

Helpers during replacement clutches buffer the impacts of late breeding on a cooperative bird

Carlos De la Cruz ^{a*}, Juliana Valencia ^{b,1}, Mónica Expósito-Granados ^{c,2},
Elena Solís ^{a,3}, Olga Jiménez ^{a,4}, Susana Alarcos ^{a,5}, José María Abad-Gómez ^{a, d,6},
María Jesús García-Baquero ^{a,7}, Jorge S. Gutiérrez ^{d, e, 8}

a Grupo de Investigación en Etología y Biología Evolutiva, Fac. de Ciencias, Univ. de Extremadura, Badajoz, Spain

b Departamento de Didáctica de las Ciencias Experimentales, Univ. de Málaga, Málaga, Spain

c Departamento de Economía y Empresa, Univ. de Almería, Almería, Spain

d Grupo de Investigación en Biología de la Conservación, Fac. de Ciencias, Univ. de Extremadura, Badajoz, Spain

e Ecología en el Antropoceno, Unidad Asociada CSIC-UEx, Fac. de Ciencias, Univ. de Extremadura, Badajoz, Spain

* Corresponding author.

E-mail address: cdacruz@unex.es (C. De la Cruz).

1 juliana@unex.es (J. Valencia).

2 moexposit@gmail.com (M. Expósito-Granados).

3 elesolis@unex.es (E. Solís).

4 olgamjg@gmail.com (O. Jiménez).

5 susalarcos@hotmail.com (S. Alarcos).

6 pipesg@yahoo.es (J. M. Abad-Gómez).

7 chusagbm@hotmail.com (M. J. García-Baquero).

8 jorgesgutierrez@unex.es (J. S. Gutiérrez).

Abstract:

Renesting is an important strategy employed by many bird species to compensate for nest failure. However, although replacement clutches may increase an individual's annual reproductive success, they impose substantial energetic and fitness costs. In some cooperatively breeding species, helpers lighten breeders' workloads thereby facilitating a second clutch within a season or increasing their survival prospects. Alternatively, renesting may increase the chances of having help in replacement clutches as some individuals that have lost their own clutch could redirect their parental effort to another nest. Here we used a 20-year dataset of a facultative cooperative breeder, the Iberian magpie, *Cyanopica cooki*, to investigate how helping and renesting behaviours combine to affect reproductive output. After controlling for clutch size and laying date, we show that helpers had a positive effect on the reproductive success of pairs, particularly in replacement clutches. Indeed, our study revealed that replacement clutches were much more common than previously thought (observed in three-quarters of the females that lost the first clutch), and that the probability of receiving help was higher in replacement clutches. As helpers increased in number over the breeding season, they could contribute to buffering the negative effects of breeding late, when environmental conditions can be more adverse, and the probability of successful independent reproduction is lower. This study indicates that species with cooperative breeding and a short lifespan can prioritize current over future reproduction by renesting at the end of the breeding season, when the benefits of having help outweigh the costs associated with deteriorating environmental conditions. We propose that renesting can be a context-dependent strategy (mediated by social and environmental factors) that may increase reproductive success in avian cooperative breeding systems.

Animals in seasonal environments time reproductive events to overlap with periods of favourable environmental conditions (Visser & Both, 2005). Notably, avian breeding schedules are synchronized with the phenology of their food supplies to meet the high energetic demands of breeding (Lack, 1968; van Noordwijk et al., 1995). If reproduction or growth takes place outside this window of optimal conditions, there are often profound fitness consequences (Burgess et al., 2018; Lack, 1968; Visser & Both, 2005). For instance, clutch size tends to be lower as the breeding season progresses (Antczak et al., 2009). This can be due to the progressive deterioration of environmental conditions and thus trophic resources ('temporality re- sources' hypothesis; Schoech, 1996; Karagicheva et al., 2016, Koenig & Walters, 2018), or to the late incorporation of the poorer-quality females that lay smaller clutches ('female quality' hypothesis; Wendeln et al., 2000; Antczak et al., 2009; Arnold et al., 2004).

Yet, despite potential phenological mismatches, re-nesting (i.e. replacement of failed clutches) is an important breeding strategy used by many bird species worldwide to compensate for nest failure (e.g. Sandercock et al., 2005; Fontaine & Martin, 2006; Arnold et al., 2010; Claassen et al. 2014). Birds could be expected always to re-nest after failure in an attempt to succeed (Wendeln et al., 2000). However, re-nesting entails extra costs (Hipfner et al., 1999): construction of a new nest in most species, additional egg production, incubation and rearing a new brood. If these costs are high, a trade-off may arise between current and future reproduction (Stearns, 1992). Furthermore, the quality and reproductive value of the fledglings in the replacement clutches may be lower than for those fledglings from first clutches because they may develop under suboptimal environmental conditions (Barba et al., 1995; Sorci et al., 1997; Verhulst & Nilsson, 2008). In temperate regions, for instance, heat stress and dehydration could negatively affect the condition of the nestlings (Salaberria et al., 2014), sometimes causing deaths (Greño et al., 2008; Rodríguez & Barba, 2016). Not surprisingly, this may have consequences for parental fitness (Amat et al., 1999; Morris et al., 2015).

Lifeshistory theory predicts that birds should adjust their reproductive effort based on the trade-off between the net benefits of current reproduction and the net costs to future reproduction and survival (Stearns, 1992). Thus, in long-lived species with a high probability of breeding in the future, individuals may skip a new breeding attempt during the current season if success probabilities are low or if the cost is high, thus saving energy and resources for a future reproductive attempt in the current or subsequent breeding seasons (Erikstad et al., 2009). In contrast, in species with a shorter lifespan, individuals are more likely to re-nest since their chances of reproducing again over the following seasons are lower (Tarwater & Arcese, 2017; Ghalambo & Martin, 2000). In cooperatively breeding species, however, the scenario can be different because parental care is shared by breeders and helpers (Brown, 1987). The presence of helpers may have a significant effect on reproductive success and can play an important role in the lifeshistory strategy of breeders, often increasing their fitness (Hatchwell et al., 2004; Canestrari et al., 2008; Cusick et al., 2018, Downing et al., 2020). Helpers can increase the total contribution of food that is provided to nestlings, often improving fledgling quality and decreasing mortality from starvation (e.g. Brown, 1987; Curry & Grant, 1990; Hatchwell, 1999). They can also reduce the parental workload of breeders, facilitating a second clutch or increasing their survival prospects (Blackmore & Heinsohn, 2007; Crick, 1992). In addition, helpers may participate in nest vigilance and defence, decreasing nest losses from predation (Canestrari et al., 2008; Curry & Grant, 1990; Mumme, 1992). Therefore, cooperative breeding is a reproductive strategy with special characteristics that must be considered when assessing fitness costs and benefits (reviewed by Cockburn, 2008).

Cooperatively breeding species, particularly those from sub-tropical areas, tend to be longlived and lay several clutches a year (Bourne et al., 2020a; Covas et al., 2008). It has been proposed that the effect of helpers may be more evident in those species that live in harsh environments, because their participation in parental care would act as a buffer against adverse conditions (Blackmore & Heinsohn, 2007, Rubenstein & Lovette, 2007; Covas et al., 2008, Rubenstein, 2011; but see Bourne et al., 2020a and 2020b and Guindre-Parker & Rubenstein, 2018 and 2020 for a lack of buffering effect of helpers on reproductive success under conditions of extreme drought and heat) or in suboptimal territories (Magrath, 2001; Capilla-Lasheras, 2020). Likewise, in many temperate regions, environmental conditions at the end of the breeding season are characterized by high temperatures and droughts (Moreno, 1998; García & Arroyo, 2001; Salaberria et al., 2014). Under these conditions, the effect of helpers may be more beneficial since they may act as a buffer against the scarcity of resources (Covas et al., 2008) and dry conditions (Capilla-Lasheras et al. 2021).

Several studies (Blackmore & Heinsohn, 2007; Crick, 1992; Hatchwell & Russell, 1996) have examined the interactive effects of cooperative breeding and re-nesting, all of which have emphasised the role of the ‘load-lightening’ hypothesis, i.e. helpers lighten breeder workloads and the energy that is saved can be allocated to other reproductive attempts. Alternatively, re-nesting could be favoured by the increased chances of having helpers in replacement clutches, as some individuals that have lost their own clutch can redirect their parental effort to another nest. Seasonally changing abiotic (including weather) and biotic (including availability of helpers and food) factors could therefore trigger re-nesting behaviour. To our knowledge, however, there are no longitudinal studies that address these two hypotheses in avian cooperative breeding systems.

Here, we used 20 years of data on the facultative cooperatively breeding Iberian magpie, *Cyanopica cooki*, to investigate associations between reproductive output, re-nesting and cooperative breeding. This species inhabits the Mediterranean region (Del Hoyo et al., 2009) and thus experiences marked environmental differences between the beginning and the end of the reproductive period, the latter being much drier and warmer (García & Arroyo, 2001; Salaberria et al., 2014). For instance, ambient temperature and heat exposure negatively influenced the body condition of spotless starling, *Sturnus unicolor*, nestlings from second (but not first) broods in central Spain (Salaberria et al., 2014). This indicates that high summer temperatures can reduce nestling fitness in this and other arid and semiarid regions.

Specifically, we set out three main objectives: (1) to determine the occurrence of re-nesting in Iberian magpies, which has not yet been reported in the literature (De la Cruz et al., 1990; Muñoz-Pulido et al., 1990; Valencia et al., 2000, 2002); (2) to test whether first and replacement clutches have different probabilities of receiving help throughout the season; and (3) to determine the factors (including laying date, clutch type, mother's age or presence/absence of helpers) that influence clutch size and reproductive success (i.e. number of 14-day-old nestlings). In doing so, we investigated the interacting effect of helping and re-nesting behaviours and evaluated whether helpers could act as a buffer against the effects of late breeding. We predicted that replacement clutches, occurring later in the season under suboptimal environmental conditions, would be less successful than first clutches. However, this trend could be reversed or compensated for if the presence of helpers is more likely in replacement than first clutches (as individuals that have lost their own clutch could redirect their parental effort to another nest) and contribute to improved probability of a successful outcome at the nest.

METHODS

Ethical Note

All procedures followed ASAB/ABS guidelines and Spanish regulation for animal behavioural research and were approved by the Ethics Committee of the University of Extremadura and the Government of Extremadura (last released licence: CN0014/18/AAN). We used 2 × 2 m wire cages with two funnel-shaped entrances and a removable roof to capture birds for marking and measuring purposes. From March to July, we left the cages in the field with the top open and we frequently put food inside so that the birds could enter and feed at will. To capture birds, we closed the top so that the birds could enter through the entrances but could not find the exit. Closed cages were observed continuously. Upon capture, birds were weighed, measured, ringed and released after a few minutes at the same location. This procedure has been employed at the study site since 1992 and birds have never been harmed. Often, they returned to the cage on the same day to resume feeding. We monitored nests every 2 days. We also observed them from 30e40 m using telescopes or video-cameras.

Study Area and Population

The Iberian magpie is a medium-sized (ca. 70 g) corvid endemic to the Iberian Peninsula. It is a colonial, cooperatively breeding bird that is typically classified as a single-brooded species (Valencia et al., 2000, 2002). Yet some pairs lay replacement clutches when nests fail (De la Cruz et al., 1990 and this study). Although in the study area we have observed long-lived individuals (up to 15 years old), average lifespan is only 2.00 ± 1.40 years and annual survival rate is about 50% (N = 236; De la Cruz, n.d.). In our study area, colonies occupy an extent of about 30-50 ha and are made up of about 20 pairs that breed in loose groups (1-5 nests/ha; De la Cruz, n.d.).

The breeding season extends from late March to mid-July (Valencia et al., 2002), so first clutches typically occur during April and the replacements during May and June, depending on when the first clutch failed (see Fig. 1). Approximately half of the breeding pairs with nestlings have helpers at the nest (Valencia et al., 2003), and these can be both yearling and older males (Valencia et al., 2003). There are two types of helpers. ‘First option helpers’ are typically yearling males of the previous breeding season who help their parents. If breeding fails and parents have a replacement clutch, they usually continue helping at this nest. ‘Second option helpers’, on the other hand, are typically males that have lost their own clutch and redirect their parental effort to another nest, generally the nest of a neighbour not far from the original nest (De la Cruz et al., 2019).

This study was conducted between 1995 and 2014 in an oak, *Quercus ilex*, forest partially converted to pasture (approximately 200 ha) in western Extremadura (Spain); that is, the middle of this species’ distribution area (Del Hoyo et al., 2009). The climate is typically Mediterranean, with cold and rainy winters and warm and extremely dry summers (average maximum temperature exceeds 35 °C and little rainfalls from late May to late September). The first half of the breeding season, when nestlings from the first clutches typically develop, coincides with milder conditions, while in the second half of the breeding season, when most of the nestlings from replacement clutches develop, environmental conditions are harsher (Pizarro, 2020; see Fig. 1).

Data Collection

Each year we surveyed one to three breeding colonies, with 17.80 ± 4.70 (mean \pm SD) breeding pairs per colony (45 colonies throughout the study period). In total, we monitored 803 breeding pairs and 1275 breeding attempts. Since 1992, Iberian magpies in this population have been captured and marked using a unique combination of metal and coloured plastic rings (2670 adults and 2128 nestlings), allowing us to identify 87% of the population's individuals each breeding season (see Valencia et al., 2006 for details). At the beginning of the breeding season, the study area was prospected to locate nests within the colonies. Every nest was either directly observed or video recorded to identify breeder and helper individuals. Helper contribution is rare during the incubation phase, so when a bird was repeatedly observed feeding a female at the nest it was identified as the breeding male. On the other hand, birds observed occasionally at the nest during this phase or those that were only present during the brooding phase were considered helpers. An individual helper may assist more than one nest within and across breeding seasons, but never two nests at once (Valencia et al., 2003).

We checked nests every 2 days to record the laying date of the first egg (laying date was standardized: day 1 $\frac{1}{4}$ 1 March) and then continued to check them every other day until the clutch was complete. We resumed visits 2 days before the estimated hatching date, i.e. 21 days after the first egg was laid (De la Cruz & Valencia, 2016). Whenever possible, the nest was monitored again every day to record the exact hatching date and overall success. During the nestling period, nests were visited every other day and observed for 1 h to record the presence of helpers at the nest.

We used two different datasets for the analyses. To estimate the frequency of the replacement clutches we used a 'full' dataset including all breeding data. This allowed us to estimate the number of first clutches and the percentage of pairs that, after failing their first attempt, laid one or more replacement clutches, although occasionally a first clutch failed before we could identify the corresponding pair. New nests that (1) we located at least 11 days after the loss of such clutches (minimal interlaying period mean: 10.57 ± 8.03 days, $N = 48$ clutches; De la Cruz, n.d.), (2) were built after a period of several days in which no other laying occurred (other than unequivocally verified replacement clutches), and (3) belonged to a pair that had not been identified previously, were considered as replacement clutches. However, to calculate and compare the different reproductive parameters between the first and replacement clutches and the effect of the help, we used a 'reduced' dataset, in which we excluded those clutches without an unequivocal indication of replacement (identification of the pairs in both breeding events). Therefore, the sample sizes vary in the different analyses.

Two age classes (first year or older, thereafter 'yearlings' or 'adults' respectively) were distinguished on the basis of plumage (De la Cruz et al., 1992). Finally, reproductive success (number of fledglings) was estimated as brood size when nestlings reached 14 days old (nestlings leave the nest at 16-17 days old but checking nests after 14 days old is dangerous because it may make nestlings jump out of the nests when disturbed). We thus assumed the number of nestlings present on day 14 was equivalent to the number of young fledged from a given nest.

Data Analyses

To assess our hypotheses, we constructed a set of linear and generalized mixed models (LMM and GLMM) using the R environment version 4.0.2 (R Core Team, 2020).

To test whether first and replacement clutches have different probabilities of receiving help throughout the season, we fitted a GLMM with a binomial error distribution and presence/absence of help as the response variable using the package ‘lme4’ (Bates et al. 2015). Clutch type (two-level factor: first versus replacement) and mother's age (two-level factor: yearling versus adult) were included as fixed factors (note that adult females might have first option helpers, i.e. offspring from the previous breeding season, and second option helpers, but yearling females can only have second option helpers). Laying date (days after 1 March) was included as a covariate. Day was also included as a second-order polynomial to allow for potential nonlinear patterns across the breeding season. However, owing to high collinearity in the models (variance inflation factor values > 10), we retained the linear effect of date, which yielded lower variance inflation factor values and a lower Akaike information criterion corrected for small sample sizes (AICc) than models considering the quadratic effect alone. Year and mother's identity were included as random factors to account for the autocorrelation structure. Temperature and precipitation were not included in the models because they were tightly correlated with Julian date ($r = 0.647$ and $r = 0.527$, respectively; see also Fig. 1), thus avoiding collinearity problems between these factors.

When clutch order affected the probability of a nest being helped, we conducted multiple Tukey post hoc comparisons using the package ‘multcomp’ (Hothorn et al., 2008) to determine which clutches had the lowest and the highest probability of being helped.

To determine the factors that influence clutch size, we first fitted a Poisson GLMM with the number of eggs as the response variable, clutch type and mother's age as fixed factors and laying date as a covariate. Again, day was included as covariate and year and mother's identity were included as random factors. In this model we did not include the interaction between help and clutch type, as helpercontribution is rare during incubation (see above). This global model was underdispersed (residual deviance = 58.563, $df = 526$) and a simulation of scaled model residuals using the R package ‘DHARMA’ (Hartig, 2020) indicated significant deviation of model residuals (500 model simulations; KolmogoroveSmirnov test: $D = 0.255$, $P < 0.001$). Thus, we fitted an LMM with the number of eggs (log) as the response variable. This model fitted the data adequately (see below).

To determine the factors that affect reproductive success, we fitted a Poisson GLMM with the number of nestlings as the response variable, presence/absence of help and clutch type as fixed factors and date as covariate. We also included the interaction between presence/absence of help and clutch type to specifically test whether the effect of helping on reproductive success differed between first and second clutches and, thus, whether the effect varied throughout the breeding season. Again, we included year and mother's identity as random factors.

Finally, to assess whether helper number varied throughout the season, we fitted a Poisson GLMM with the number of helpers as the response variable, laying date as covariate, and year and mother's identity as random factors.

In all the analyses we subjected the chosen predictor variables to variance inflation factor analyses to assess collinearity in the full models and retained variables that had variance inflation factor values < 4 (Dormann et al., 2013). As noted earlier, we only had to remove day2 from the global model. Then, we compared alternative models, based on their AICc, using packages ‘lme4’ (Bates et al., 2015) and ‘MuMIn’ (Barton, 2020). Models within 2 units of DAICc were considered equally good. We calculated Akaike weights (w_i) for the 95% confidence set of models to determine the weight of evidence in favour of each model. When no single model was clearly superior to the

others in a set of models (model with $w_i < 0.9$, i.e. in mixed models explaining the likelihood of receiving help in first and replacement clutches), we additionally used model averaging (Burnham & Anderson, 2002). We used the entire set of plausible models (95% confidence set of best-ranked models) to calculate model-averaged estimates for variables included in the confidence set of models and their unconditional standard errors. This reduces bias effects on regression coefficient estimates in the selected subsets (Burnham & Anderson, 2002). Next, we explored model residuals using a simulation-based approach to create readily interpretable scaled (quantile) residuals for the fitted GLMM (Hartig, 2020).

Results were qualitatively similar to those presented here when the effect of help was tested as a count variable (i.e. number of helpers) instead of a binary variable (Appendix Tables A2 and A3). Model averaging and best-ranked regression models generated similar conclusions (Appendix Tables A1-A3).

RESULTS

Renesting and Helping Occurrence

Overall, 70.73% of birds lost their first clutch and, of these, 75.42% attempted a replacement clutch. The percentage of pairs attempting a second replacement clutch was low (11.59%) and these had a relatively low probability of success (16.21%). A few pairs that failed on their third or fourth attempt ($N = 8$) laid another replacement clutch, but these were always unsuccessful.

When considering all the first and replacement clutches that hatched ($N = 606$), 28.84% had at least one helper. The best-supported model ($w_i = 0.54$) explaining the likelihood of receiving help in first and replacement clutches only included clutch type. Both model selection and model averaging showed that breeding pairs were more likely to receive help in first replacement clutches than in first clutches (Table 1, Figs. 2 and 3; for the 95% confidence set of best-ranked models see Appendix Table A1).

The higher probability of helping behaviour in replacement clutches is probably due to the number of helpers (first and second option helpers) increasing throughout the breeding season (Poisson GLMM with number of helpers at the nest as response and laying date as predictor: $Z = 4.124$, $P < 0.0001$; Fig. 3). Finally, we found no significant effect of laying date and age, albeit adult females showed a marginally higher probability of receiving help (Table 1).

Clutch Size and Reproductive Success

The 95% confidence set of best-ranked models explaining variation in clutch size consisted of a single model ($w_i = 0.77$) including mother's age and laying date. On average, adult females had larger clutch sizes than yearling ones (Table 2). Moreover, clutch size decreased as the breeding season progressed in both first and replacement clutches (Table 2, Fig. 4).

Overall, reproductive success was relatively low with 27.51% of successful clutches ($N = 1275$), and only 1.08 ± 1.90 nestlings per nest ($N = 1005$). When we considered only successful clutches (those with at least one 14-day-old nestling, $N = 511$), the number of nestlings increased to 2.13 ± 2.21 . Of the total number of successful clutches ($N = 350$), 32.87% correspond to replacement clutches, which produced 23.15% ($N = 193$) of the total fledglings. A single model stood out as being the best model ($w_i = 1.00$, Table 2), so we did not perform model averaging. This top-ranked

model showed that reproductive success increased significantly with the presence of help and decreased with laying date (Table 2). Moreover, the interaction between help and clutch type was significant and positive, indicating that the effect of help was more beneficial in replacement clutches (Table 2). Reproductive success decreased throughout the breeding season, although significantly so only in the absence of help (Fig. 5, Table 2).

DISCUSSION

Our study reveals that replacement clutches in a facultative cooperative breeder, the Iberian magpie, are much more common than previously thought (De la Cruz et al., 1990, Muñoz-Pulido et al., 1990; Valencia et al., 2000, 2002). Indeed, reneating in this study was an important strategy in the Iberian magpie accounting for nearly a third of annual breeding success and around a quarter of total nestlings produced. The importance of reneating in this species can be attributed to two main factors. First, the low residual reproductive value of this species (Valencia et al., 2006; De la Cruz & Valencia, 2016), as a result of its relatively low annual survival rate and short lifespan, means that any further breeding attempt in the current season may increase fitness even if costs are high. Second, the greater probability of having helpers at the nest in replacement clutches can overcome these costs and increase the chances of success. Notably, helpers can provide different sorts of benefits to breeders. (1) Helpers could compensate for the lower size of replacement clutches. (2) They could avoid high rates of predation (Valencia et al., 2006). (3) They contribute to the parental workload, particularly at the end of the breeding season, potentially reducing the detrimental effects of heat exposure and dehydration (Greño et al., 2008; Salaberria et al., 2014; Rodríguez & Barba, 2016). (4) They could also reduce deaths from starvation when resources are scarce and nestlings receive less food (De la Cruz et al., 2019; Garcia-Navas & Sanz, 2011). This agrees with the ‘hard life’ hypothesis, which proposes that in some cooperative breeding species the effects of helpers are detectable mostly under unfavourable conditions (Blackmore & Heinsohn, 2007; Covas et al., 2008; Magrath, 2001). Although we did not explicitly test the buffering effect of helpers against adverse environmental conditions (temperature and precipitation were tightly correlated with date), our longitudinal study indicates that helpers can buffer the effects of late breeding, as they had a more positive effect on the success of replacement clutches than on that of first clutches.

Renesting, Clutch Size and Helping

Clutch sizes of many temperate bird species decrease as the breeding season progresses and late clutches (including replacement ones) tend to be smaller than earlier clutches (Antczak et al., 2009). Two nonexclusive hypotheses have been proposed to explain this decline (Koenig & Walters, 2018). First, the ‘temporality resources’ hypothesis, advocates the progressive deterioration of environmental conditions and, consequently, the decreased availability of food, and thus smaller clutch sizes, as the breeding season advances (Schoech, 1996; Karagicheva et al., 2016). Second, the ‘female quality’ hypothesis proposes that females that begin reproduction later will be of lower quality, thereby laying smaller clutches (Wendeln et al., 2000; Antczak et al., 2009; Arnold et al., 2004). In the Iberian magpie, we also observed a notable decrease in clutch size as the breeding season progressed, in both first and replacement clutches. The first clutches laid by yearling females were, on average,

about half an egg smaller than those laid by adult females. However, yearling females laid only 3 days later than adult females on average. Smaller replacement clutches were also not explained by age differences because the laying date of replacement clutches was primarily determined by the date of the loss of the first clutch. Therefore, our data seem to support the ‘temporality resources’ hypothesis, although we cannot rule out that female age may have a minimal influence. The apparent differences in clutch size between first (6.33 ± 0.82 , $N = 339$) and replacement clutches (5.67 ± 0.83 ; $N = 139$) in Iberian magpie are mostly likely to be an artefact of later laying, as demonstrated in other bird species (Arnold, 1993; Karagicheva et al., 2016).

In this study, we found no effect of help on clutch size. In other cooperatively breeding species, females that receive help appear to modulate their investment in their current clutch by decreasing egg size (Canestrari et al., 2011, Paquet et al., 2013, but see Langmore et al. 2016 and Fortuna et al., 2021) or increasing clutch size (Woxvold & Magrath, 2005; Koenig et al., 2009; Savage et al., 2013, but see ; Fortuna et al., 2021). Most of this evidence, however, comes from studies on territorial species (individuals living in flocks of relatives and within a defined territory), where the presence of helpers can be predictable even before the start of reproduction. Thus, females might adjust their investment in clutches based on the potential presence of helpers in the flock (Canestrari et al., 2011; Paquet et al., 2013; Santos & Macedo, 2011). These features do not apply to the Iberian magpie, as it is a colonial species and the presence of helpers is not always predictable, depending largely on the fate of nearby nests (see below).

As expected, adult females had more help than yearlings. Unlike yearlings, adult females could have first option helpers (mainly offspring from the previous breeding season) in both the first and replacement clutches, while yearling females could only be aided by second option helpers if a neighbour failed to breed. In addition, the probability of helping behaviour was higher in replacement (delayed) than in first clutches (35% versus 22%), most likely because the number of helpers increases throughout the breeding season (see also De la Cruz et al., 2019).

Renesting, Reproductive Success and Helping

Life history theory predicts a trade-off between current and future reproduction (Tarwater & Arcese, 2017; Ghalambo & Martin, 2000). The resolution of this trade-off depends on life history strategies. Females in long-lived species may utilize strategies other than or additional to renesting, to save energy and resources for a future reproductive attempt. In contrast, short-lived species invest more in current reproduction (for example, by laying an additional clutch) even though this may lead to a decrease in adult survival or in the probability of reproductive success in the future (Tarwater & Arcese, 2017).

Many cooperatively breeding species have relatively long life- spans and low annual mortality rates (e.g. Arnold & Owens, 1998; Hammers et al., 2019). However, this does not apply to the Iberian magpie (see above). Renesting could, therefore, be an advantageous strategy in this (and other) species with low residual reproductive value (Valencia et al., 2006; De la Cruz & Valencia, 2016). Iberian magpies appear to prioritize current over future reproduction, despite the potentially high costs associated with late breeding (Atczak et al., 2009; Suárez et al. 2005), when environmental conditions are generally more adverse (also see Verhulst & Nilsson, 2008). Our study area is characterized by high temperatures and little rain from late May onwards (Valencia et al., 2000). However, despite the extra costs of renesting and the suboptimal

environmental conditions when doing so, the decision to reneest could be favoured by the higher probability of receiving help: as the breeding season progresses and nests are lost, the number of potential helpers (specifically second option helpers) in the colony increases. Breeders laying a replacement clutch are more likely to have both primary and secondary option helpers (De la Cruz et al., 2019) and thus be successful in breeding.

In many cooperatively breeding species, there is evidence that the presence of helpers increases the number of fledglings produced in a reproductive attempt (Canestrari et al., 2008; Rubenstein, 2011; Guindre-Parker & Rubenstein, 2018; Bourne et al. 2020b; Downing et al., 2020). Helpers can increase the amount of food that nestlings receive, preventing their death by starvation (Hatchwell et al., 2004; Canestrari et al., 2008; Cusick et al., 2018). Additionally, by actively participating in the defence of the nests, they can reduce the incidence of predation (Canestrari et al., 2008; Rubenstein, 2016). In the Iberian magpie, helpers have a significant effect on the survival of nestlings, partly because they reduce the incidence of nest predation, the main cause of nest loss in our population (De la Cruz et al., 1990; Valencia et al., 2006). Helpers' contributions to feeding nestlings adds to parental effort (De la Cruz et al., 2019; Valencia et al., 2006), reducing the incidence of nestling death by starvation (De la Cruz & Valencia, 2016). Moreover, parents with helpers make a greater parental effort than when they lack help, further increasing the amount of food the young receive in the presence of helpers (Valencia et al., 2006, Carranza et al., 2008; see also Guindre-Parker & Rubenstein, 2018 for a similar behaviour in the superb starling, *Lamprolornis superbus*). Our results show that, in the presence of helpers, the number of failed nests was similar in first and replacement clutches and reproductive success did not decrease as the season progressed. However, this was not the case in the absence of help (Fig. 5c). In this study, we did not find that helpers lightened breeders' work-loads or that they facilitated reneesting. On the contrary, our results suggest that breeders reneested because they had a high chance of having helpers, and helpers increased their chances of reproductive success.

In conclusion, replacement clutches represent an important and frequent strategy in the life history of the Iberian magpie. They account for one-third of the species' annual reproductive success even though they occur when environmental conditions are generally suboptimal. However, the negative effects of late breeding can be largely offset by the presence of helpers. A similar buffering effect has been proposed for other cooperatively breeding species under adverse conditions (Magrath, 2001; Covas et al., 2008). Our study supports the notion that cooperatively breeding species with low residual reproductive value also prioritize current over future reproduction. Lastly, it also suggests that reneesting is a context-dependent strategy (i.e. mediated by seasonally changing social and environmental factors such as the availability of helpers and food) that can increase reproductive success in some avian cooperative breeding systems. Our long-term study adds substantially to previous knowledge of the benefits of help in cooperative birds breeding in highly variable environments, as evidence supporting the notion that helpers increase the reproductive output of breeders is inconsistent and strongly affected by study design (Downing et al., 2020).

Author Contributions

Carlos De la Cruz: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Resources, Supervision Writing. Juliana Valencia: Funding acquisition, Investigation. Mónica Expósito-Granados: Investigation. Elena Solís:

Funding acquisition, Investigation. Olga Jiménez: Investigation. Susana Alarcos: Investigation. José María Abad-Gómez: Investigation. María Jesús García-Baquero: Investigation. Jorge S. Gutiérrez: Conceptualization, Formal análisis, Software, Supervisión, Writing.

Acknowledgments

We thank M.A. Pitarch for permission and facilities and all students (too many to be cited here) from the University of Extremadura who collaborated at different stages of the fieldwork. This study was supported by the Government of Extremadura, co-financed by FEDER Funds through the projects IPR99A020, 2PR02A080, PRI09A057 and PRI09A057 to C.C. and funds for research group GR15117 to M.E-G. and O.J. and J.V. was supported by a postdoctoral grant from Ministerio de Educación y Ciencia of Spain and CSIC grant (JAEdoc); E.S. was supported by a post-graduate research grant from Junta de Extremadura; and J.S.G. was supported by the Government of Extremadura (grant no. TA18001). We also thank Pablo Capilla-Lasheras and two anonymous referees for comments that helped improve the manuscript.

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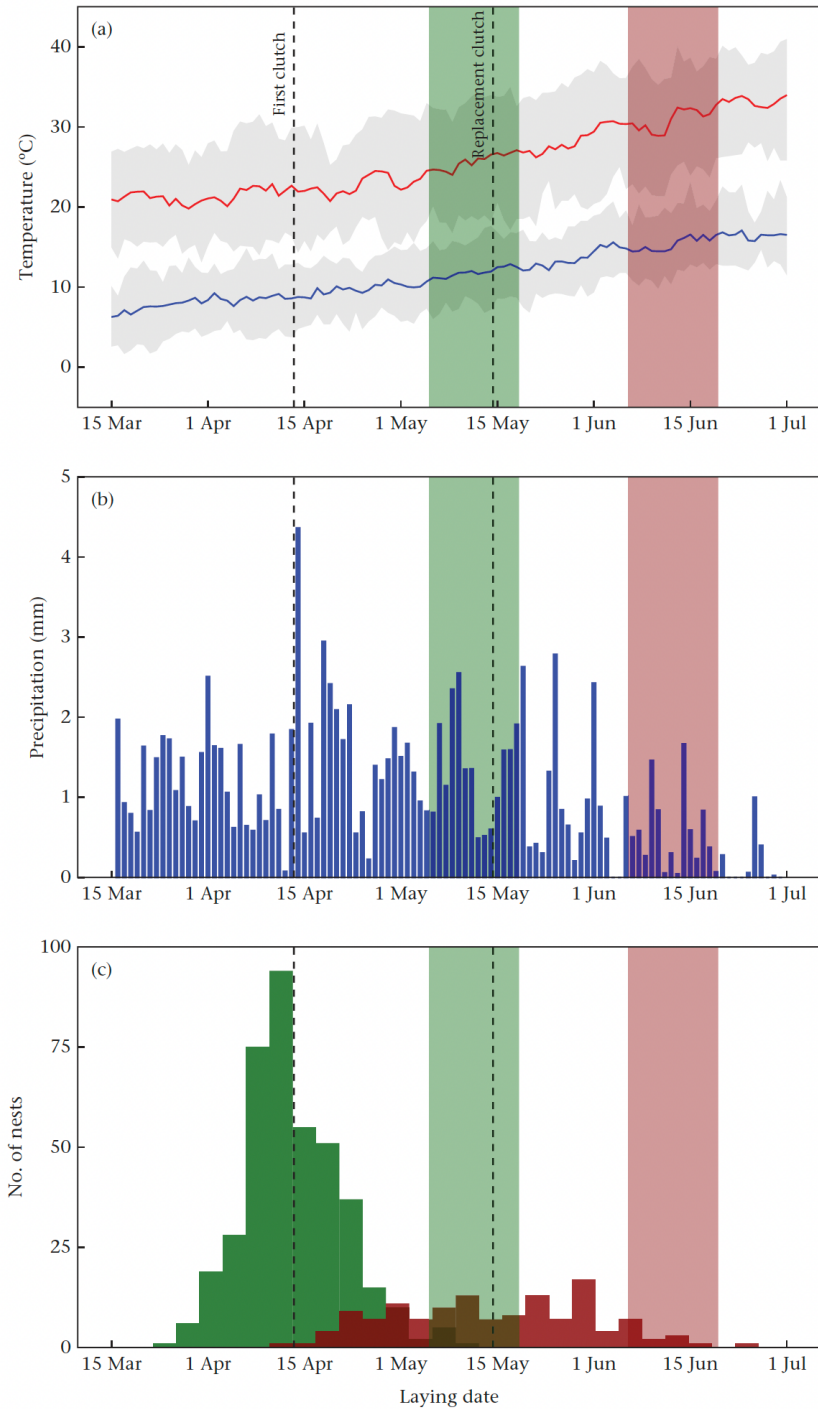


Figure 1. (a) Maximum (red) and minimum (blue) temperatures averaged across each day during the 20 years of the study (1995–2014; means \pm 95% quartiles). (b) Averaged daily precipitation during the study period. Temperature and precipitation data were recorded at a local meteorological observatory ca. 15 km from the study area. Data were extracted using the package ‘climaemet’ (Pizarro, 2020). (c) Histogram showing the frequency of first clutches (green bars) and replacement clutches (red bars) over the study period. Vertical dashed lines represent historical means for the onset of first and replacement clutches and shaded areas represent the corresponding nestling periods (green and red, respectively).

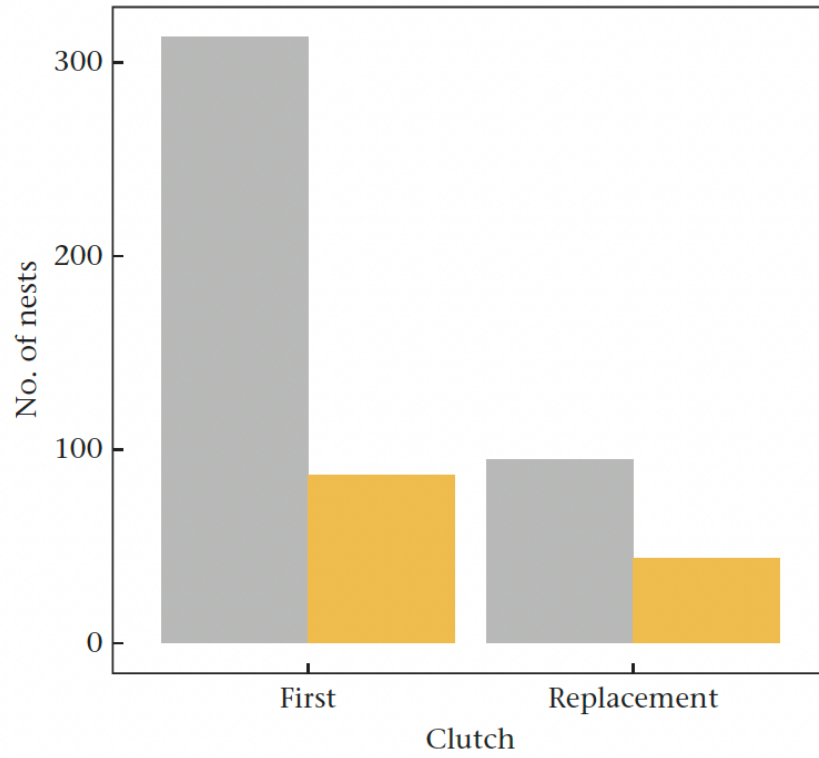


Figure 2. Occurrence of helping behaviour in first and replacement clutches: without help (grey bars) and with help (orange bars).

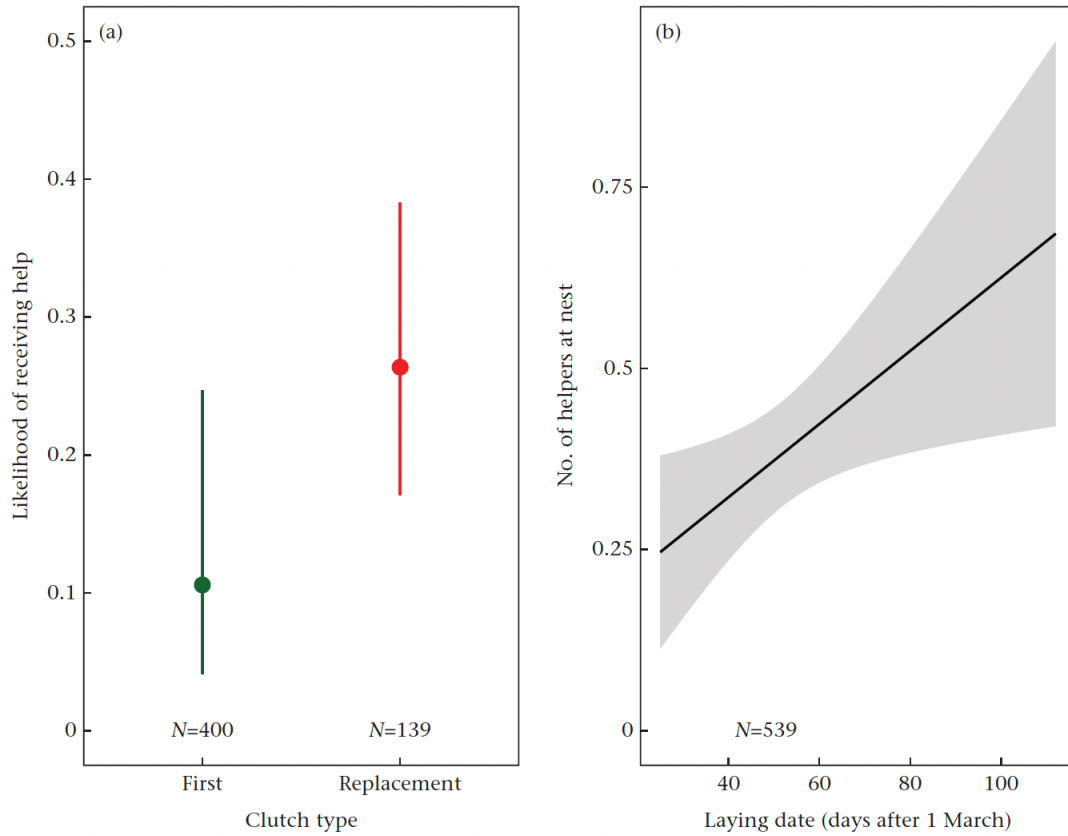


Figure 3. (a) Predicted likelihood of receiving help in first and replacement clutches when accounting for laying date, clutch type and female age. Dots are predicted estimates from the GLMM and vertical lines are the 95% confidence intervals (CI) based on fixed-effect uncertainty. (b) Relationship between the number of helpers at the nest and laying date. The grey shaded area represents a 95% CI of a fitted linear model of the number of helpers against laying date.

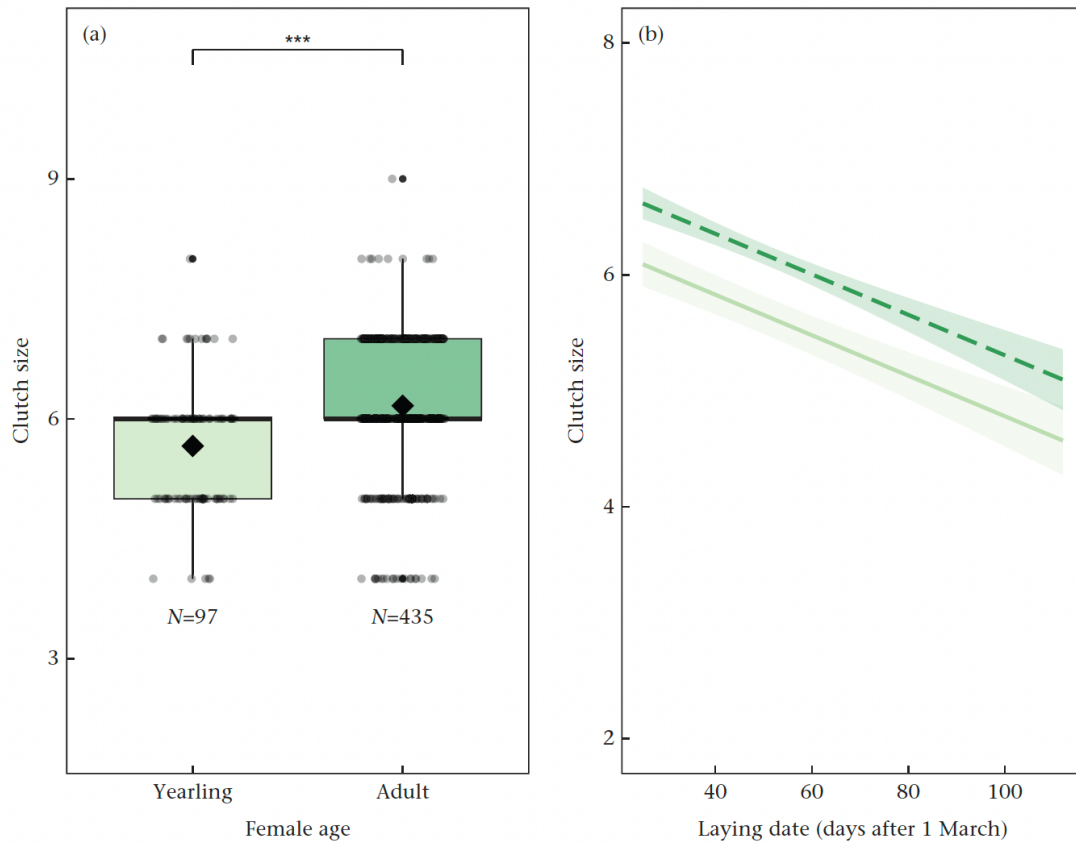


Figure 4. (a) Clutch size for yearling and adult females. Box plots give medians (horizontal line within plot, overlapping with upper and lower interquartile ranges, respectively), means (diamond), interquartile ranges (box) and 1.5 times the interquartile range (whiskers); circles represent individual data points. *** $P < 0.001$. (b) Model predictions for clutch size as a function of female age and laying date. Green shaded areas represent 95% CI for clutch size in adult females (dark shading and dashed line) and yearling females (light shading and solid line). For clarity, predictions of clutch size (i.e. the untransformed values) were obtained by taking the antilogarithm of log-transformed values (see Methods for details).

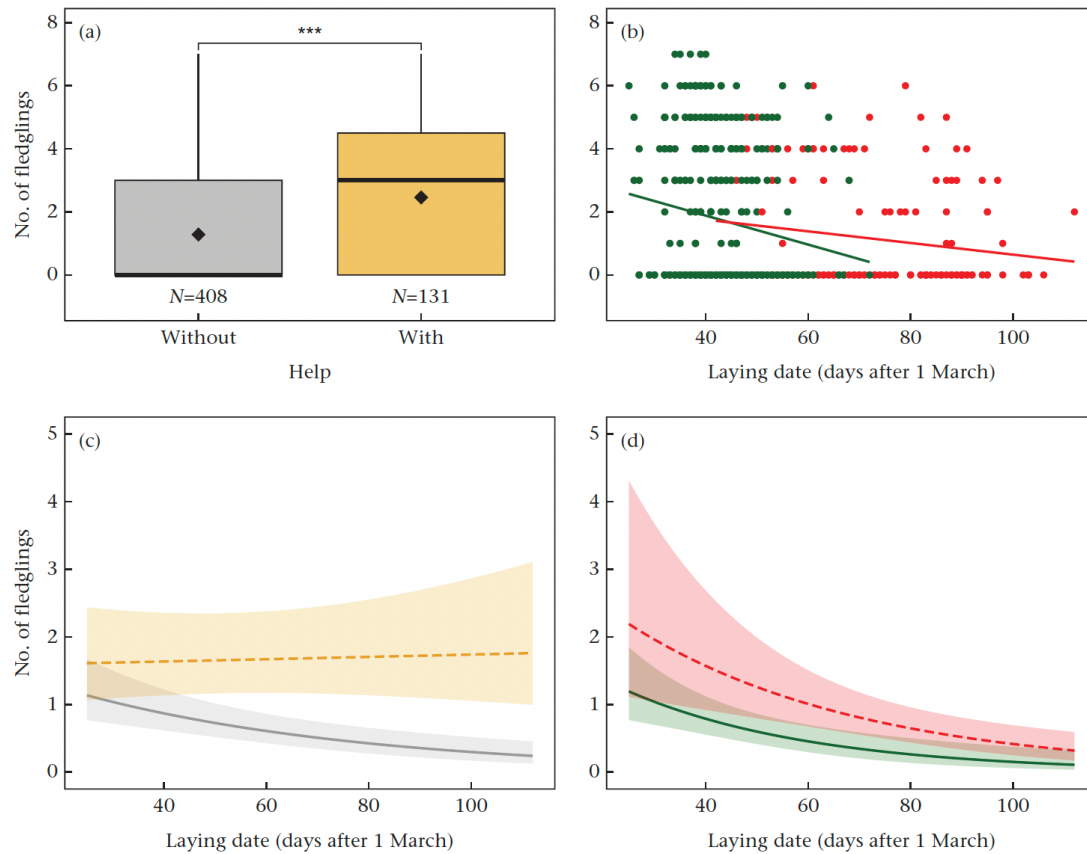


Figure 5. (a) Reproductive success (number of 14-day-old nestlings) from clutches without and with help. Box plots give medians (horizontal line within plot, overlapping with lower interquartile range for clutches without help), means (diamond), interquartile ranges (box) and 1.5 times the interquartile range (whiskers). $***P < 0.001$. (b) Reproductive success from first (green line and dots) and replacement (red line and dots) clutches throughout the breeding season. (c) Model predictions showing the reproductive success as a function of helping behaviour and laying date. The orange dashed line and orange shaded area represent predictions and 95% CI, respectively, for clutch size in females with help; whereas the grey solid line and grey shaded area represent predictions and 95% CI, respectively, for clutch size in females without help. (d) Model predictions showing the reproductive success for first clutches (green solid line and green shaded areas represent predictions and 95% CI, respectively) and replacement clutches (red dashed line and red shaded areas represent predictions and 95% CI, respectively) throughout the breeding season.

Table 1

Model-averaged values from mixed models explaining the likelihood of receiving help in first and replacement clutches

Model	Estimate	SE	Z	P
Intercept	-1.449	0.518	2.796	0.005
Laying date	-0.010	0.015	0.673	0.501
Clutch type	0.853	0.418	2.038	0.041
Random effects	Variance	SD		
Individual	0.965	0.983		
Year	0.289	0.537		

Reference level for clutch type is 'first' and for age 'yearling'. See Methods for details. Significant explanatory variable is in bold.

Table 2

Best-ranked mixed models ($\Delta AIC_c > 2$) explaining variation in clutch size and reproductive success

Model	Estimate	SE	t/Z	P
Clutch size (LMM)				
Intercept	1.871	2.293e-2	81.583	<0.0001
Mother's age	8.810e-02	1.583e-02	5.564	<0.0001
Laying date	-2.966e-03	3.567e-04	-8.316	<0.0001
Random effects	Variance	SD		
Individual	2.2624e-3	0.0476		
Year	1.749e-7	0.0008		
Reproductive success (GLMM)				
Intercept	0.892	0.280	3.185	0.001
Laying date	-0.027	0.005	-5.285	<0.0001
Helping	0.576	0.112	5.167	<0.0001
Clutch type	0.369	0.207	1.781	0.075
Help*clutch type	0.981	0.225	4.369	<0.0001
Random effects	Variance	SD		
Individual	0.788	0.888		
Year	0.448	0.669		

Reference level for mother's age is 'yearling', for helping 'yes' and for clutch type 'first'. See Methods for details. Significant explanatory variables are in bold.

Appendix

Table A1

The 95% confidence set of best-ranked models (with a cumulative Akaike weight, $\text{acc } w_i, \leq 0.95$) explaining the likelihood of receiving help in first and replacement clutches

Candidate models	<i>df</i>	logLik	AIC _c	ΔAIC_c	w_i	acc w_i
1. Clutch type	4	-285.272	578.600	0.000	0.537	0.537
2. Clutch type + laying date	5	-284.688	579.500	0.870	0.348	0.885
3. Laying date	4	-287.443	583.0	4.340	0.061	0.946

Table A2

Model-averaged values from mixed models explaining the likelihood of receiving help in first and replacement clutches

Model	Estimate	SE	<i>Z</i>	<i>P</i>
Intercept	-1.449	0.518	2.796	0.005
Laying date	-0.010	0.015	0.673	0.501
Clutch type	0.853	0.418	2.038	0.041
Random effects	Variance	SD		
Individual	0.965	0.983		
Year	0.289	0.537		

Reference level for clutch type is 'first' and for age 'yearling'. Unlike results from models shown in [Table 1](#), helping was entered as a count variable (no. of helpers); again, this predictor variable was not in the confidence set of models and thus its model-averaged estimates were not calculated. Significant explanatory variable is in bold.