Fitness benefits of alternated chick provisioning in cooperatively breeding carrion crows

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Running headline: Alternated chick provisioning in carrion crows

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Abstract

In most bird species, parents raise offspring cooperatively. In some cases, this cooperation extends to helpers-at-the-nest who assist the breeders with a range of tasks. While cooperative food provisioning might merely arise incidentally, as a result of the efforts of carers that act independently from each other, recent studies suggest that birds may coordinate by taking turns in visiting the nest. However, evidence that such coordination emerges because individuals actively respond to each other's behaviour is controversial, and the potential benefits of carers' alternation remain unknown. We addressed this knowledge gap by analysing a multi-year dataset for cooperatively breeding carrion crows *Corvus corone*, comprising 8,693 nest visits across 50 groups. Our results reveal that turn taking does occur in this species and that all group members, regardless of their sex and social role (breeder/helper), tend to alternate at the nest with other carers rather than to make repeat visits. Importantly, we found that the body mass of nestlings increased significantly with the degree of carers' alternation, possibly because well-coordinated groups provided food at more regular intervals. Using earlier monitoring data, the observed increase in body mass is predicted to substantially boost post-fledging survival rates. Our analyses demonstrate that alternation in nestling provisioning has measurable fitness benefits in this study system. This raises the possibility that cooperatively breeding carrion crows, as well as other bird species with similarly coordinated brood provisioning, exhibit specialized behavioural strategies that enable effective alternation.

Keywords: cooperative breeding, brood provisioning, turn taking, alternation, coordination, helping at the nest, nestling body mass

Introduction

Cooperation – typically defined as a behaviour that provides a benefit to another individual and has evolved at least partly because of this benefit (West et al., 2007) – is a central theme in evolutionary biology. Exploring the paradox of the apparently altruistic behaviour of individuals who invest time and energy to increase the fitness of others, has led to groundbreaking contributions, like Hamilton's theory of inclusive fitness (Hamilton,1964). An economic, game theory-based approach (see Schuster & Perelberg, 2004) that focuses on the outcomes of alternative strategies (e.g., cooperation *vs.* defection) has also proved fruitful (for a review, see Bshary & Bergmüller, 2008), showing that cooperation may depend on an ability to monitor the behaviour of others, to adjust one's own behaviour in response to the behaviour of others, to learn from previous experience and interactions, and to specialize in specific tasks. A plethora of experiments across different animal species (Noë, 2006) have illustrated that understanding how cooperation is achieved is essential to studying its evolution and maintenance.

Cooperation can arise incidentally among individuals that act independently form each other's, or can instead be achieved through active coordination amongst multiple individuals, who adjust their behaviour to that of their group mates (Noë, 2006). An example of incidental cooperation is 'milk dumping' in evening bats *Nycticeius humeralis*, where lactating females with excess milk reduce their body mass before a foraging trip by nursing unrelated pups, which benefit from the provision of extra food (Wilkinson, 1992). Active coordination, in contrast, occurs in communal fishing of American white pelicans *Pelecanus erythrorhynchos* (McMahon &Evans, 1992), in which individuals synchronously dip their bills in the water to herd fish towards the shore where they can be caught more easily, or in hunting associations between different species of fish (Bshary et al., 2006). Distinguishing cases in which parties act independently from each other from those in which they actively coordinate is a critical first step for studying the evolution of specialized behavioural or cognitive capacities that may be required to achieve more complex forms of cooperation. This task, however, poses major empirical challenges, because apparent forms of coordination can arise passively among individuals that, in fact, are not responding at all to the behaviour of group members. Cooperatively breeding bird societies provide excellent models for distinguishing incidental and active forms of cooperation.

In birds, parents typically raise their offspring together, but in a notable proportion of species (9%; Cockburn, 2006), more than two birds attend the brood, contributing to provisioning the chicks, defending the nest, and other tasks. Most studies so far have focused on group members' investment into brood provisioning and any associated effects on chick survival (Cockburn, 1998), while other important aspects of carer behaviour, such as the timing of nest visits, have received much less attention (Savage & Hinde, 2019). Pioneering studies on bird species with biparental care (i.e., breeders without helpers) have recently revealed that the timing of nest visits often deviates from random expectations, typically with parents taking turns (Baldan et al., 2019; Johnstone et al., 2014) in feeding the young. This 'active alternation', in which pair mates monitor each other's behaviour and adjust their own behaviour accordingly, has been suggested to help resolve the conflict over biparental care. This conflict, first described by Trivers (1972), arises because each parent stands to gain in terms of survival or future fecundity if the other does more of the work. By strictly taking turns, the male and female would ensure that any increase of their own feeding rate is followed by a matched increase of their partner's efforts (conditional cooperation) leading to an egalitarian share of duties (Johnstone et al., 2014). Johnstone and Savage

(2019) extended this theoretical work, showing that 'imperfect' turn taking can also be effective at solving the conflict over care under certain conditions (e.g., when clumped feeding visits compromise the survival of the offspring), and that alternation can persist even when the parents have incomplete information on each other's contribution to brood care.

Conceivably, such active turn taking could also be an effective mechanism for stabilizing cooperation among multiple carers, both breeders and helpers. Methods for measuring potential deviation of nest visit alternation from random expectations have recently been adapted for cooperatively breeding species, using the runs test (Khwaja et al., 2017; Sheskin, 2011) and Continuous Time Markov Models (Savage et al., 2017). Furthermore, randomizations of inter-visit intervals have been implemented to account for the fact that turn taking may arise simply due to the 'refractory period' between subsequent visits of the same individual, (Santema et al., 2019; Savage et al., 2017). Indeed, birds usually need to forage away from the nest before coming back to feed the brood, making alternated visits by different carers more likely than consecutive visits of the same individual ('passive turn taking'; Savage et al., 2017). The few relevant studies currently available confirmed that alternation can occur in groups with more than two carers (Halliwell et al., 2022; Koenig & Walters, 2016; Savage et al., 2017), supporting the view that cooperative care results from individuals responding to the investment of others and adjusting their own behaviour accordingly. An interesting exception is that of the rifleman *Acanthisitta chloris,* where carers do not coordinate, possibly because of the low level of potential conflict over nestling care in this species (Khwaja et al., 2017).

Despite notable progress in this field, questions were recently raised about whether non-random nest-visit alternation truly reflects active coordination, casting doubt on earlier interpretations. Specifically, Schlicht et al. (2016) pointed out that patterns in the visit sequence may result not only from carers responding to each other's behaviour, but also from a multitude of environmental factors (e.g., temporal variation in food availability, changing weather conditions, the appearance of predators) that could introduce a correlation between the inter-visit intervals of carers. A randomization of inter-visit intervals does not only remove the effect that carers can have on each other, which is key for testing conditional cooperation, but it also eliminates the environmental component that may affect the visit sequence. Thus, if the observed degree of alternation is higher than that measured in randomized sequences, this would raise the question of whether turn taking is driven by environmental variability or by carers responding to the behaviour of their group mates (Savage & Hinde, 2019). Ilhe et al. (2019) showed that, when multiple recording bouts are available for the same reproductive unit, a randomization 'within bouts' (Johnstone et al., 2014; Savage et al., 2017) is more conservative than a randomization 'across bouts' and should therefore be adopted. That said, the same authors also warn that, even in this case, evidence of active turn alternation would remain weak, especially if observation bouts are long (Ihle et al., 2019).

Apart from the necessary step of showing that turn taking deviates from random expectations, it is important to ask if alternated provisioning has measurable fitness consequences (Ihle et al., 2019; Savage et al., 2017). Showing an effect on the number of nestlings produced, or their quality, would support the idea that alternation has adaptive benefits, creating exciting opportunities to explore underlying proximate mechanisms. To the best of our knowledge, however, no clear evidence has been reported of fitness benefits of turn taking in cooperatively breeding species.

Here, we investigate the fitness benefits of coordination with a detailed study of a population of cooperatively breeding carrion crows *Corvus corone* in which dominant breeding pairs are assisted by one to three helpers (Baglione et al., 2002a; Canestrari et al., 2005). Based on video-recorded observations at 50 nests, we analyse, first, whether the degree of alternation of nest visits differs from random expectations, and second, whether it is related to the number of fledglings produced and their body mass, with the latter being a reliable proxy of post-fledging survival probability (Canestrari et al., 2011).

Methods

Study area and population

We studied a population of carrion crows in a 45-km^2 study area in low-intensity farmland at La Sobarriba, northern Spain (42° 37' N, 5° 26' W). Unlike birds in socially monogamous populations of this species, or of the closely related hooded crow *Corvus cornix*, our study subjects form cohesive groups (average size ± SE = 3.2 ± 0.08; (Baglione et al., 2002a; 2010) that live year-round in all-purpose territories (Baglione et al., 2005). In this population, pairs represent only about 25% of the reproductive units. Groups are enlarged families comprising a dominant breeding pair, some non-dispersing offspring of both sexes, and/or individuals (mostly males) fledged in other territories (called 'immigrants'), that are related to the resident breeder of the same sex (average coefficient of relatedness ± SE = 0.23 ± 0.07; Baglione et al., 2003). It has been shown that the alliances between dominant residents and immigrants do not arise through population viscosity, but because crows actively choose relatives to cooperative with (Baglione et al., 2003 for details), proving the role of kin selection in shaping this complex society. Male immigrants, unlike non-dispersing offspring, can sire offspring alongside the dominant male (12.9% of young produced in groups with immigrants belong to the subordinate; Baglione et al., 2002b), therefore obtaining also direct fitness benefits from cooperation. Extra-group paternities can also occur, but at a lower rate (5.6% of nestlings; Canestrari et al., 2023, Baglione et al. unpublished data), and we never found a brood entirely sired by external males. Subordinates feed the incubating female and – later in the season – the nestlings, significantly boosting brood survival rates (Canestrari et al., 2008). Brood care in crows is costly in terms of loss of body mass, both in breeders and helpers (Canestrari et al., 2007), and the contribution of subordinates varies largely, with some birds refraining from providing any care at all (Canestrari et al., 2005).

Data collection and video-analyses

Data were collected as part of a long-term population study. All procedures followed ASAB/ABS guidelines (ASAB Ethical Committee/ABS Animal Care Committee, 2023) and Spanish regulations for animal behavioural research and were approved by Junta de Castilla y León (reference of first released licenses: EP/LE/177-1999; last released licence: EP/LE/681-2019). All nestlings were measured and banded just before fledging (i.e., when the eldest chick of the brood was 28–30 days old; for details, see Canestrari et al., 2007). Body mass was measured with 1,000-g Pesola Precision Scales. Since hatching is asynchronous in crows, siblings from the same brood could differ in age by 0–4 days, as documented by measuring the length of the sixth primary feather (Canestrari et al., 2008). We also captured adult group members (for details on trapping methods, see Baglione et al., 2002a) and marked them with colour rings and wing tags. Trapped birds were aged as one, two, or more-than-two years old according to the colour of the internal upper mandible (Svensson, 1992). We collected 50–200 μl of blood from the brachial vein of each banded individual. A microsatellites-based parentage analysis established which male group members sired nestlings in broods. In our sample, one brood was fathered by two males, which were therefore considered 'co-breeders' (Baglione et al., 2002b). However, we could not always exclude that, in other groups, two males shared paternity sequentially (e.g., in two different years). Therefore, the categorization as 'helper' corresponds here to individuals that did not sire young in the current brood. The P2/P8 molecular method was used to sex all birds (Griffiths et al., 1998).

During the breeding seasons of 1999–2000, 2003–2007, 2015, 2018 and 2019, we monitored a total of 50 nests from 37 different territories with camouflaged small video-cameras from a distance of ca. 1.5–2 m (Canestrari et al., 2005). All carers in sampled groups were individually recognizable (see above). Our total sample included 6 unassisted pairs, 25 groups with one helper, 14 groups with two helpers, and 5 groups with three helpers (for details, see Table 1). Daily recording bouts lasted between ca. 4 and 15 hours (average ± SE = 6.31 ± 0.25) and took place between 5:00 a.m. and 8:00 p.m., typically on consecutive days. For the present study, we considered only video-recordings with chicks older than 14 days, which is the age at which breeding females substantially reduce brooding and fully engage in provisioning food to the brood (Bolopo et al., 2015). We collected on average (± SE) 32.4 ± 4.3 hours of video-recordings per nest, with a total of 1,622 hours of footage documenting 8,693 nest visits. For each visit, we noted the identity of the carer, the exact time of entrance and departure from the nest (according to the UTC time stamp displayed on all recordings), the nestlings that were fed and the time allocated to any other duty (e.g., nest or chick sanitation, such as fecal sac removal). In 22 broods, all nestlings were recognizable (n = 57 nestling), because we had marked them individually with a non-toxic marker on the top of the head (18 broods) or because they contained a single chick (four). This subsample was used to assess the food intake of each nestling and to measure the time intervals between consecutive feedings. Data were extracted by E.T. and D.C. from videos using VLC media player, with footage being viewed in slow motion where necessary. Inter-observer agreement for nest-visit times (defined as scores that differed by 5 seconds or less) and carer identification were checked on a subsample of 200 nest visits by 10 individuals and was 99.5% and 100%, respectively.

Following the STRANGE framework for animal behaviour research (Webster & Rutz, 2020), we explored scope for sampling biases. Each year, we tried to find all carrion crow breeding groups in our study area (Baglione et al., 2002a) and surveyed all their nesting attempts (birds may re-nest after an early failure). In total, we identified 228 successful (i.e., at least one fledgling produced) breeding groups over the ten-year study period. Candidate groups for nest recording were selected at the beginning of each breeding season, stratifying the overall sample according to group size. Nests on trees that were unsuitable for installing video-camaras (e.g., because trees could not be climbed safely or because no appropriate branch was available for mounting the camara) were excluded. Some adjustments to the planned sample were inevitable because of nest losses (e.g., due to predation or early brood starvation) or our failure to trap adults for tagging. Whenever possible, we tried to replace a lost group with another one of the same size, eventually achieving our final sample of 50 nests. For nestling head marking, we selected a subsample of 18 nests that could be climbed easily, given that the head paint faded quickly and needed to be replaced approximately every other day during the recording period. Overall, we conclude that scope for sampling biases was relatively low and that the nests yielding data for final analyses adequately captured the variation in ecological context and bird behaviour present in our long-term study population. We therefore expect that our findings should generalize well to other populations of cooperatively breeding carrion crows.

Alternation analyses

We investigated if turn taking occurred in our study population, that is, if the observed proportion of alternated nest visits in groups differed from random expectations and if the tendency to alternate varied among types of carers (i.e., breeders and helpers). To do so, we first performed an initial analysis based on *k*-category runs tests (Savage et al., 2017; Sheskin, 2011), implemented in the R package *trqwe* (Ching, 2018) for each group.

Random expectations based on the *k*-category runs tests *k*-category runs tests could be improved by accounting for the refractory time between successive provisioning visits of a carer, which includes the time needed to reach a foraging patch, collect food, and return to the nest. This refractory time inevitably increases turn taking simply by generating a time window during which other carers can visit the nest, but the focal individual cannot (Santema et al., 2019; Savage et al., 2017). To control for this, and to test whether the observed proportion of alternated visits still differed from random, we performed a randomization test following Savage et al. (2017). Within each group and recording bout, we measured all the inter-visit intervals for every carer and constructed a new sequence of visits by randomizing these intervals within bouts. Subsequently, we obtained ‘randomized recording bouts’ by merging the randomized sequences of all carers. We repeated this procedure and re-fitted each randomized sequence 1,000 times per bout, generating a distribution of expected turn taking based solely on the effect of group size, unequal visitation rate, and refractory periods. For each group, the observed degree of turn taking was calculated as the average within-bouts proportion of alternated visits. We then compared, for groups of equal size, if the median of observed proportions of alternated visits differed from the median of the randomized values, taken as the reference level in a one-sample Wilcoxon test (Sheskin, 2011).

It should be noted that synchronous trips to the nest by multiple individuals may lead to a quick succession of arrivals by different carers, causing alternation without any ‘intention’ to take turns (passive turn taking; see above, and Savage et al., 2017). If this was the case, in each group, short consecutive inter-visit intervals should occur more frequently than would be expected by chance (Savage et al., 2017). To test this, we categorized inter-visit intervals as either ‘short’ or ‘long’ (using the within-bout median of inter-visit intervals as the threshold value) and performed a Wald-Wolfowitz run test of randomness (Caeiro & Mateus, 2014; Sheskin, 2011) where fewer runs than expected by chance would indicate synchrony.

We also examined whether the tendency to alternate nest visits was exhibited by all categories of group members (i.e., breeding males, breeding females, and helpers). To do so, we fitted Continuous Time Markov Models to each breeding group, using the *msm* package (Jackson, 2011) in R (R Core Team, 2021). These models are suited to analyzing behavioural sequences (Bishir et al., 2004) and have been adapted successfully for investigating the timing of brood provisioning both in biparental (Bremaud, 2001; Harcourt et al., 2010; Johnstone et al., 2014) and cooperatively breeding bird species (Savage et al., 2017). Briefly, each nest visit was treated as a discrete event, and the model state was defined by the identity of the last bird visiting the nest. To allow the model to interpret repeated visits by the same individual as transitions of the state of the system, a dummy state was used (for details, see Savage et al., 2017). This way, *msm* could compute individuals’ transition rate following any bird other than themselves (λ) as well as their rate (μ) of repeated visits (Johnstone et al., 2014). Carers in this species vary greatly in their provisioning effort (Canestrari et al., 2005), especially helpers. Following earlier recommendations (Savage et al., 2017), we removed from the sample 8 helpers whose nest-visitation rate was less than 20% of the mean rate for the rest of the group, as they had little opportunity to coordinate with other carers (Table 1). As a consequence, only three groups of five carers remained and could not be included in the analyses because this sample was too small for meaningful comparison. The group with male co-breeders (see above) was one of the excluded groups.

For the purposes of the Continuous Time Markov analysis, helpers were named according to their relative contribution to chick provisioning within their groups (‘primary’ and ‘secondary’ helpers hereafter), following the terminology of Savage et al. (2017). In this way, within each group, every social category comprised only one individual, making all group members identifiable for the model. Continuous Time Markov Models were fitted allowing either: (a) for each individual as many λ visitation rates as there are carers, therefore assuming that individuals may react differently to each of the other carers (full model); or (b) for each individual only one λ visitation rate, therefore assuming that the probability of following another individual is independent of the identity of this bird (reduced model 1; model λ_i, μ_i); or (c) identical λ and μ for all individuals of the group (reduced model 2; model λ_0, μ_0). Models were compared using likelihood ratio tests and estimates of transition rates are reported for the best-fitting model.

We compared Continuous Time Markov estimated rates at which crows alternated visits (λ) with the rates at which they repeated visits (μ) for all the categories of carers, within groups of equal size. Non-overlapping 95% confidence intervals were interpreted as indicating significant differences. We also tested if the tendency for individual crows to exhibit turn taking rate (λ/μ; Savage et al., 2019) in fitted Continuous Time Markov models was lower in the randomization tests than in the observed data. For each group, we averaged the λ/μ ratio of all individuals and, for each group size separately, we compared the median of these values with the median of expected ratios obtained by randomizing individual inter-visit intervals 1,000 times, using the one-sample Wilcoxon test.

Fitness consequences of alternation

A key objective of this study was to test if better alternation among carers was linked to higher reproductive output (number of chicks fledged) and/or to nestling quality. To examine this, we first ran Generalized Linear Mixed Models (GLMMs) with a binomial error distribution and logit link function in the package *lme4* in R (Bates et al., 2015) where the response variable is a matched pair of counts of the number of eggs that successfully developed into fledglings and those that did not, combined into a single object with the R function *cbind* (Crawley, 2012). This variable, which represents the proportion of eggs that led to fledglings, has the advantage of taking into consideration the information on the size of the sample from which it was estimated, i.e. clutch size. Therefore, it is best suited for our case, in which the size of the clutch varies considerably among nests (2–7 eggs; average ± SE = 4.6 ± 0.05; Canestrari et al., 2011). There were three fixed factors relevant for this analysis, namely the degree of carer alternation (measured as the proportion of alternated visits over the total of all nest visits performed by carers), group size, and total brood feeding rate (i.e., number of feeding events per hour by all carers). Since these factors should not be included in the same model because of their interdependence (for details, see Ihle et al., 2019 and

Santema et al., 2019), we ran separate models, including a null model, and compared them using corrected Akaike's Information Criterion values (AICc; Hurvich & Tsai, 1989). Following Burnham et al. (2011), models with ΔAICc in the 0–2 range were considered equivalent, models in the 2–4 range received less support, and models with ΔAICc > 7 received scarce support.

In all models, laying date of the first egg (Julian date, counted with reference to 1 March) was also accounted for, and year was fitted as random term. Territory identity was not included as a random term because there were too few repeated measures from the same territories; in those cases, groups had always changed, totally or partially. Normality of scaled residuals, heteroscedasticity and outliers were checked for the best model with the package *DHARMa* (Hartig, 2022), while multicollinearity between fixed factors was tested by computing variance inflation factors (VIFs) with the package *performance* (Lüdecke et al., 2021). All other analyses described below followed the same model checking procedure.

The relationship between nestling body mass and degree of carer alternation, group size and total brood feeding rate was explored in three separate Linear Mixed Models (LMM) fitted by Maximum Likelihood (ML), using the package *lmerTest* (Kuznetsova et al., 2017). Following the procedure explained above, models were compared with AICc. The best model was rerun using Restricted Maximum Likelihood (REML), which produces more accurate estimates and p-values for fixed terms (Zuur et al., 2009). All models included the length of the sixth primary feather (to account for nestling age), laying date, and sex as fixed factors. The sample comprised multiple chicks from the same territories, allowing territory identity (nested within year) to be fitted as a random term.

Although body mass alone is considered a reliable indicator of condition in birds (Labocha & Hayes, 2012), ratio indices that divide body mass by some linear measure of structural size are also commonly used. To check the robustness of our results, we repeated analyses using body mass divided by tarsus length (Stauss et al., 2005) as a measure of condition. Like nestling body mass, this index also correlated with post-fledging survival in our study population (see Table S1).

It is possible that a correlation between the degree of carers' alternation and fitness metrics (here, number and/or quality of fledglings) is spurious. For example, breeders that are of high quality and/or that occupy prime territories may lay larger clutches or larger eggs, which then produce heavier hatchlings and, ultimately, heavier fledglings (Alquati et al., 2007; Krist, 2011). Carer and territory quality may also translate into higher feeding rates, resulting in higher degrees of alternation. To address this issue, we ran: (a) a GLMM with a Poisson error distribution and log link function to investigate whether carer alternation was linked to larger clutches, fitting group size and laying date as additional fixed terms and year as a random term; (b) an LMM to examine whether females belonging to well-coordinated groups gave their nestling a 'better start' by laying larger eggs – this model was run on a subsample of 64 eggs (14 clutches) of known volume (Canestrari et al., 2011), and included clutch size as a fixed term in addition to the variables used in the previous model; and (c) an LMM where total brood feeding rate was the dependent variable and the degree of alternation, group size, brood size, and laying date were included as fixed terms and year as a random term.

One of the nestlings in our sample was found injured under the nest tree on the day of chick banding. During a previous visit to the nest, this individual had already shown signs of sickness (it was conspicuously underdeveloped and lost feathers during handling), although a proper diagnosis was not carried out. This nestling was formally identified as an outlier in the corresponding analysis performed with *DHARMa* (see above) and hence excluded. That said, we checked the robustness of the relationship between nestling body mass and carer alternation by also running models including this datum, confirming that results remained qualitatively unchanged.

Finally, in the reduced sample of broods where chicks were individually recognizable, we measured both the feeding rate and the time intervals between consecutive feedings of each individual nestling. We then calculated the corresponding coefficients of variation (CVs) of these feeding intervals to quantify the regularity of food provisioning of each chick. To analyse whether higher degrees of alternation among group members resulted in the provision of more food and/or in a more regular feeding pattern, we ran two LMMs where chick feeding rate and CV values were separately modelled with the proportion of alternated nest visits, group size, and brood size as fixed terms and territory identity as a random term.

Results

Alternation in food provisioning

The *k*-category runs tests of randomness indicated a degree of nest-visit alternation significantly higher than expected by chance in 45 out of 50 broods (Table S2). Turn taking in provisioning was confirmed after randomizing inter-visit intervals. Indeed, the degree of observed alternation was higher than that in the randomized samples for all group sizes (Fig. 1), and where sample sizes allowed statistical comparison, the median of the observed values significantly differed from the median of the randomized samples, taken as the reference level in one-sample Wilcoxon tests ($V = 249$, $N = 25$ and $p = 0.02$ for groups of three; $V = 85$, $N = 12$ and $p = 0.04$ for groups of four).

Alternation could not have arisen through carers synchronizing their feeding trips and visiting the nest in rapid succession. In fact, short and long inter-visit intervals were distributed randomly in all recording bouts (Wald-Wolfowitz runs test of randomness; $p > 0.05$ for all tests).

Continuous Time Markov Models further confirmed the occurrence of turn taking in crows regardless of group size. Indeed, full models, which allowed a different λ transition rate for each individual following any other carer of the group, significantly outperformed reduced models (equal λ or equal λ and μ) for every group size considered (Table S3). Continuous Time Markov estimated transition rates also showed that individuals were significantly more likely to alternate visits rather than to repeat visits (Fig. 2; Table S4), regardless of their social role (breeding male, breeding female, primary and secondary helpers), with the only exception being breeding females in groups of four carers (for which the estimated proportion of repeated visits was similar to that of alternated visits with the secondary helpers; Table S4). The median turn-taking ratios (λ/μ) for individual crows in fitted Continuous Time Markov models were also lower in randomized visits than in the observed data, for group sizes for which meaningful comparisons could be performed (one-sample Wilcoxon Test: $V = 347$ and $p < 0.01$ for groups of three; $V = 91$ and $p < 0.01$ for groups of four; Fig. 3).

Fitness consequences of alternation

When analysing the proportion of eggs that led to fledglings, none of the models performed better than the null model (ΔAICc < 2; Table 2). Conversely, in the analysis of nestling body mass, the alternation model outperformed all other models (ΔAICc > 7; Table 2). Nestling mass increased significantly with the degree of carers' alternation (Fig. 4) and with nestling age, and decreased with laying date (Table 3). Male nestlings were found to be heavier than female nestlings, as expected based on previous results (Canestrari et al., 2011). All the results held when the outlier mentioned above was included in the analyses (Table S5).

Canestrari et al. (2011) had previously shown that, in this study population, nestling body mass substantially affects post-fledging survival (the 3-month period of maximum mortality risk; Baglione et al., 2002a, 2010). Based on these earlier findings, an increment in group alternation from 0.7 to 0.9 (an interval that comprised 70% of the empirically observed values of alternation; Fig. 4) corresponded to an estimated survival benefit of 12.9% and 13.3% for males and females, respectively. Analyses based on the body mass/tarsus length index of body condition returned qualitatively similar results, which are reported in the Supplementary Materials (Table S6 and S7, Fig. S1).

Females in better coordinated groups neither laid larger clutches (estimate ± SE= -0.1 ± 0.79, *z* = -0,13, p = 0.89; Table S8) nor, more importantly, larger eggs (estimate ± SE= -12.49 ± 8.8, df = 8.91, *t* = -1.42, p = 0.19; Table S9). Nestlings provisioned by well-coordinated carers therefore did not have a ‘better start’ than those raised by less-coordinated groups, suggesting that the observed differences in nestling body mass must have arisen during the nestling period. Furthermore, the degree of carers’ alternation did not correlate with total brood feeding rate (estimate ± SE = 0.18 ± 0.46, df = 44.23, *t* = 0.4, p = 0.69; Table S10), so it seems unlikely that the relationship between the degree of alternation and nestling body mass arose through a positive effect of feeding rate on both variables.

While better carer alternation did not result in higher nestling food intake rates (estimate ± SE= 1.03 ± 1.0, df = 18.50, *t* = 1.04, p = 0.31; Table S11), it ensured more constant food provisioning (i.e., lower CV values for time intervals between consecutive feedings; estimate ± SE= -1.12 ± 0.45, df = 14.45, t = -2.52, p = 0.02; Table S12, Fig. S2).

Discussion

Cooperatively breeding carrion crows in our long-term study population alternate in provisioning the brood. The *k*-category runs test showed that the degree of alternation of carers at the majority of nests (90%) was significantly higher than would be expected by chance. The randomization of inter-visit intervals, which removes the relationship between the visit times of different individuals, suggested that the observed turn taking did not arise merely as a by-product of the refractory time that birds require to forage away from the nest. Finally, Continuous Time Markov Models revealed that this tendency to alternate nest visits was common across carer types (breeders, primary and secondary helpers) and did not depend on group size. A plausible explanation of these results is that alternation in this system is an active process, with carers adjusting the timing of their provisioning visits according to the behaviour of other group members (Savage et al., 2017).

Despite consistent findings across different analytical approaches, this interpretation should be treated cautiously. It has been argued that a multitude of external factors can either decrease or increase inter-visit intervals. For example, the presence of a predator or changing weather conditions may increase the time between subsequent visits of carers, hindering a more constant provisioning rate. Combining periods of high and low activity into a single sequence of feeding events inevitably reduces the degree of alternation after randomization of inter-visit intervals, as compared to observed sequences (for a demonstration, see Santema et al., 2019). Although the randomization ‘within bouts’ approach followed here (Johnstone et al., 2014; Savage et al., 2017) has been shown to be the most conservative (Ihle et al., 2019), deviation from randomness may therefore be less informative than previously thought, particularly when, as in our case, observation bouts are long. Distinguishing between active and passive alternation would therefore require accounting for the environmental conditions that birds experienced during the sampling period with a resolution that is not normally achievable, or performing experiments that would be difficult to conduct in most study systems (for notable examples, see Hinde, 2006; Meade et al., 2011).

In the present study, we took a different perspective by also examining potential fitness consequences of carers' alternation. We found a strong effect on the body mass of nestlings, which likely translates into significantly enhanced post-fledging survival rates (Baglione et al., 2002a; Canestrari et al., 2011). This illustrates the potential adaptive significance of alternation and a role for natural selection in shaping mechanisms that allow carers to monitor the provisioning behaviour of others, and to adjust their own behaviour accordingly. In other words, our results show that the way cooperation is achieved (coordinated *vs.* uncoordinated behaviours) affects fitness payoffs, setting the stage for complex forms of interaction among group members to arise.

It is conceivable that high-quality carers achieve higher degrees of alternation and are also able to colonize and defend better territories. In other words, carer and territory quality may ultimately cause the relationship between the degree of alternation and nestling body mass, rather than turn taking *per se*. If this was the case, however, we would have expected to find positive correlations between the degree of alternation and other parameters that are linked to carer and territory quality, such as the size of clutch or the eggs, or the number of fledglings produced, but this was not the case. Most importantly, nestlings raised by well-coordinated groups did not hatch from larger eggs, and therefore did not enjoy a ‘better start’, which, in birds, can lead to heavier mass at fledging (Alquati et al., 2007; Krist, 2011). Moreover, we also failed to find a correlation between the degree of alternation and total brood feeding rate, allowing us to tentatively reject the hypothesis that high-quality carers (and/or carers that occupy high-quality territories) alternate more simply because they feed the brood more often. Despite the correlational nature of our study, we argue that, on current evidence, a causal effect of group alternation on offspring condition is a plausible explanation of our results.

If good alternation in brood provisioning does not translate into more food delivered to the chicks (see above), what mechanism might underlie the correlation between the degree of turn taking and nestling body mass? Our data on the sample of broods where all chicks were individually recognizable revealed that nestlings were provisioned more regularly in well-coordinated groups. It has been shown in birds that regular, and hence predictable, feeding intervals can improve nestling body condition (Clark, 2002; Cohen et al., 2014; Mariette & Griffith, 2015; Royle et al., 2006; Weimerskirch et al., 2000), although some exceptions have been reported (Grissot et al., 2019; Grodzinski et al., 2009). Interestingly, regular food intake also prevents mass loss and improves health in adult hooded crows (Acquarone et al., 2002), which are closely related to the carrion crow (Poelstra et al., 2014). In conclusion, it seems to be the regularity of feeding that causally links carers’ alternation and nestling body mass – an idea that should be amenable to experimental investigation in future studies.

The benefits of regular nestling feeding would promote alternation even in the case of imperfect monitoring of group members’ behaviour, a condition that is likely to apply to most avian systems, including the carrion crow. Johnstone and Savage (2019) proposed a model that addresses why strict turn taking, where a carer invariably refrains from visiting the nest until another one has done so, virtually never occurs in birds. Indeed, although several species show significant alternation in nest visits, turn taking is always imperfect (e.g., Bebbington & Hatchwell, 2016; Koenig & Walters, 2016; Savage et al., 2017; this study), contradicting the predictions of an earlier model based on conditional cooperation (Johnstone et al., 2014). The new model (Johnstone & Savage, 2019) incorporates several factors that may affect the tendency of carers to alternate, among which two are particularly relevant to our study, namely: (a) imperfect monitoring of each other's provisioning behaviour; and (b) time-dependent costs and benefits of care. The model shows, on the one hand, that imperfect monitoring disrupts the alternation of carers leading to bursts of frequent feeding visits separated by longer intervals of fasting. On the other hand, it demonstrates that, when clumped feeding visits are costly for the offspring, turn taking is restored despite the limitations in monitoring, and that, when this occurs, carers' alternation is no longer perfect. Although Johnstone and Savage (2019) address the case of a species with biparental care, our findings for carrion crows fit their predictions well, suggesting that the model generalises to cooperatively breeding species.

The positive fitness consequences of turn taking might select for mechanisms that improve individuals' ability to monitor the behaviour of other carers and to adjust the timing of their own nest visits. Our analyses suggest that cooperative offspring care in carrion crows is a coordinated behaviour rather than arising merely as the sum of independent actions. If that is the case, coordination may be achieved through communication, as highlighted by simulated biological systems where the amount of information shared among agents improves the likelihood of resolving a cooperative task (Miglino et al., 2008). Interestingly, cooperative breeding is associated with richer vocal repertoires in birds and, in particular, with a larger variability of contact calls (Leighton, 2017). In light of the findings presented here, cooperatively breeding carrion crows are a particularly valuable model system for investigating communicative cooperation (*sensu* Noë 2006) in non-human animals. This work will be aided by the use of advanced machine-learning methods for charting the vocal repertoires of pairs with and without helpers, detecting context dependence in crows' communicative behaviour, and ultimately, functional decoding of call types that may be involved in coordination (Rutz et al., 2023).

In conclusion, our study highlights the importance of the temporal dimension of brood care, revealing a possible effect of carers' alternation on (predicted) post-fledging survival. On current evidence, turn taking seems common in birds (e.g., Halliwell et al., 2022; Koenig & Walters, 2016; Savage et al., 2017; Johnstone et al., 2014; but see Khwaja et al., 2017), and may therefore afford fitness benefits in many species, including both biparental and cooperative breeding systems. Future research on environmental (e.g., habitat type, weather, predator density, distribution of food) and social factors (e.g., familiarity between carers) that may affect carers' alternation behaviour will provide a more nuanced understanding of parental care in birds, and could also prove important for species conservation. Furthermore, analyses of alternation promise novel insights into many other behaviours where coordination may boost shared benefits, such as vigilance in groups of foraging animals or predator mobbing in colonial species. This approach has the potential to unveil a surprising degree of behavioural complexity, illuminating the adaptations that enable cooperation in non-human animals.

Conflict of interest declaration

The authors declare no conflict of interest.

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Data accessibility

Analyses reported in this article can be reproduced using the data provided by Trapote et al., 2023 in *Dryad*.

Author contributions

T.E., C.D., R.C. and B.V. conceived the ideas and designed methodology; T.E., C.D., and B.V. collected the data; T.E., M-G.V and B.V. analysed the data; T.E., R.C. and B.V. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Table 1. Summary of groups sampled. Helpers are classified according to sex and category (offspring from previous brood that remained at the natal territory or immigrants).

	Number of sampled individuals				
Group type (N)	Male offspring helpers	Female offspring helpers	Male immigrant helpers	Female immigrant helpers	Unknown
Unassisted pairs (6)	-	-	-	-	-
Groups with three carers (25)	11[1]	9[1]	5	-	-
Groups with two helpers (14)	10	10[2]	4	3[1]	1
Groups with three helpers (5)	6[1]	7[2]	2	-	-

[1] Among these individuals, one 'non-significant carer', that is, a bird that provisioned less than 20% of the mean rate of the rest of other carers of its group, was excluded from Continuous Time Markov analyses (see Methods).

[2] Among these individuals, two non-significant carers were excluded from Continuous Time Markov analyses.

Table 2. Corrected Akaike based comparison of models for nestling survival (n = 50 broods) and body mass (n = 81 chicks), measured when the eldest chick of the brood was 28–30 days old.

Response term	Fixed terms	df	AICc	ΔAICc
Nestling survival	Null model	2	148.8928	0.1
	Total brood feeding rate, laying date	4	148.7682	0.0
	Alternation, laying date	4	150.1104	1.3
	Group size, laying date	4	151.0252	2.3
Body mass	Null model	4	841.0693	49.6
	Total brood feeding rate, age, laying date, sex	8	803.6508	12.2
	Alternation, age, laying date, sex	8	791.4916	0.0
	Group size, age, laying date, sex	8	801.7390	10.2

Table 3. Effects of predictors in the best model for nestling body mass. Results of Linear Mixed Models (LMMs) fitted by Restricted Maximum Likelihood (REML), using Satterthwaite's method. Significant p-values are highlighted in bold.

Fixed terms	Estimate ± SE	d.f.	*t* value	*P* value
Alternation	186.23 ± 49.37	37.21	3.77	**< 0.001**
Age	3.74 ± 2.11	70.88	1.78	0.08
Laying date	-1.18 ± 0.34	28.05	-3.51	**0.002**
Sex1	-22.82 ± 3.18	66.65	-7.18	**< 0.001**

Figure legends

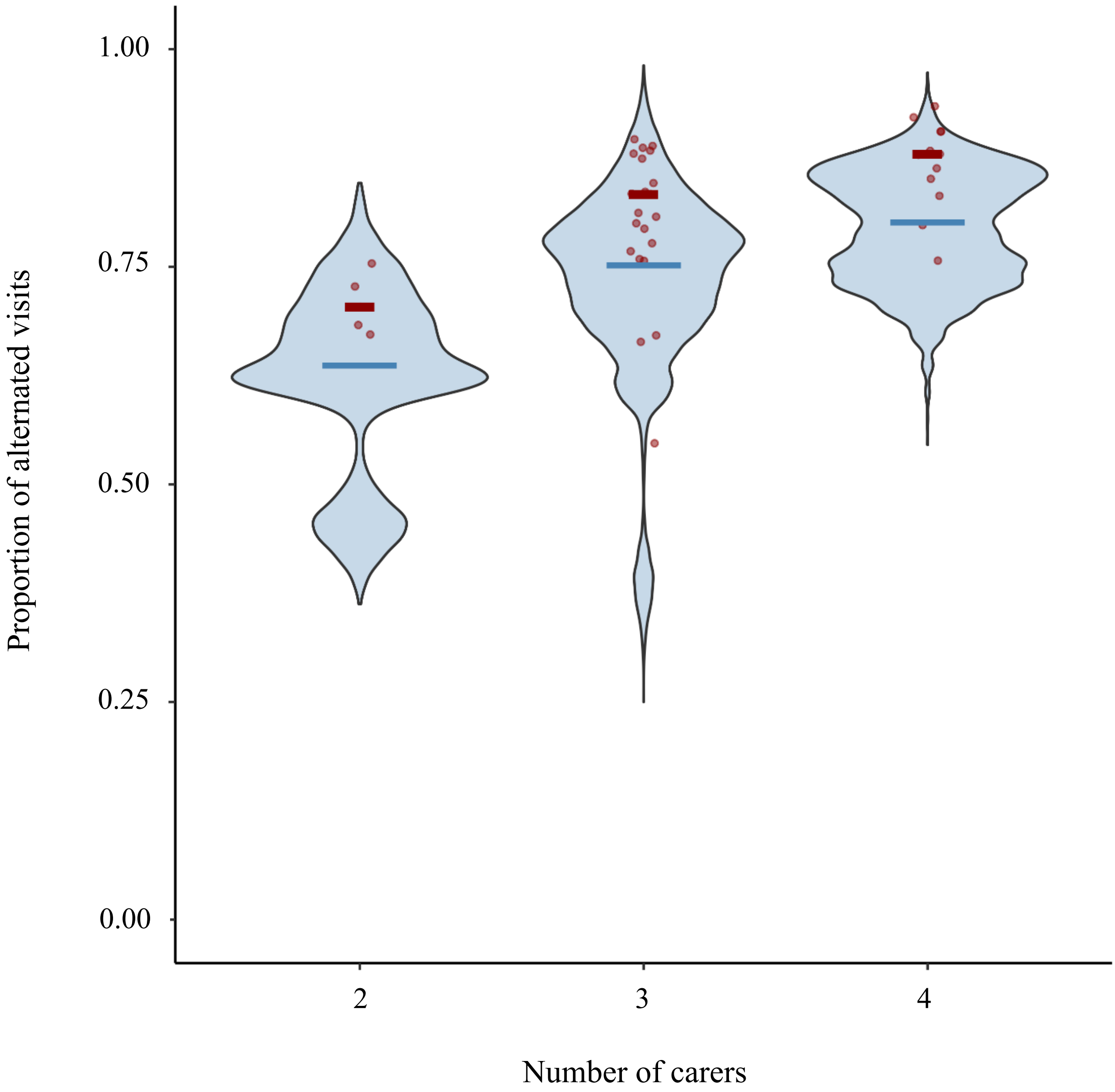
Figure 1. Observed degree of turn taking (proportion of alternated visits) in nests with different number of carers (individual nests: red dots; median: red line) compared to simulated distributions obtained by randomizing inter-visit intervals 1,000 times (see Methods). For every group size, the median of observed alternation is greater than expected by randomization (blue line), suggesting that crows take turns in provisioning.

Figure 2. Mean of individual estimated transition rates for breeding females (Bf), breeding males (Bm), primary helpers (H1) and secondary helpers (H2), calculated according to Continuous Time Markov Models in groups of two (**A**), three (**B**) and four (**C**) carers. Arrow widths are proportional to the estimated transition rates. The within-individual transition rate μ, that is, the rate of subsequent visits of the same individual (within individual arrows) was significantly lower (non-overlapping confidence intervals, see Table S4) than estimated transition rates λ between different individuals (between-individuals arrows) for each bird category, except Bf->H2, suggesting that crows were more likely to alternate, rather than to repeat, visits.

Figure 3. Individual turn-taking rate (λ/μ), averaged within each group, in fitted Continuous Time Markov models. Observed ratios (crosses) were compared with expected ratios obtained by randomizing individual inter-visit intervals 1,000 times.

Figure 4. Fitted values of nestling body mass (measured just before fledging, that is, when the eldest chick was 28–30 days old; see Methods) plotted against the proportion of alternated visits (n = 81 nestlings). The shadowed area indicates 95% confidence

limits. The graph does not include the outlier mentioned in the Method section (see above).



1.00
0.75
0.50
0.25
0.00
Proportion of alternated visits
2
3
4
Number of carers

Figure 1.

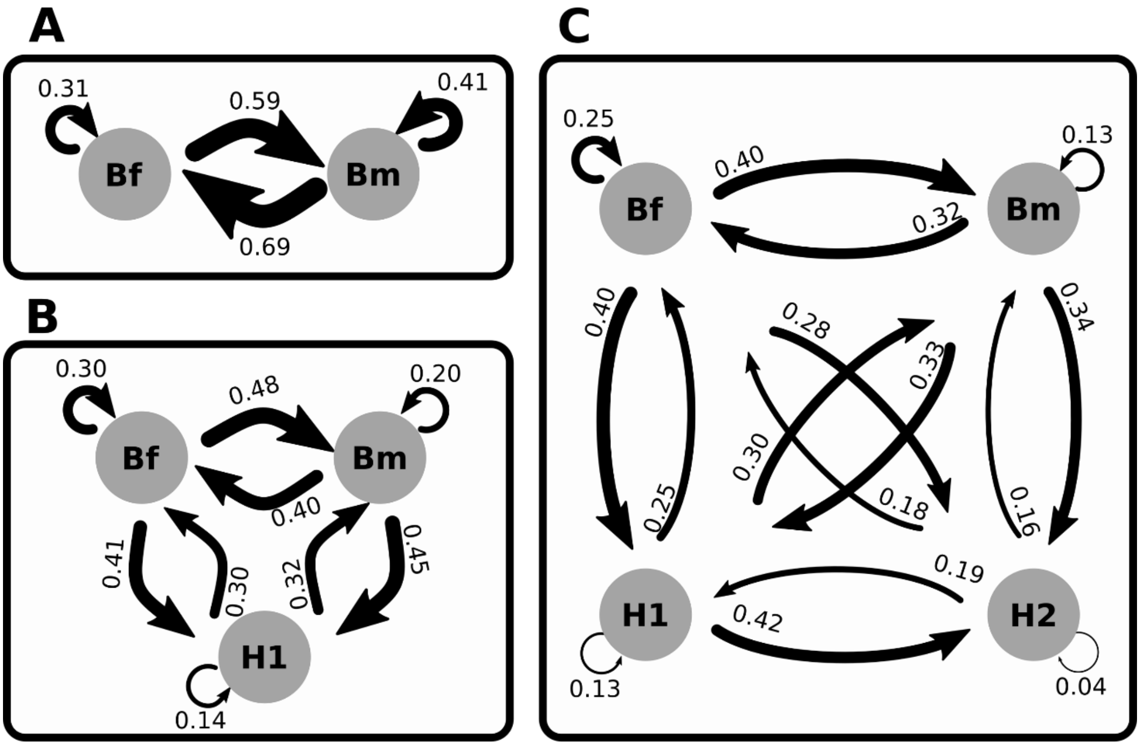

A
0.31
0.59
0.41
Bf
Bm
0.69
B
0.30
0.48
0.20
Bf
Bm
0.40
0.41
0.30
0.32
0.45
H1
0.14
C
0.25
0.40
0.13
Bf
Bm
0.32
0.40
0.28
0.33
0.34
0.30
0.18
0.25
0.16
0.19
H1
H2
0.42
0.13
0.04

Figure 2

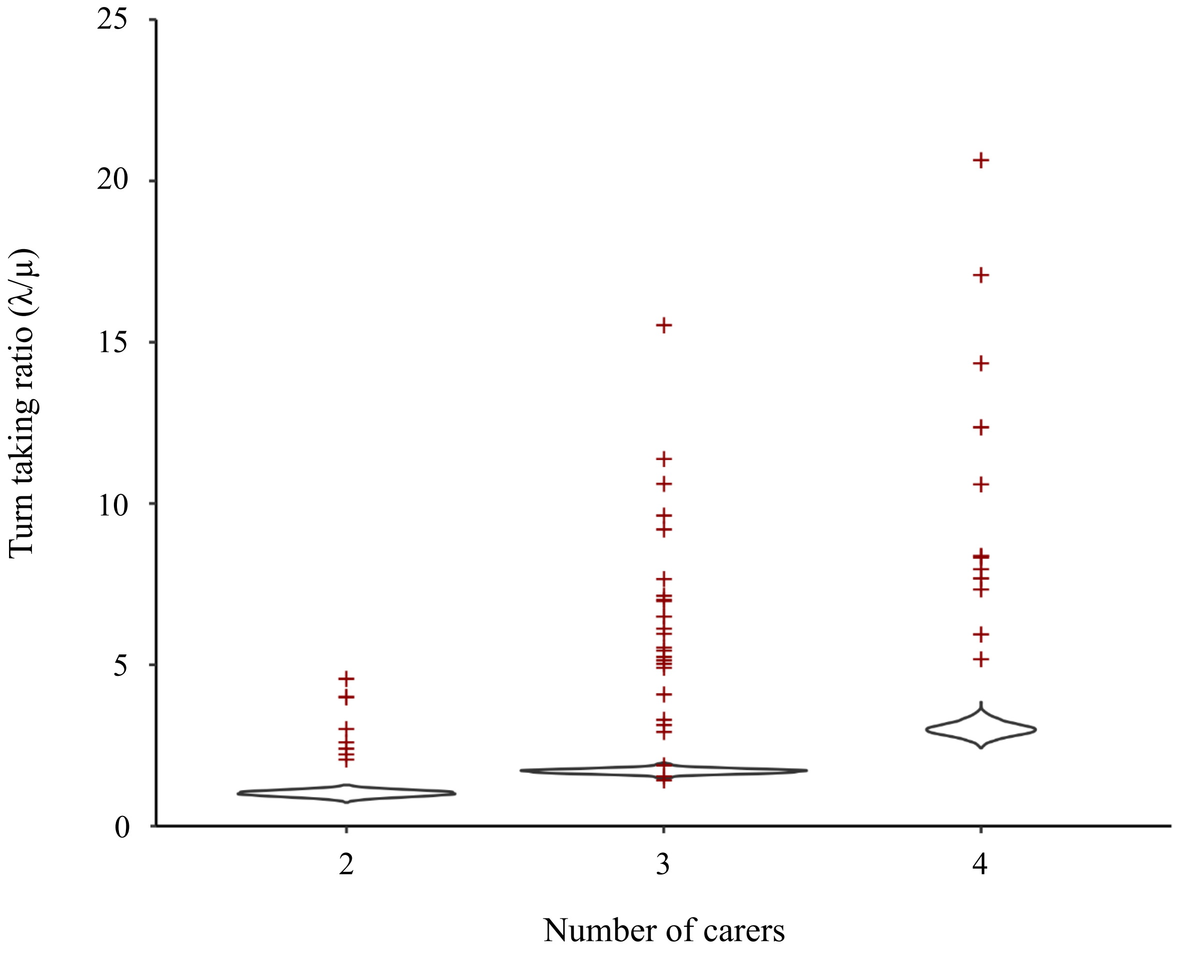
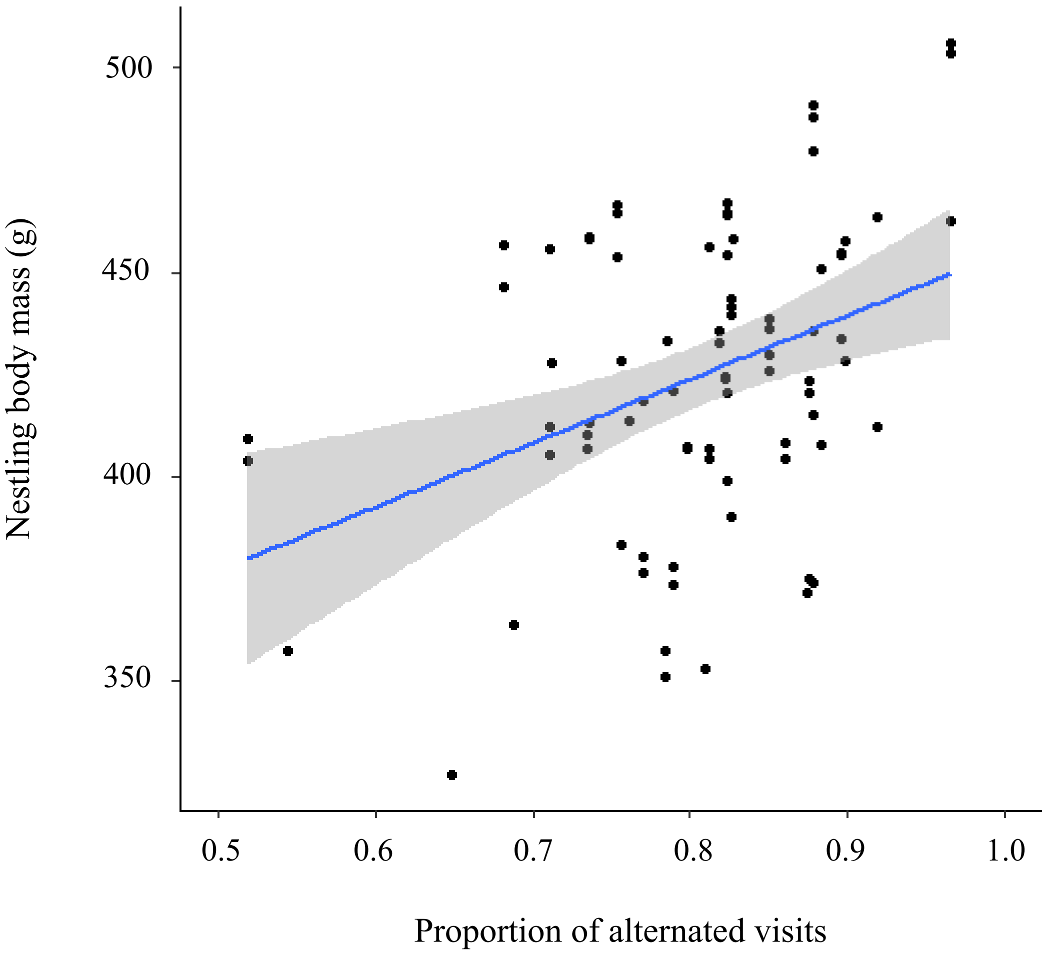


Figure 3.



Nestling body mass (g)
500
450
400
350
0.5
0.6
0.7
0.8
0.9
1.0
Proportion of alternated visits

Figure 4.

SUPPLEMENTARY MATERIAL

Table S1. Effect of body condition (body mass/tarsus length), brood size and sex on the survival probability of fledglings (n = 144) in the first three months after leaving the nest. Results of a Generalized Linear Mixed Model (GLMM) with binomial error distribution. Year was fitted as a fixed term instead of random term because of insufficient levels (3). Based on data presented in Canestrari et al., 2011. Significant p values are highlighted in bold.

Fixed terms	Estimate ± SE	*Z* value	*P* value
Body condition	1.14 ± 0.45	2.55	**0.01**
Brood size	0.21 ± 0.22	0.93	0.35
Sex 1	0.21 ± 0.24	0.88	0.38
Year 1	0.17 ± 0.35	0.48	0.63
Year 2	-0.36 ± 0.33	-1.08	0.28

Table S2. k-category runs test of randomness for 50 sampled nests. P-values were adjusted following the Benjamini-Hochberg method. Significant p values are highlighted in bold.

Nest ID	Trials	Runs	Expected μ	Expected σ	z statistic	p value	Adjusted p value
1	174	128	113.92	6.09	2.31	0.0207	**0.0242**
2	74	65	55.62	3.64	2.58	0.0100	**0.0127**
3	68	37	36.65	3.43	0.10	0.9182	0.9182
4	139	109	90.83	5.43	3.35	0.0008	**0.0014**
5	65	49	33.49	4.00	3.88	0.0001	**0.0003**
6	220	187	159.72	6.33	4.31	<0.0001	**0.0001**
7	142	117	93.89	5.54	4.18	<0.0001	**0.0001**
8	72	62	47.56	3.87	3.73	0.0002	**0.0005**
9	332	305	240.55	7.91	8.14	<0.0001	**<0.0001**
10	143	117	94.01	5.14	4.47	<0.0001	**<0.0001**
11	60	58	48.37	3.02	3.19	0.0014	**0.0022**
12	58	52	37.72	3.40	4.19	<0.0001	**0.0001**
13	137	120	102.85	5.02	3.42	0.0006	**0.0012**
14	132	109	87.36	5.31	4.07	<0.0001	**0.0001**
15	53	46	35.94	3.35	3.00	0.0027	**0.0040**
16	66	47	33.73	4.00	3.32	0.0009	**0.0015**
17	83	73	62.81	3.87	2.64	0.0084	**0.0110**
18	161	127	102.59	5.85	4.17	<0.0001	**0.0001**
19	90	74	59.84	4.39	3.23	0.0013	**0.0020**
20	81	55	39.72	4.27	3.58	0.0003	**0.0008**

21	62	57	45.48	3.37	3.42	0.0006	**0.0012**
22	42	34	26.10	2.75	2.88	0.0040	**0.0058**
23	74	48	45.00	3.87	0.78	0.4377	0.4484
24	222	199	160.68	6.48	5.91	<0.0001	**<0.0001**
25	170	127	105.38	5.78	3.74	0.0002	**0.0005**
26	155	137	122.88	4.95	2.85	0.0044	**0.0061**
27	199	174	131.99	6.58	6.38	<0.0001	**<0.0001**
28	40	30	27.20	2.88	0.97	0.3315	0.3481
29	80	55	38.98	4.22	3.80	0.0001	**0.0004**
30	261	215	190.22	7.00	3.54	0.0004	**0.0008**
31	157	121	104.44	5.84	2.83	0.0046	**0.0062**
32	178	142	127.97	5.70	2.46	0.0138	**0.0166**
33	255	217	169.84	7.48	6.31	<0.0001	**<0.0001**
34	59	53	40.19	3.55	3.61	0.0003	**0.0007**
35	63	48	39.16	3.54	2.50	0.0126	**0.0155**
36	121	95	77.88	5.08	3.37	0.0008	**0.0014**
37	37	28	24.35	2.68	1.36	0.1739	0.1873
38	33	29	25.30	2.37	1.56	0.1186	0.1311
39	654	429	361.80	10.79	6.23	<0.0001	**<0.0001**
40	612	417	305.82	12.31	9.03	<0.0001	**<0.0001**
41	289	213	197.98	7.07	2.13	0.0335	**0.0380**
42	656	543	434.14	11.99	9.08	<0.0001	**<0.0001**
43	74	60	48.43	3.96	2.92	0.0034	**0.0050**
44	335	225	221.00	8.55	3.97	<0.0001	**0.0002**

45	211	145	105.64	7.19	5.48	<0.0001	**<0.0001**
46	170	95	79.22	5.98	2.64	0.0083	**0.0106**
47	285	255	212.61	7.28	5.82	<0.0001	**<0.0001**
48	239	121	97.44	6.22	3.79	0.0002	**0.0003**
49	315	254	207.62	8.27	5.61	<0.0001	**<0.0001**
50	295	248	227.18	7.02	2.93	0.0030	**0.0044**

Table S3. Comparison of Continuous Time Markov Models. Complete models allow, for each individual, a different λ transition rate following any other particular carer of the group. Reduced models 1 allow only one λ visit rate, therefore assuming that the probability of following another individual is independent of the identity of this bird (model λ_i, μ_i). Finally, reduced models 2 assume identical λ and μ for all individuals of the group (model λ_0, μ_0). P-values refer to comparisons with the complete model. Note that the complete model and reduced model 1 are equivalent for groups of two carer. Nest with five significant carers were omitted because of small sample size (n = 3).

	AIC	BIC	log(lik)	LRT (p-value)	Number of nests
2 significant carers					
Complete model	24706.39	24727.71	-12349.19		8
Reduced model 1 (λ i, μ i)	-	-	-		
Reduced model 2 (λ 0, μ 0)	24771.04	24781.70	-12383.52	**< 0.001**	
3 carers					
Complete model	86084.08	86141.46	-43003.04		27
Reduced model 1 (λ i, μ i)	86171.40	86209.56	-43079.70	**< 0.001**	
Reduced model 2 (λ 0, μ 0)	86369.40	86382.15	-43182.70	**< 0.001**	
4 carers					
Complete model	38903.69	38995.65	-19435.83		12
Reduced model 1 (λ i, μ i)	38948.97	38994.96	-19446.48	**<0.001**	
Reduced model 2 (λ 0, μ 0)	39145.09	39156.59	-19570.55	**<0.001**	

Table S4. Mean ± 95% Confidence intervals of individual estimated transition rates for breeding females (Bf), breeding males (Bm), primary helpers (H1) and secondary helpers (H2), calculated according to Continuous Time Markov Models in groups of two, three and four carers. The within-individual transition rate μ, i.e., the rate of subsequent visits of the same individual was significantly lower (non-overlapping confidence intervals) than estimated transition rates λ between different individuals for each bird category, suggesting that carrion crows are more likely to alternate visits rather than repeating them. The only exception is that of breeding females in groups of four carers, for which the estimated proportion of repeated visits was similar to that of alternating visits with the secondary helpers. The sample comprises 47 breeding males, 47 breeding females, 39 primary helpers and 13 secondary helpers.

	Transition	Estimate	Lower confident limit	Upper confident limit
2 carers				
Bf -> Bf	μ	0.31	0.27	0.34
Bf -> Bm	λ	0.59	0.55	0.63
Bm -> Bf	λ	0.69	0.66	0.73
Bm -> Bm	μ	0.41	0.37	0.45
3 carers				
Bf -> Bf	μ	0.30	0.28	0.32
Bf -> Bm	λ	0.48	0.46	0.51
Bf -> H1	λ	0.41	0.38	0.44
Bm -> Bf	λ	0.40	0.38	0.43
Bm -> Bm	μ	0.20	0.18	0.22
Bm -> H1	λ	0.45	0.42	0.48
H1 -> Bf	λ	0.30	0.27	0.32

H1 -> Bm	λ	0.32	0.29	0.34
H1 -> H1	μ	0.14	0.12	0.16
4 carers				
Bf -> Bf	μ	0.25	0.22	0.29
Bf -> Bm	λ	0.40	0.36	0.44
Bf -> H1	λ	0.40	0.36	0.45
Bf -> H2	λ	0.29	0.24	0.34
Bm -> Bf	λ	0.32	0.29	0.36
Bm -> Bm	μ	0.14	0.11	0.17
Bm -> H1	λ	0.33	0.29	0.38
Bm -> H2	λ	0.32	0.27	0.38
H1 -> Bf	λ	0.25	0.21	0.28
H1 -> Bm	λ	0.30	0.27	0.35
H1 -> H1	μ	0.08	0.06	0.11
H1 -> H2	λ	0.34	0.29	0.40
H2 -> Bf	λ	0.18	0.15	0.21
H2 -> Bm	λ	0.16	0.13	0.19
H2 -> H1	λ	0.19	0.15	0.23
H2 -> H2	μ	0.04	0.03	0.07

Table S5. Effect of the degree of alternation, nestling age and sex, and laying date on nestling body mass and the body mass/tarsus length condition index, after adding the one outlier (see main text; n = 82). Results of Linear Mixed Models (LMMs) fitted by Restricted Maximum Likelihood (REML), using Satterthwaite's method. Significant p values are highlighted in bold.

Model	Fixed terms	Estimate ± SE	d.f.	*t* value	*P* value
Body mass	Alternation	167.07 ± 52.56	38.33	3.18	**0.003**
	Age	4.95 ± 2.32	69.05	2.14	**0.036**
	Laying date	-1.46 ± 0.36	29.78	-4.03	**< 0.001**
	Sex1	-19.89 ± 3.6	71.15	-5.52	**< 0.001**

Table S6. Corrected Akaike based comparison of models for nestling body condition (body mass/tarsus length) measured when the eldest chick of the brood was 28-30 days old (n = 81 chicks).

a		df	AICc	ΔAICc
Body condition	Null model	4	152.7749	26.1
	Total brood feeding rate, age, laying date, sex	8	142.2948	15.6
	Alternation, age, laying date, sex	8	126.6782	0.0
	Group size, age, laying date, sex	8	140.0881	13.4

Table S7. Effect of predictors in the best model for nestling body condition . Results of two Linear Mixed Models (LMMs) fitted by Restricted Maximum Likelihood (REML), using Satterthwaite's method. The first model excludes the one outlier (n = 81 nestling), while the second model includes it (n = 82). Significant p values are highlighted in bold.

b					
Model	Fixed terms	Estimate ± SE	d.f.	*t* value	*P* value
Body condition (without outlier)	Alternation	3.17 ± 0.75	39.23	4.22	**< 0.001**
	Age	0.05 ± 0.03	66.89	1.43	0.16
	Laying date	-0.02 ± 0.01	26.19	-3.42	**0.002**
	Sex female	-0.18 ± 0.05	72.60	-3.35	**0.001**
Body condition (with outlier)	Alternation	2.92 ± 0.83	40.09	3.5	**0.001**
	Age	0.07 ± 0.04	67.78	1.87	0.066
	Laying date	-0.02 ± 0.01	25.86	-3.82	**< 0.001**
	Sex female	-0.14 ± 0.06	72.95	-2.42	**0.018**

Table S8. Effect of the degree of alternation, group size and lying date on clutch size (n = 50). Results of a Generalized Linear Mixed Model (GLMMs) with Poisson error distribution.

Model	Fixed terms	Estimate ± SE	*z* value	*P* value
Clutch size	Alternation	-0.10 ± 0.79	-0.13	0.896
	Group size	-0.01 ± 0.09	-0.04	0.968
	Laying date	-0.01 ± 0.00	-0.43	0.666

Table S9. Effect of the degree of alternation, group size, laying date and clutch size on the egg size (n = 64 eggs from 14 clutches). Results of Linear Mixed Models (LMMs) fitted by Restricted Maximum Likelihood (REML), using Satterthwaite's method. Significant p values are highlighted in bold.

Model	Fixed terms	Estimate ± SE	d.f.	*t* value	*P* value
Egg size	Alternation	-12.49 ± 8.8	8.91	-1.42	0.190
	Group size	0.66 ± 0.76	4.65	0.87	0.429
	Laying date	-0.23 ± 0.05	31.90	-4.67	**<0.001**
	Clutch size	-2.72 ± 0.88	5.99	-3.1	**0.021**

Table S10. Effect of the degree of alternation, group size, laying date and brood size on the total brood feeding rate (n = 50 broods). Results of Linear Mixed Models (LMMs) fitted by Restricted Maximum Likelihood (REML), using Satterthwaite's method. Significant p values are highlighted in bold.

Model	Fixed terms	Estimate ± SE	d.f.	*t* value	*P* value
Total brood feeding rate	Alternation	0.18 ± 0.46	44.23	0.40	0.690
	Group size	0.11 ± 0.05	43.13	2.13	**0.039**
	Laying date	-0.01 ± 0.01	43.42	-1.25	0.217
	Brood size	0.11 ± 0.04	44.87	2.87	**0.006**

Table S11. Effect of the degree of alternation, group size and brood size on the nestling food intake rates (n = 57 individually recognizable nestlings). Results of Linear Mixed Models (LMMs) fitted by Restricted Maximum Likelihood (REML), using Satterthwaite's method. Significant p values are highlighted in bold.

Model	Fixed terms	Estimate ± SE	d.f.	*t* value	*P* value
Nestling food intake rates	Alternation	1.03 ± 1.00	18.50	1.04	0.313
	Group size	0.02 ± 0.12	17.99	0.20	0.84
	Brood size	-0.18 ± 0.07	18.66	-2.66	**0.02**

Table S12. Effect of the degree of alternation, group size and brood size on the coefficient of variation (CV) of the time intervals between consecutive feeds of each individual nestling (higher CVs indicate less constant feeding), calculated for 57 individually recognizable nestlings. Results of Linear Mixed Models (LMMs) fitted by Restricted Maximum Likelihood (REML), using Satterthwaite's method. Significant p values are highlighted in bold.

Model	Fixed terms	Estimate ± SE	d.f.	*t* value	*P* value
CV of time intervals between consecutive feedings	Alternation	-1.12 ± 0.45	14.44	-2.52	**0.024**
	Group size	0.07 ± 0.05	12.51	1.33	0.208
	Brood size	-0.01 ± 0.03	14.74	-0.29	0.775

Figure legends

Figure S1. Fitted values of fledgling body condition (body mass/tarsus length; n = 81 nestlings) plotted against the degree of alternation of the carers (proportion of alternated visits). The shadowed area indicates 95% confidence limits.

Figure S2. Fitted values of coefficient of variation of the time intervals between consecutive feeds of nestlings plotted against the degree of alternation of the carers (n = 57 individually recognizable nestlings). The shadowed area indicates 95% confidence limits.

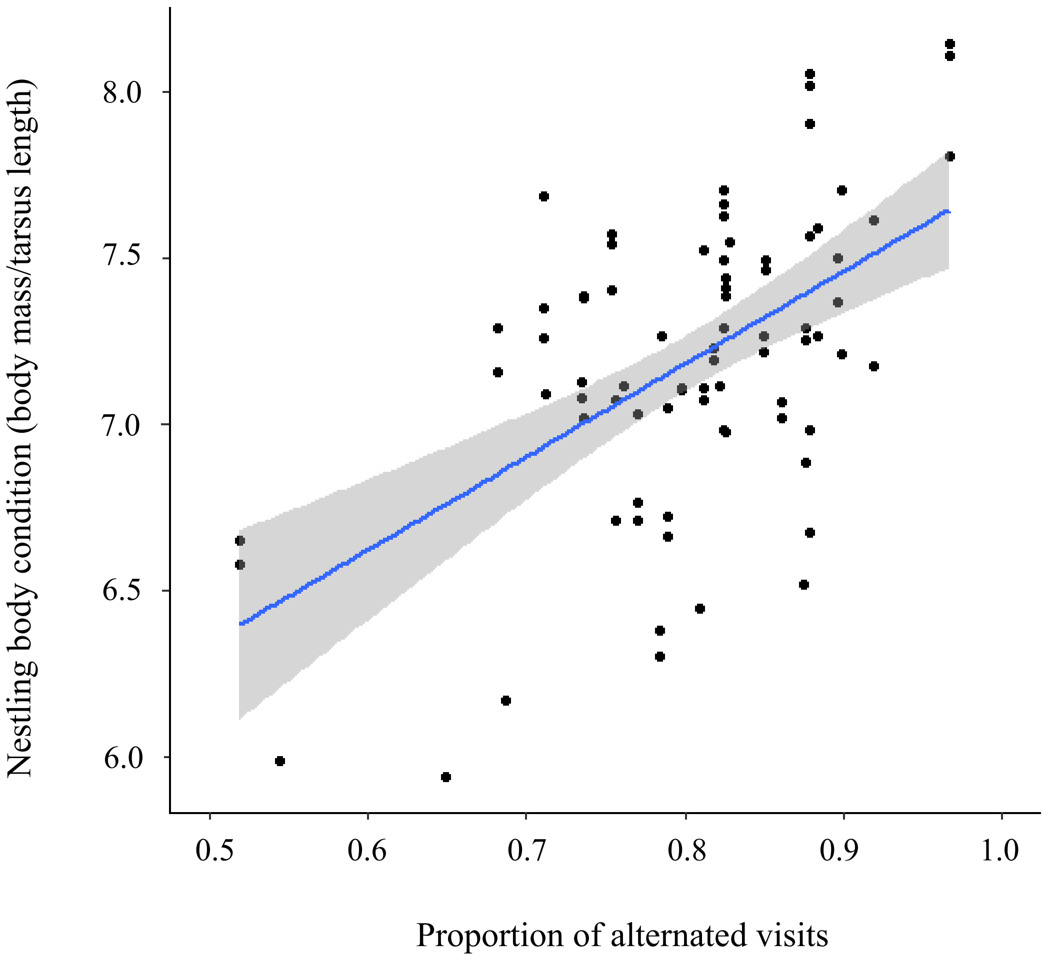

Nestling body condition (body mass/tarsus length)
8.0
7.5
7.0
6.5
6.0
0.5
0.6
0.7
0.8
0.9
1.0
Proportion of alternated visits

Figure S1.

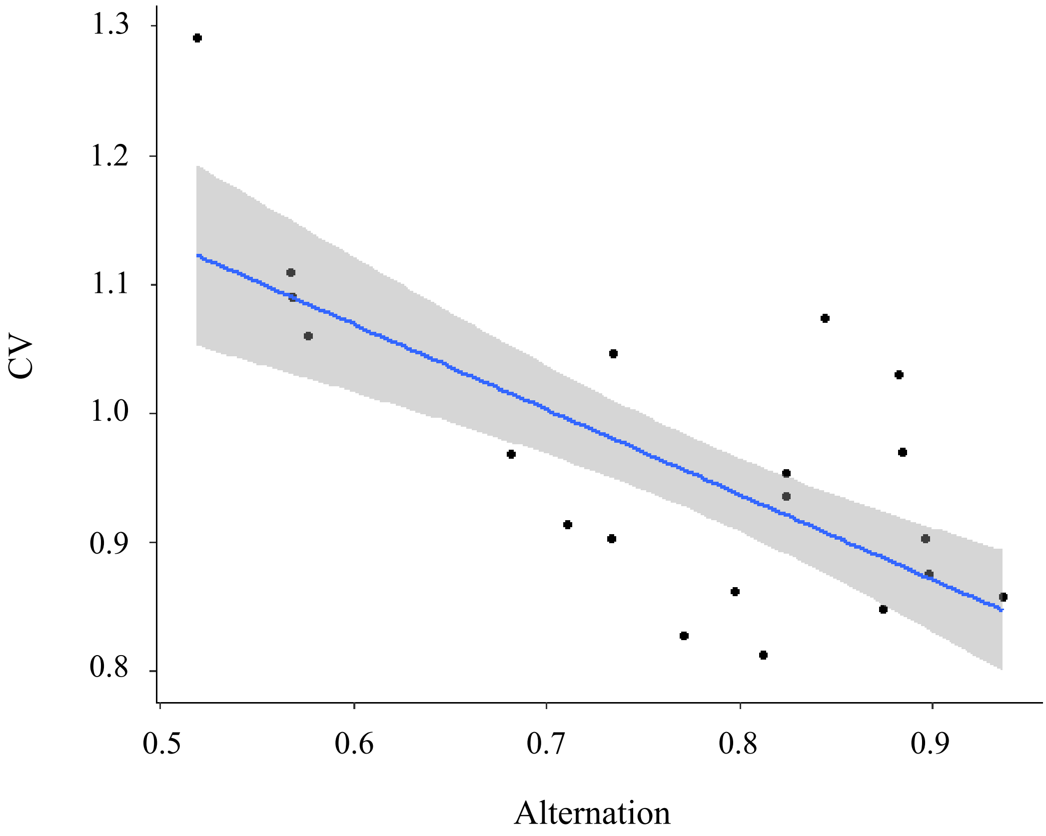


Figure S2.