., & Michl, G. (2004). Effect of timing and female quality on clutch size in the collared flycatcher *Ficedula albicollis*. *Bird Study*, 51(3), 270–277. <https://doi.org/10.1080/00063650409461363>
- Geltsch, N., Hauber, M. E., Anderson, M. G., Bán, M., & Moskát, C. (2012). Competition with a host nestling for parental provisioning imposes recoverable costs on parasitic cuckoo chick's growth. *Behavioural Processes*, 90(3), 378–383. <https://doi.org/10.1016/j.beproc.2012.04.002>
- Grim, T. (2006). Cuckoo growth performance in parasitized and unused hosts: Not only host size matters. *Behavioral Ecology and Sociobiology*, 60(5), 716–723. <https://doi.org/10.1007/s00265-006-0215-z>
- Grim, T., & Rutila, J. (2017). Cuckoo–host coevolutionary interactions across all breeding stages: Unusual ecological setting of a cavity-nesting host. In M. Soler (Ed.), *Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution* (pp. 287–303). Springer International Publishing. https://doi.org/10.1007/978-3-319-73138-4_16
- Grim, T., Rutila, J., Cassey, P., & Hauber, M. E. (2009a). Experimentally constrained virulence is costly for common cuckoo chicks. *Ethology*, 115(1), 14–22. <https://doi.org/10.1111/j.1439-0310.2008.01574.x>
- Grim, T., Rutila, J., Cassey, P., & Hauber, M. E. (2009b). The cost of virulence: An experimental study of egg eviction by brood parasitic chicks. *Behavioral Ecology*, 20(5), 1138–1146. <https://doi.org/10.1093/beheco/arp108>
- Grim, T., & Smaš, P. (2016). Growth performance of nestling cuckoos *Cuculus canorus* in cavity nesting hosts. *Acta Ornithologica*, 51(2), 175–188. <https://doi.org/10.3161/00016454A02016.51.2.004>
- Grim, T., Smaš, P., Moskát, C., Kleven, O., Honza, M., Moksnes, A., Røskaft, E., & Stokke, B. G. (2011). Constraints on host choice: Why do parasitic birds rarely exploit some common potential hosts? *Journal of Animal Ecology*, 80(3), 508–518. <https://doi.org/10.1111/j.1365-2656.2010.01798.x>
- Grim, T., Smaš, P., Procházka, P., & Rutila, J. (2014). Are tits really unsuitable hosts for the Common Cuckoo? *Ornis Fennica*, 91, 166–177. <https://doi.org/10.51812/of.133853>
- Grim, T., Tyllner, Z., & Smaš, P. (2017). Unusual diet of brood parasitic nestlings and its fitness consequences. *Auk*, 134(3), 732–750. <https://doi.org/10.1642/AUK-16-242.1>
- Hector, K. L., & Nakagawa, S. (2012). Quantitative analysis of compensatory and catch-up growth in diverse taxa. *Journal of Animal Ecology*, 81(3), 583–593. <https://doi.org/10.1111/j.1365-2656.2011.01942.x>
- Houston, D. C., Jones, P. J., & Sinly, R. M. (1983). The effect of female body condition on egg laying in Lesser black-backed gulls *Larus fuscus*. *Journal of Zoology*, 200(4), 509–520. <https://doi.org/10.1111/j.1469-7998.1983.tb02812.x>
- Jelínek, V., Procházka, P., Požgayová, M., & Honza, M. (2014). Common cuckoos *Cuculus canorus* change their nest-searching strategy according to the number of available host nests. *Ibis*, 156(1), 189–197. <https://doi.org/10.1111/ibi.12093>
- Kattan, G. H. (1997). Shiny cowbirds follow the 'shotgun' strategy of brood parasitism. *Animal Behaviour*, 53(3), 647–654. <https://doi.org/10.1006/anbe.1996.0339>
- Kilner, R. M., Noble, D. G., & Davies, N. B. (1999). How should cuckoo chicks signal in different host nests? *Trends in Ecology & Evolution*, 14(8), 322. [https://doi.org/10.1016/S0169-5347\(99\)01675-4](https://doi.org/10.1016/S0169-5347(99)01675-4)
- Kleven, O., Moksnes, A., Røskaft, E., Rudolfsen, G., Stokke, B. G., & Honza, M. (2004). Breeding success of common cuckoos *Cuculus canorus* parasitising four sympatric species of Acrocephalus warblers. *Journal of Avian Biology*, 35(5), 394–398. <https://doi.org/10.1111/j.0908-8857.2004.03359.x>
- Koleček, J., Piálková, R., Piálek, L., Šulc, M., Hughes, A. E., Brlík, V., Procházka, P., Požgayová, M., Capek, M., Sosnovcová, K., Štětková, G., Valterová, R., & Honza, M. (2021). Spatiotemporal patterns of egg laying in the common cuckoo. *Animal Behaviour*, 177, 107–116. <https://doi.org/10.1016/j.anbehav.2021.04.021>
- Koleček, J., Procházka, P., Brlík, V., & Honza, M. (2020). Cross-continental test of natal philopatry and habitat-imprinting hypotheses to explain host specificity in an obligate brood parasite. *Science and Nature*, 107, 12. <https://doi.org/10.1007/s00114-020-1667-0>
- Korpimäki, E., & Hakkariainen, H. (1991). Fluctuating food supply affects the clutch size of Tengmalm's owl independent of laying date. *Oecologia*, 85(4), 543–552. <https://doi.org/10.1007/BF00323767>
- Korpimäki, E., & Wiehn, J. (1998). Clutch size of kestrels: Seasonal decline and experimental evidence for food limitation under fluctuating food conditions. *Oikos*, 83(2), 259–272. <https://doi.org/10.2307/3546837>
- Louder, M. I. M., Schelsky, W. M., Albores, A. N., & Hoover, J. P. (2015). A generalist brood parasite modifies use of a host in response to reproductive success. *Proceedings of the Royal Society B: Biological Sciences*, 282(1814), Article 20151615. <https://doi.org/10.1098/rspb.2015.1615>
- Lyon, B. E. (1993). Tactics of parasitic American cots: Host choice and the pattern of egg dispersion among host nests. *Behavioral Ecology and Sociobiology*, 33(2), 87–100. <https://doi.org/10.1007/BF00171660>
- Møller, A. P., Adriaenssen, F., Artemyev, A., Bañbura, J., Barba, E., Biard, C., Blondel, J., Bouslama, Z., Bouvier, J.-C., Camprodon, J., Cecere, F., Charmantier, A., Charter, M., Cichoń, M., Cusimano, C., Czeszczewik, D., Demeyrier, V., Doligez, B., Doutrelant, C., ... Lambrechts, M. M. (2014). Variation in clutch size in relation to nest size in birds. *Ecology and Evolution*, 4(18), 3583–3595. <https://doi.org/10.1002/ece3.1189>
- Marshall, D. J., & Uller, T. (2007). When is a maternal effect adaptive? *Oikos*, 116(12), 1957–1963. <https://doi.org/10.1111/j.2007.0030-1299.16203.x>
- Martinez, N. (2012). Sparse vegetation predicts clutch size in common redstarts *Phoenicurus phoenicurus*. *Bird Study*, 59(3), 315–319. <https://doi.org/10.1080/00063657.2012.672949>
- Martinez, N., Jenni, L., Wyss, E., & Zbinden, N. (2010). Habitat structure versus food abundance: The importance of sparse vegetation for the common redstart *Phoenicurus phoenicurus*. *Journal of Ornithology*, 151(2), 297–307. <https://doi.org/10.1007/s10336-009-0455-6>
- Martínez, J. G., Soler, M., & Soler, J. J. (1996). The effect of magpie breeding density and synchrony on brood parasitism by great spotted cuckoos. *Condor: Ornithological Applications*, 98(2), 272–278. <https://doi.org/10.2307/1369145>
- Marton, A., Fülöp, A., Ozogány, K., Moskát, C., & Bán, M. (2019). Host alarm calls attract the unwanted attention of the brood parasitic common cuckoo. *Scientific Reports*, 9, Article 18563. <https://doi.org/10.1038/s41598-019-54909-1>
- Moksnes, A., Røskaft, E., & Tysse, T. (1995). On the evolution of blue cuckoo eggs in Europe. *Journal of Avian Biology*, 26(1), 13–19. <https://doi.org/10.2307/3677207>
- Molina-Morales, M., Martínez, J. G., & Avilés, J. M. (2016). Criteria for host selection in a brood parasite vary depending on parasitism rate. *Behavioral Ecology*, 27(5), 1441–1448. <https://doi.org/10.1093/beheco/aww066>
- Moreras, A. (2023). *Frontline strategies in the arms race between hosts and their brood parasites: The case of the common redstart*. University of Cape Town [Ph.D. thesis].
- Moreras, A., Tolvanen, J., Kysučan, M., Smaš, P., Grim, T., & Thomson, R. L. (2025). Can nest design hinder brood parasitism success? *Journal of Avian Biology*, 2, Article e03300. <https://doi.org/10.1111/jav.03300>
- Moreras, A., Tolvanen, J., Morosinotto, C., Bussiere, E., Forsman, J., & Thomson, R. L. (2021). Choice of nest attributes as a frontline defense against brood parasitism. *Behavioral Ecology*, 32(6), 1285–1295. <https://doi.org/10.1093/beheco/arab095>
- Moreras, A., Tolvanen, J., Tornberg, R., Mönkkönen, M., Forsman, J. T., & Thomson, R. L. (2022). Breeding near heterospecifics as a defence against brood parasites: Can redstarts lower probability of cuckoo parasitism using neighbours? *Oecologia*, 199(4), 871–883. <https://doi.org/10.1007/s00442-022-05242-4>
- Moskát, C., Bán, M., Fülöp, A., Bereczki, J., & Hauber, M. E. (2019). Bimodal habitat use in brood parasitic Common Cuckoos (*Cuculus canorus*) revealed by GPS telemetry. *Auk*, 136(2), 1–12. <https://doi.org/10.1093/auk/uky019>
- Moskát, C., Hauber, M. E., Růžicková, J., Marton, A., Bán, M., & Elek, Z. (2020). Female-female aggression and male responses to the two colour morphs of female common cuckoos. *Science and Nature*, 107(4), 28. <https://doi.org/10.1007/s00114-020-01680-3>
- Naef-Daenzer, B., & Gruebler, M. U. (2016). Post-fledging survival of altricial birds: Ecological determinants and adaptation. *Journal of Field Ornithology*, 87(3), 227–250. <https://doi.org/10.1111/jof.12157>
- Nakamura, H., & Miyazawa, Y. (1997). Movements, space use and social organization of radio-tracked common cuckoos during the breeding season in Japan. *Japanese Journal of Ornithology*, 46, 23–54. <https://doi.org/10.3838/jjo.46.23>
- Nakamura, H., Miyazawa, Y., & Kashiwagi, K. (2005). Behavior of radio-tracked common cuckoo females during the breeding season in Japan. *Ornithological Science*, 4(1), 31–41. <https://doi.org/10.2326/osj.4.31>
- O'Brien, E. L., & Dawson, R. D. (2005). Perceived risk of ectoparasitism reduces primary reproductive investment in tree swallows *Tachycineta bicolor*. *Journal of Avian Biology*, 36(4), 269–275. <https://doi.org/10.1111/j.0908-8857.2005.03562.x>
- Orians, G. H., Røskaft, E., & Beletsky, L. D. (1989). Do brown-headed cowbirds lay their eggs at random in the nests of red-winged blackbirds? *Wilson Bulletin*, 101(4), 599–605.
- Pagani-Núñez, E., & Senar, J. C. (2014). Are colorful males of great tits *Parus major* better parents? Parental investment is a matter of quality. *Acta Oecologica*, 55, 23–28. <https://doi.org/10.1016/j.actao.2013.11.001>
- Poláčiková, L., Procházka, P., Cherry, M. I., & Honza, M. (2009). Choosing suitable hosts: Common cuckoos *Cuculus canorus* parasitize great reed warblers *Acrocephalus arundinaceus* of high quality. *Evolutionary Ecology*, 23(6), 879–891. <https://doi.org/10.1007/s10682-008-9278-9>
- R Core Team. (2023). R: A language and environment for statistical computing. *Computer Software*. <http://www.R-project.org/>
- Refsnider, J. M., & Janzen, F. J. (2010). Putting eggs in one basket: Ecological and evolutionary hypotheses for variation in oviposition-site choice. *Annual Review of Ecology, Evolution, and Systematics*, 41(1), 39–57. <https://doi.org/10.1146/annurev-ecolsys-102209-144712>
- Richards, S. A., Whittingham, M. J., & Stephens, P. A. (2011). Model selection and model averaging in behavioural ecology: The utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology*, 65(1), 77–89. <https://doi.org/10.1007/s00265-010-1035-8>
- Ricklefs, R. E. (1968). Patterns of growth in birds. *Ibis*, 110(4), 419–451. <https://doi.org/10.1111/j.1474-919X.1968.tb00058.x>
- Rutilla, J., Latja, R., & Koskela, K. (2002). The common cuckoo *Cuculus canorus* and its cavity nesting host, the redstart *Phoenicurus phoenicurus*: A peculiar cuckoo-host system? *Journal of Avian Biology*, 33(4), 414–419. <https://doi.org/10.1034/j.1600-048X.2002.02937.x>

- Šulc, M., Hughes, A. E., Troscianko, J., Štětková, G., Procházka, P., Požgayová, M., Piálek, L., Piálková, R., Brlík, V., & Honza, M. (2022). Automatic identification of bird females using egg phenotype. *Zoological Journal of the Linnean Society*, 195(1), 33–44. <https://doi.org/10.1093/zoolinnean/zlab051>
- Samaš, P., Rutíla, J., & Grim, T. (2016). The common redstart as a suitable model to study cuckoo-host coevolution in a unique ecological context. *BMC Evolutionary Biology*, 16(1), 255. <https://doi.org/10.1186/s12862-016-0835-5>
- Schwagmeyer, P. L., & Mock, D. W. (2008). Parental provisioning and offspring fitness: Size matters. *Animal Behaviour*, 75(1), 291–298. <https://doi.org/10.1016/j.anbehav.2007.05.023>
- Silva, M. C., Boersma, P. D., Mackay, S., & Strange, I. (2007). Egg size and parental quality in thin-billed prions, *Pachyptila belcheri*: Effects on offspring fitness. *Animal Behaviour*, 74(5), 1403–1412. <https://doi.org/10.1016/j.anbehav.2007.01.008>
- Slagsvold, T., & Lifjeld, J. T. (1988). Ultimate adjustment of clutch size to parental feeding capacity in a passerine bird. *Ecology*, 69(6), 1918–1922. <https://doi.org/10.2307/1941168>
- Slagsvold, T., & Lifjeld, J. T. (1990). Influence of male and female quality on clutch size in tits (*Parus* Spp.). *Ecology*, 71(4), 1258–1266. <https://doi.org/10.2307/1938263>
- Soler, J. J., Martínez, J. G., Soler, M., & Møller, A. P. (2001). Life history of magpie populations sympatric or allopatric with the brood parasitic great spotted cuckoo. *Animal Behaviour*, 82(6), 1621–1631. [https://doi.org/10.1890/0012-9658\(2001\)082\[1621:LHOMPS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1621:LHOMPS]2.0.CO;2)
- Soler, M., Pérez-Contreras, T., & Soler, J. J. (2020). Great spotted cuckoos show dynamic patterns of host selection during the breeding season. The importance of laying stage and parasitism status of magpie nests. *Behavioral Ecology*, 31(2), 467–474. <https://doi.org/10.1093/beheco/arz208>
- Soler, M., & Soler, J. J. (1999). The cuckoo chick tricks their reed warbler foster parents, but what about other host species? *Trends in Ecology & Evolution*, 14(8), 296–297. [https://doi.org/10.1016/S0169-5347\(99\)01648-1](https://doi.org/10.1016/S0169-5347(99)01648-1)
- Soler, J. J., Soler, M., Møller, A. P., & Martínez, J. G. (1995). Does the great spotted cuckoo choose magpie hosts according to their parenting ability? *Behavioral Ecology and Sociobiology*, 36(3), 201–206. <https://doi.org/10.1007/BF00177797>
- Starck, J. M., & Ricklefs, R. E. (1998). *Avian Growth and Development: Evolution Within the Altricial-precocial Spectrum*. Oxford University Press.
- Stoddard, M. C., & Stevens, M. (2011). Avian vision and the evolution of egg color mimicry in the common cuckoo. *Evolution*, 65(7), 2004–2013. <https://doi.org/10.1111/j.1558-5646.2011.01262.x>
- Stokke, B. G., Hafstad, I., Rudolfsen, G., Bargain, B., Beier, J., Bigas Campàs, D., Dyrce, A., Honza, M., Leisler, B., Pap, P. L., Patapavičius, R., Procházka, P., Schulze-Hagen, K., Thomas, R., Moksnes, A., Møller, A. P., Røskaft, E., & Soler, M. (2007). Host density predicts presence of cuckoo parasitism in reed warblers. *Oikos*, 116(6), 913–922. <https://doi.org/10.1111/j.0030-1299.2007.15832.x>
- Szymkowiak, J., & Schmidt, K. A. (2022). Deterioration of nature's information webs in the Anthropocene. *Oikos*, 2022(10), Article e08504. <https://doi.org/10.1111/oik.08504>
- Teuschl, Y., Taborsky, B., & Taborsky, M. (1998). How do cuckoos find their hosts? The role of habitat imprinting. *Animal Behaviour*. <https://doi.org/10.1006/anbe.1998.0931>
- Thomson, R. L., Tolvanen, J., & Forsman, J. T. (2016). Cuckoo parasitism in a cavity nesting host: Near absent egg-rejection in a northern redstart population under heavy apparent (but low effective) brood parasitism. *Journal of Avian Biology*, 47(3), 363–370. <https://doi.org/10.1111/jav.00915>
- Tolvanen, J., Forsman, J. T., & Thomson, R. L. (2017). Reducing cuckoo parasitism risk via informed habitat choices. *Auk*, 134(3), 553–563. <https://doi.org/10.1642/AUK-17-30.1>
- Tomás, G., Martín-Gálvez, D., Ruiz-Rodríguez, M., & Soler, J. J. (2017). Intraspecific avian brood parasites avoid host nests infested by ectoparasites. *Journal of Ornithology*, 158(2), 561–567. <https://doi.org/10.1007/s10336-016-1409-4>
- Trnka, A., Požgayová, M., Procházka, P., Prokop, P., & Honza, M. (2012). Breeding success of a brood parasite is associated with social mating status of its host. *Behavioral Ecology and Sociobiology*, 66(8), 1187–1194. <https://doi.org/10.1007/s00265-012-1372-x>
- Visser, M. E., & Lessells, C. M. (2001). The costs of egg production and incubation in great tits (*Parus major*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268(1473), 1271–1277. <https://doi.org/10.1098/rspb.2001.1661>
- Vogl, W., Taborsky, B., Taborsky, M., Teuschl, Y., & Honza, M. (2004). Habitat and space use of European cuckoo females during the egg laying period. *Behaviour*, 141(7), 881–898. <https://doi.org/10.1163/1568539042265671>
- Wang, L., & Liang, W. (2023). Random egg laying in host nests, rather than egg-matching, explains patterns of cuckoo parasitism: a comment on Zhang et al. (2023). *Proceedings of the Royal Society B: Biological Sciences*, 290(2006), Article 20231018. <https://doi.org/10.1098/rspb.2023.1018>
- Wang, L., Yang, C., He, G., Liang, W., & Møller, A. P. (2020). Cuckoos use host egg number to choose host nests for parasitism. *Proceedings of the Royal Society B: Biological Sciences*, 287(1928), Article 20200343. <https://doi.org/10.1098/rspb.2020.0343>
- Westneat, D. F., Schofield, M., & Wright, J. (2013). Parental behavior exhibits among-individual variance, plasticity, and heterogeneous residual variance. *Behavioral Ecology*, 24(3), 598–604. <https://doi.org/10.1093/beheco/ars207>
- White, T. E., Latty, T., & Umbers, K. D. L. (2022). The exploitation of sexual signals by predators: A meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, 289(1976), Article 20220444. <https://doi.org/10.1098/rspb.2022.0444>
- Wilkin, T. A., King, L. E., & Sheldon, B. C. (2009). Habitat quality, nestling diet, and provisioning behaviour in great tits *Parus major*. *Journal of Avian Biology*, 40(2), 135–145. <https://doi.org/10.1111/j.1600-048X.2009.04362.x>
- Williams, H. M., Willemoes, M., Klaassen, R. H. G., Strandberg, R., & Thorup, K. (2016). Common cuckoo home ranges are larger in the breeding season than in the non-breeding season and in regions of sparse forest cover. *Journal of Ornithology*, 157(2), 461–469. <https://doi.org/10.1007/s10336-015-1308-0>
- Winder, L. A., Simons, M. J. P., & Burke, T. (2023). The optimal clutch size revisited: Separating individual quality from the costs of reproduction. *eLife*, 12, Article RP87018. <https://doi.org/10.7554/eLife.87018.1>
- Winnicki, S. K., Strausberger, B. M., Antonson, N. D., Burhans, D. E., Lock, J., Kilpatrick, A. M., & Hauber, M. E. (2021). Developmental asynchrony and host species identity predict variability in nestling growth of an obligate brood parasite: A test of the “growth-tuning” hypothesis. *Canadian Journal of Zoology*, 99(3), 213–220. <https://doi.org/10.1139/cjz-2020-0147>
- Wood, S. N. (2006). Low-rank scale-invariant tensor product smooths for generalized additive mixed Models. *Biometrics*, 62(4), 1025–1036. <https://doi.org/10.1111/j.1541-0420.2006.00574.x>
- Wood, S. N. (2017). *Generalized Additive Models: An Introduction with R, Second Edition*. CRC Press.
- Zárybnická, M., Riegert, J., Břejšková, L., Šindelář, J., Kouba, M., Hanel, J., Popelková, A., Menclová, P., Tomásek, V., & Šťastný, K. (2015). Factors affecting growth of Tengmalm's owl (*Aegolius funereus*) nestlings: Prey abundance, sex and hatching order. *PLoS One*, 10(10), Article e0138177. <https://doi.org/10.1371/journal.pone.0138177>
- Zanette, L. Y., White, A. F., Allen, M. C., & Clinchy, M. (2011). Perceived predation risk reduces the number of offspring songbirds produce per year. *Science*, 334(6061), 1398–1401. <https://doi.org/10.1126/science.1210908>
- Zhang, J., Santema, P., Lin, Z., Yang, L., Liu, M., Li, J., Deng, W., & Kempnaers, B. (2023). Experimental evidence that cuckoos choose host nests following an egg matching strategy. *Proceedings of the Royal Society B: Biological Sciences*, 290(1993), Article 20222094. <https://doi.org/10.1098/rspb.2022.2094>
- Zuur, A. F., Saveliev, A. A., & Ieno, E. N. (2014). *A beginner's guide to generalised additive mixed models with R*. Highland Statistics.