

## **Maternal allocation in eggs when counting on helpers in a cooperatively breeding bird**

Juliana Valencia, Concha Mateos, Carlos de la Cruz, Juan Carranza

### **Abstract**

For cooperatively breeding birds, it has been proposed that breeders should reduce their investment in eggs when they count on helpers, because this can be compensated for by helpers provisioning of nestlings. Data from some species have supported this prediction, but this is not the case in others. It has also been proposed that mothers should not reduce but rather increase investment if the presence of helpers enhances the reproductive value of offspring, a pattern that might also influence egg production as long as helpers are predictable for laying females. Here, we studied maternal expenditure in eggs and clutches in the Iberian magpie, to see whether mothers reduce their expenditure at the egg stage in the presence of helpers. Our results show that investment in clutches varied depending on the year, date in the season and age of the mother, but there were no reductions in maternal expenditure per individual egg when they counted on helpers. On the contrary, a pattern emerged in the opposite direction of more investment in eggs associated with the future presence of helpers at the nestling stage. Our data suggest that the predictability of helpers, along with the type of benefits accrued from the contribution of helpers, may be crucial to understanding the reaction of mothers at egg production.

Selection is expected to act on parents to maximise lifetime reproductive success by adjusting parental investment trade-offs (Pianka 1976, Stearns ). One of these trade-off is between propagule size and number (Lack 1954, Smith and Fretwell 1974, Tuomi 1990). Another one is between investment in current and future reproduction (Pianka 1976). In birds, investing in the present clutch may reduce future reproduction by affecting the survival of the parents (Santos and Nakagawa 2012). In birds, investment in egg size may affect hatching success and different traits related to offspring fitness (Krist 2011).

Current investment by mothers on egg and clutch sizes may be influenced by the quality or commitment of their mates (Reyer 1994, Houston et al. 2005). For instance, mothers may increase effort when mating with genetically superior males (differential allocation hypothesis: Burley 1986, 1988, Sheldon 2000) or may compensate effort when mating with males who can contribute more to parental care (Reyer 1994, Houston et al. 2005, Harris and Uller 2009).

Cooperative breeding birds face an additional source of variation: the presence of helpers at the nest (Brown 1978). Helpers may improve the environment of the chicks by providing them with more and/or better-quality food as well as protection from predation (Cockburn 1998). Thus, parents who count on helpers are expected to take these advantages into account and modulate their investment in the present clutch. One possible reaction of parents is to reduce their investment per individual egg because the contribution of helpers might compensate for it during chick development. Russell et al. (2007) showed that *Malurus cyaneus* females who counted on helpers laid smaller eggs with a lower nutritional content, which produced lighter chicks, compared with females without helpers. Despite such a reduction in maternal investment, compensation due to the contribution of helpers to the brood meant that the mass and survival of chicks at the

end of the nestling period were not different from broods without helpers (Dunn et al. 1995). Russell et al. (2007) proposed that this reduction in investment per egg should be a general strategy for females in cooperatively breeding species, although it may not have been detected so far in many species due to the concealed effect of helpers. A reduction in female investment in eggs in the presence of helpers has been shown for the southern lapwings *Vanellus chilensis* (Santos and Macedo 2011), the carrion crow *Corvus corone* (Canestrari et al. 2011), and the social weaver *Philetairus socius* (Paquet et al. 2013). Even for fish, Taborsky et al. (2007) showed that in *Neolamprologus pulcher*, a cichlid species with cooperative breeding, females reduced investment per individual egg as a function of the number of helpers.

Helpers may also affect total maternal investment in the clutch, not only per individual egg. Woxvold and Magrath (2005) found for apostlebirds *Struthidea cinerea* that females that counted on helpers laid larger clutches. In the acorn woodpecker *Melanerpes formicivorus*, Koenig et al. (2009) found that females laid more eggs when they counted on helpers, and suggested that adjustments per individual should be primarily at the nestling rather than at the egg stage. Especially if production costs are low compared to rearing costs, the prospect of receiving aid at rearing might lead mothers to increase the clutch size (Savage et al. 2013), and even more if expenditure per individual egg can be compensated for.

At the nestling stage, parents may also modulate their expenditure per offspring in the presence of helpers. This compensation by parents at the nestling stage in cooperative breeders was initially proposed by Emlen and Wrege (1991). Interspecific comparisons showed that this compensation at the nestling stage may be highly variable, depending on the balance of costs and benefits for the parents related to the type of contribution from helpers (Hatchwell 1999, Valencia et al. 2006, Carranza et al. 2008). In particular, for the cooperatively breeding Iberian magpie *Cyanopica cooki*, the presence of helpers has been associated with greater effort by parents in feeding the chicks, probably due to the increased reproductive value of the brood when parents count on helpers (Valencia et al. 2006, Carranza et al. 2008).

For the production of individual eggs, however, predictions might differ (reviewed by Russell and Lummaa 2009). Savage et al. (2015) modelled maternal pre-birth investment by considering two different modes by which maternal allocation per egg might benefit offspring, either substituting later investment (the 'head start' effect) or increasing the value of later investment (the 'silver spoon' effect). Their model predicted that mothers should take advantage by investing more in individual eggs, only for the silver spoon assumptions. Unfortunately, the model did not incorporate the variations in the type of benefits that helpers may provide (e.g. provisioning and anti-predatory defence) or their effects on the reproductive value of offspring, as mentioned above (Valencia et al. 2006, Carranza et al. 2008). In the absence of a formal model, we may envisage that incorporating these aspects might promote higher investment by parents on eggs when the reproductive value of offspring increases.

A further complication comes from the fact that there are two types of helpers in the Iberian magpie (Valencia et al. 2003). First option (FO) helpers are those that do not initiate their own breeding in that season and only assist others' nests. They are typically juveniles that help others before starting their own reproduction. On the other hand, second option (SO) helpers are typically adult birds that attempted their own breeding

but help others after their own nest fails. Since second option helpers only assist the nests of other birds after failure of their own breeding nests, we may assume that their presence must be unpredictable for breeding pairs at the egg laying stage. On the contrary, first option helpers may assist from the beginning of the breeding tasks, even during nest building although they mostly incorporate after hatching (Valencia et al. 2003). Therefore, we may hypothesise that breeding pairs at laying might be aware of the availability of FO helpers but this is probably not the case for SO helpers.

Here, we studied maternal investment in clutches and individual eggs in the Iberian magpie in the presence of helpers. In particular, we were interested to see whether mothers compensated their investment per egg when counting on helpers (Russell et al. 2007) or, alternatively, if they would follow the same patterns as at the nestling stage (Valencia et al. 2006), hence increasing investment when helpers are available to predictably contribute to raising the brood. We base this latter hypothesis on previous evidence that the presence of helpers reduces predation risk (Valencia et al. 2003) and hence increases the reproductive value of the clutch/brood (Carranza et al. 2008). A higher reproductive value of offspring may promote an increase in optimal maternal allocation in that season compared to other seasons throughout the mothers' reproductive lifetime. In this sense, this effect may supersede the relative costs of production and rearing (Savage et al. 2013) and to the types of maternal benefits to offspring (as considered by Savage et al. 2015), likely biasing predictions towards increasing rather than compensating for maternal allocation to individual eggs. On the other hand, as mentioned above, our study species presents two types of helpers that are not equally predictable for mothers at the laying stage, which might produce differential effects.

## Methods

We studied a population of Iberian magpie *Cyanopica cooki* in south-western Spain. The study area is 22 km north the city of Badajoz (39°03'N, 6°48'W), in the middle of the Iberian distribution of the species (Del Hoyo et al. 2009). The predominant habitat is a dehesa (open holm oak *Quercus ilex* woodland). The climate is typically Mediterranean, with dry-hot summers and mild-wet winters. Iberian magpies in this area breed between late March and early July typically producing a single brood that may be replaced in the case of failure (Valencia et al. 2000, 2002). Since 1992, Iberian magpies in this population have been captured and marked with metal and coloured plastic rings. From late March or early April onwards the study area was searched for nests at least twice weekly. Trees containing nests were marked, with the nests being inspected at least once every two days until the clutch was completed. Observations on nests were done with a telescope from a hidden position for a minimum of one hour every second day. Observations of individual nests were intensified on days just after they were found and maintained until fledging (up to three hours of continuous observation), in order to identify the members of the pair and the presence of helpers. The sex of breeders was assigned according to their behaviour, only females incubate the eggs and brood the young (see Hosono 1966 and Komeda et al. 1987 for the sister species *C. cyana*). We considered the laying date for an individual female as the date when she laid the first egg of the clutch. Eggs were individually marked as they were laid so that the addition or loss of any egg was recorded at each inspection. Note that this did not allow us to register the exact laying order because several new eggs could be found at each nest inspection. We took egg measurements during the breeding

seasons from 1995 to 1997 and resumed measurements in 2008, 2009 and 2012. There was ongoing fieldwork in intermediate years, but not egg measurements, due to prioritizing different projects and objectives. Thus, the data used in this study cover those six years.

We measured the length and width of each egg with a digital caliper to the nearest 0.1 mm. We measured a total of 221 clutches with 6.04 eggs on average (SD = 0.830). The volume of each egg was calculated from the equation  $V = 0.51 LB^2$  (Hoyt 1979), where V is egg volume (in mm<sup>3</sup>), L is egg length and B is egg width (both in mm). Some clutches may be laid by the same individual female.

Laying dates (first egg of the clutch) were computed in days with respect to the date when the first egg was laid in the colony. This could be accurately done in 210 out of the 221 clutches.

To consider the environmental conditions over the studied period, we obtained for each year data for the March mean temperature (mean March T) and winter rainfall during the three winter months before the breeding season (January, February and March). Data were obtained from the Valdesequera meteorological station located within the study area until 1997. After 1997, the Valdesequera station ceased working, so we used the data from the Villar del Rey station, 10 km northwards.

In a sub-sample of 166 clutches, two age-classes were distinguished for mother birds on the basis of plumage (Cruz et al. 1992): juveniles (birds up to one year old, presenting a partial moult, duller plumage and whitish fringes on the tail feathers) and adults (more than one year old, showing a complete moult, with rich azure-blue wings and brighter plumage).

Although helpers may assist parents before chicks hatch (Valencia et al. 2003), most helpers were observed and accurately assigned to a nest only when they provided feeding visits to the brood. This could only be done in a sub-sample of 154 nests after removing data from all those nests that did not succeed to hatching. In summary, we had in total 127 different clutches laid by 91 different mothers (29 clutches laid by juvenile mothers and 98 clutches laid by adult mothers).

Along with the effects of the presence of any helpers, we were interested in testing the potential effect of the type of helpers. Previous fieldwork has shown that both FO and SO helpers provisioned the chicks but the rate per hour was higher for FO ( $1.76 \pm 1.31$  SD, n = 718) compared to SO ( $1.37 \pm 1.08$ , n = 286;  $t = 2.06$ ;  $p < 0.001$ ; Cruz and Valencia unpubl.). There were 31 nests with FO helpers and 11 nests with SO helpers (Table 1).

**Table 1.** Number of clutches laid by juvenile and adult mothers that were assisted by helpers of one or another type, or had no helpers, in the sample of nests used in this study

Age	FO helpers	SO helpers	No helpers	Total
Juvenile	2	3	24	29
Adult	29	8	61	98
Total	31	11	85	127

### *Statistical analyses*

We analysed our data on clutch size and egg volume by using linear mixed models fitted by restricted maximum likelihood (REML). The main fixed factors in both models were the date of laying, environmental conditions (mean March T and winter rainfall), mother's age (juveniles vs adults) and the type of helpers present at the nest (FO helpers, SO helpers and no helpers). The random factor 'female identity' was included to control for non-independence between observations of the same female at different nesting attempts. Plots of fitted values against residuals were used to verify normality and homoscedasticity. We started by fitting models with all the main factors and their meaningful two-way interactions (type of helpers  $\times$  environmental conditions, type of helpers  $\times$  mother's age, type of helpers  $\times$  date of laying, environmental conditions  $\times$  date of laying and date of laying  $\times$  mother's age). Then, the full models were simplified by removing the non-significant interactions, one at a time, using backward elimination based on the p-values. However, all main factors were maintained regardless of their statistical significance, as recommended by Forstmeier and Schielzeth (2011).

When egg volume was the dependent variable, we used the nested term 'number of nests  $\times$  year' as the subjects to identify the 127 different clutches, and selected a repeated measures design to control for non-independence between egg volume within the same clutch. The chosen covariance structure for the residuals was compound symmetry. This covariance structure assumes a correlation between measurements of the same clutch, and that the correlation does not depend on the order of the observations per subject, which was appropriate in our case since the order of eggs in each nest was randomly assigned. This covariance structure produced the best AICc value (the smallest form of the corrected Akaike's information criterion) and the simplest model. All analyses were conducted by using SPSS software (ver. 22).

### *Ethical note*

To catch birds, we used wire cages (2  $\times$  2 m and 2 m high) with two funnel-shaped entrances and a removable top. During the breeding period (March July), cages were continuously in the field with the top open and we frequently put food inside, so that the birds became used to entering them to feed. To catch birds, we closed the top so that birds entered through the gates but they could not leave the cage. The closed cage was continuously observed. When birds entered, the observer approached. If the birds were already marked, we simply opened the top to free them. If not, we caught them with a piece of cloth. Every bird was then weighed, measured, ringed and released after a few minutes. This procedure has been used in the study area since 1992. Birds never suffered any harm during capture, and they frequently returned to feed in the cage very quickly after release, even on the same day.

Nests were inspected every two days. We used an aluminium ladder leant against the tree branch to reach the nests. We took and carefully lowered the eggs to the ground using a tissue bag to allow for safer measurement, and then returned them to back the nest. This manipulation was as brief as possible (a few minutes). No egg were damaged during the study, and in all cases parents quickly returned to the nest and no nest was abandoned as the result of our work.

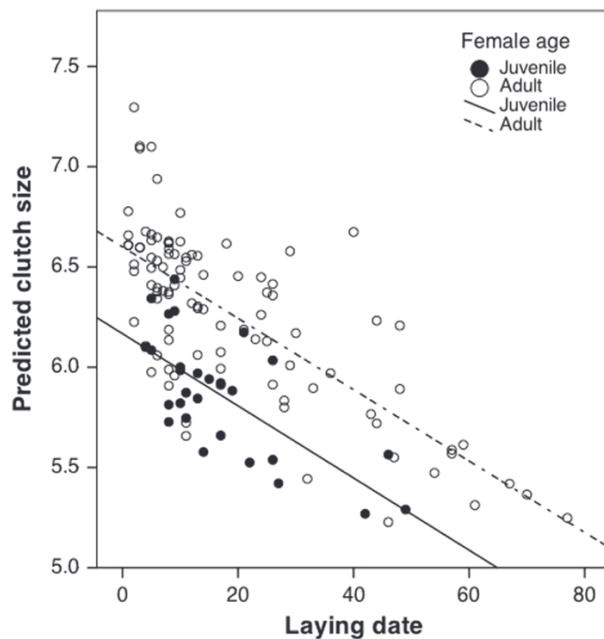
The Consejería de Agricultura y Medio Ambiente of Junta de Extremadura provided the authorisation for the study.

Data available from the Dryad Digital Repository:  
<<http://dx.doi.org/10.5061/dryad.4n2th>> (Valencia et al. 2016).

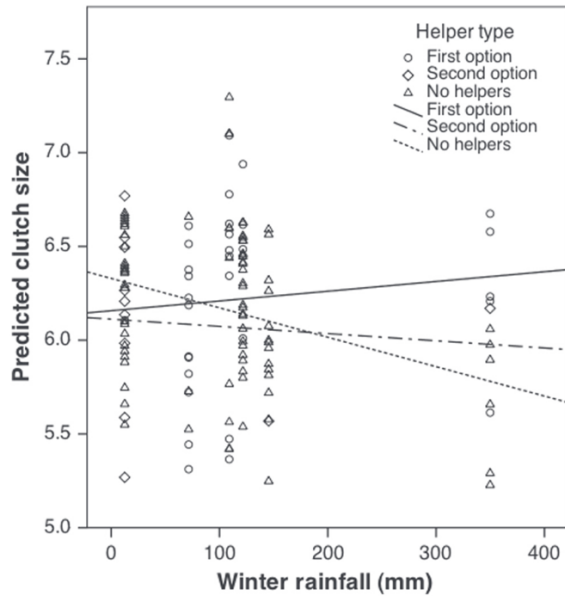
## Results

### *Clutch size*

The number of eggs laid per clutch depended mainly on the laying date, decreasing as the breeding season progressed (Fig. 1). Adult females laid more eggs per clutch than juveniles (estimated effect size  $\pm$  SE =  $0.434 \pm 0.159$ ; 95% CI = 0.118–0.749;  $p = 0.008$ ), but the random factor ‘female identity’ did not significantly contribute to explaining clutch size. Clutch size tended to increase with the March temperature, although this relationship was only marginally significant. There was no significant effect of the type of helping factor on clutch size (Table 2). However, we found a significant interaction between winter rainfall and the type of helping. More winter rainfall (before laying started) appeared to be negatively related to the size of clutches in nests without helpers, while in nests with FO helpers, this did not happen and the tendency was even the opposite, which produced a significant difference between nests with FO helpers and nests without helpers. The situation with SO helpers was intermediate and non-significant (Table 2, Fig. 2).



**Figure 1.** Clutch size values predicted from model in Table 2 for juvenile and adult mothers depending on the date of laying.



**Figure 2.** Clutch size values predicted from model in Table 2 for nests with FO helpers, SO helpers and with no helpers and depending on the total rainfall during January, February and March.

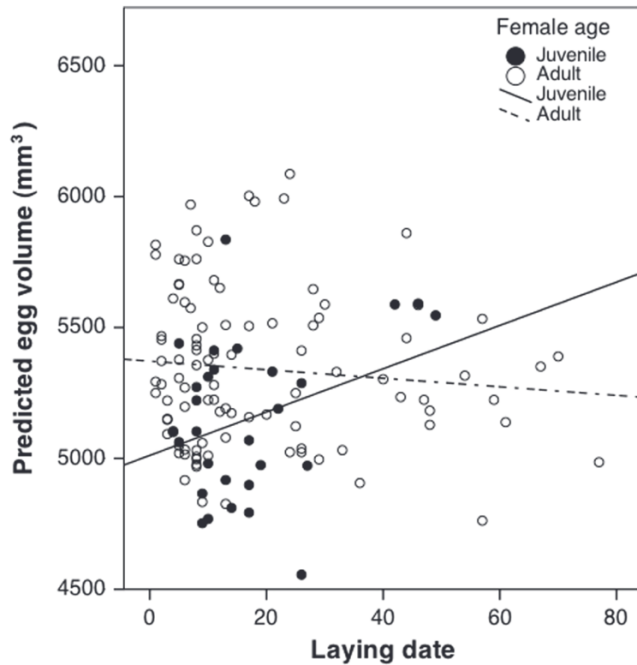
**Table 2.** Results of the linear mixed model on clutch size. Denominator degrees of freedom of the t statistic were computed following the Satterthwaite's approximation. Reference categories for the fixed factors were 'no helpers' and 'juveniles'. The estimate variance  $\pm$  SE for the random effect 'female identity' was  $0.131 \pm 0.094$  (Wald  $Z = 1.379$ ,  $p = 0.168$ )

Parameter	Estimate	Std. Error	DF	t	p
Intercept	5.579	0.618	105.763	9.034	<0.001
Age (adult)	0.434	0.159	114.923	2.719	0.008
FO helpers	-0.479	0.257	117.147	-1.866	0.065
SO helpers	-0.062	0.275	113.484	-0.226	0.821
Date	-0.019	0.004	83.141	-4.943	<0.001
Winter rainfall	-0.001	0.001	112.868	-1.238	0.218
March temperature	0.080	0.041	98.546	1.944	0.055
FO helpers $\times$ Winter rainfall	0.004	0.001	90.594	2.713	0.008
SO helpers $\times$ Winter rainfall	0.002	0.002	86.007	0.840	0.403

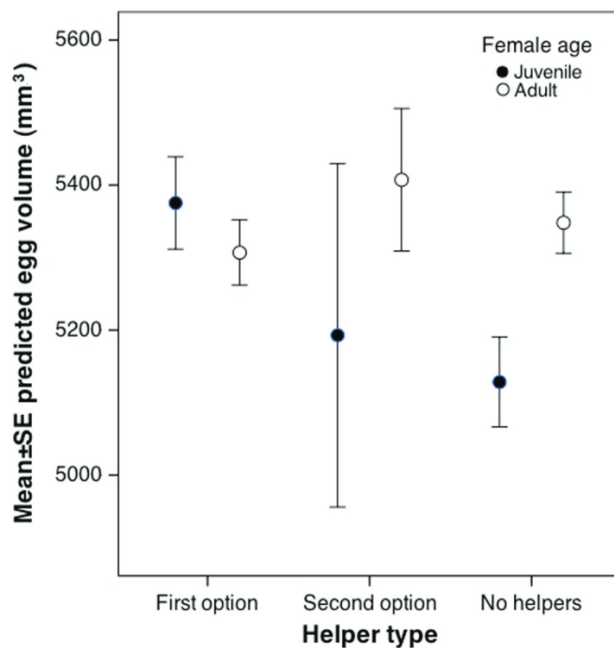
### *Egg volume*

The size (volume) of individual eggs varied considerably between mothers, and also depended on the mother's age, as adult females laid larger eggs than juveniles (estimated effect size  $\pm$  SE =  $295.148 \pm 98.634$ ; 95% CI = 98.937–491.359;  $p = 0.004$ ). There was no relationship between egg volume and environmental conditions, either temperature or rainfall. We found a nearly significant ( $p = 0.054$ ) interaction between laying date and mother's age, the laying date had no effect on egg volume for adult females, while juvenile females laid smaller eggs at the beginning of the season and larger eggs later in the season (Fig. 3). As for the effect of the type of helping, there was no difference between having SO helpers or no helpers, but the presence of FO helpers produced an almost significant increase in egg volume (Table 3). When we ran the analysis considering only two categories of helping (FO helpers versus SO helpers/no helpers), the presence of FO helpers became significant (estimated effect size  $\pm$  SE =  $139.198 \pm$

65.642; 95% CI = 8.434–269.960;  $p = 0.037$ ). Finally, although we did not have enough data for juvenile females to test the interaction between the mother's age and the type of helpers on egg volume, the predicted values from the model in Table 3 suggest that the main effect was due to juvenile mothers, who tended to lay smaller eggs than adult mothers only when they did not count on FO helpers (Fig. 4).



**Figure 3.** Egg volume values predicted from model in Table 3 for juvenile and adult mothers depending on the date of laying.



**Figure 4.** Mean ( $\pm$  SE) predicted values of egg volume (from model in Table 3) for nests with FO helpers, SO helpers and with no helpers and for juvenile and adult mothers.

**Table 3.** Results of the linear mixed model on egg volume. Denominator degrees of freedom of the t statistic were computed following the Satterthwaite's approximation. Reference categories for the fixed factors were 'no helpers' and 'juveniles'. The estimate variance  $\pm$  SE for the random effect 'female identity' was  $114601.042 \pm 21714.812$  (Wald  $Z = 5.278$ ,  $p < 0.001$ ), and the estimate covariance  $\pm$  SE for the repeated measures (eggs volume of the same clutch) was  $16701.474 \pm 6456.126$  (Wald  $Z = 2.587$ ,  $p = 0.010$ )

Parameter	Estimate	Std. Error	DF	t	p
Intercept	5293.520	216.680	55.538	24.430	<0.001
Age (adult)	295.148	98.634	82.097	2.992	0.004
FO helpers	124.096	68.045	79.909	1.824	0.072
SO helpers	-76.970	84.963	57.521	-0.906	0.369
Date	-1.077	1.252	40.885	-0.860	0.395
Winter rainfall	0.185	0.263	55.772	0.703	0.485
March temperature	0.562	14.040	49.836	0.040	0.968
Age (adult) $\times$ Date	-7.821	3.964	46.708	-1.973	0.054

Some of the FO helpers (only in four nests) were observed assisting the couple during incubation. We may assume that these helpers should have been more predictable than others at laying. Eggs in these nests with helpers at the incubation stage tended to be bigger than those from the remaining nests ( $5579 \pm 285$ SD mm<sup>3</sup>  $n = 4$ ; compared with  $5273 \pm 448$ SD mm<sup>3</sup>,  $n = 217$ ), although the sample was obviously highly unbalanced and the difference was not significant (mixed linear model controlling for other factors, including female identity:  $t = 1.589$ ; DF 59;  $p = 0.117$ ).

## Discussion

We have shown that the presence of helpers in the Iberian magpie was not associated with lower maternal expenditure in eggs (nor in the whole clutch). In contrast, mothers who counted on helpers whose assistance was predictable as early as at the time of egg laying (i.e. FO helpers; Valencia et al. 2003) produced larger eggs.

When the future contribution of helpers is predictable at the laying stage, some species appear to actually reduce maternal expenditure in eggs, thus relying on future compensation by the workforce of assistants. This pattern has been shown so far for the superb fairy-wren *Malurus cyaneus* (Russell et al. 2007), the carrion crow *Corvus corone* (Canestrari et al. 2011), the southern lapwing *Vanellus chilensis* (Santos and Macedo 2011) and the social weaver *Philetairus socius* (Paquet et al. 2013). However, Russell and Lummaa (2009) revealed for chestnut-crowned babbler *Potatostomus ruficeps* that mothers may not reduce and may even increase investment in individual eggs in the presence of helpers potentially because their probability of future reproduction is low. Savage et al. (2013) also stated that mothers should be more prone to compensating the size of eggs in the presence of helpers when the probability for future breeding is high. In our study area, Iberian magpie females rarely breed for more than two consecutive years, probably due to the high mortality rate (Valencia et al. 2003), so the relatively low probability of future reproduction might also contribute to the lack of compensation found in egg expenditure in the presence of helpers.

We also found that juvenile females who increased egg volume in the presence of helpers, while there was no change in the size of eggs laid by adult females. The presence of helpers may be particularly beneficial for young females in terms of

reproductive success (Magrath 2001) and survival (Paquet et al. 2015). Our results suggest that the assistance of helpers might increase the optimal expenditure in eggs by young females, while for adult mothers perhaps egg volume is already closer to the optimum either with or without helpers, although this idea deserves further research attention.

An alternative, potential cause for not reducing egg volume is that the presence of helpers may not be so predictable at the egg stage. In the Iberian magpie, most helpers do not incorporate until the nestlings hatch (Valencia et al. 2003). However, social relationships prior to egg laying might provide clues for mothers to predict the future assistance of helpers. Valencia et al. (2003) reported for this species that some individuals collaborated during nest building or in feeding the female. However, the subsequent role of these birds was variable, and not all of them continued assisting the same breeding pair at the nestling phase. We have separately considered the two types of helpers occurring in the Iberian magpie: FO helpers who are normally juveniles that help instead of breeding themselves, and SO helpers who are those birds that attempted to breed as a first choice but lost their brood and then redirected their behaviour towards helping others. We can expect that FO helpers are more predictable for mothers at the egg laying stage than SO helpers, because a) FO helpers are usually the previous offspring of the female, while SO helpers are only neighbours (Valencia et al. unpubl.), and b) the latter will help others only after failing in their own breeding attempt. Even so, colonial breeding, rather than territorial breeding as observed in other species (Russell et al. 2007), may add further uncertainty to the predictability of the assistance of helpers, since their presence in the colony does not guarantee that they will actually help in a particular nest when nestlings hatch.

We found that FO helpers were associated with increased egg volume. This finding contradicts our hypothesis that the lack of compensation is caused by helper unpredictability, since when helpers were more, predictable egg volume was not reduced but rather increased. Hence, our results indicate that the effect of helpers in the Iberian magpie is to increase the expenditure of young females in terms of egg volume. This recalls the previous finding at the nestling stage that parents increased provisioning in the presence of helpers (Valencia et al. 2006, Carranza et al. 2008), and suggests that factors affecting parents' decisions at the nestling stage may also play a role at the egg laying stage. In the Iberian magpie the main reported effect of helpers was to reduce the predation risk for the brood (Valencia et al. 2003, 2006). In such a situation, helpers may produce an important effect by increasing the reproductive value of the whole brood along with contributing to feeding the young. Under these conditions, the theoretical model by Carranza et al. (2008) predicts that parents should not reduce their expenditure but rather increase it, as they actually do (Valencia et al. 2006). Egg weight was the main variable that Russell et al. (2007) predicted to be reduced in the presence of helpers. Our results on egg volume do not support this prediction for the Iberian magpie and reveal the opposite pattern.

Nevertheless, a positive relationship between egg volume and the presence of helpers could be the result of at least two, not mutually exclusive, mechanisms. One of them, in agreement with the results found for provisioning rates to chicks in this same population (Valencia et al. 2006, Carranza et al. 2008), may be that mothers can predict the future assistance of helpers and increase their expenditure in eggs as an optimal investment in relation to the increased reproductive value of the offspring. Another explanation may

be that the association between helpers and nests with bigger eggs is arranged after laying, either because helpers select these nests or because better parents may have greater success in recruiting helpers. However, the predictability of helpers stands is an important element to associated with larger eggs. This rests on the finding that only FO helpers were associated with larger eggs, as well as the tendency in the same direction found for the few cases when helpers were already present at the incubation stage. These results support an advanced reaction of young females to future assistance by helpers, rather than an association between nests with bigger eggs and helpers after laying.

Our results also provide evidence for an interaction between helpers and factors that affect expenditure in clutches. Clutch size increased with the mother's age, as has been observed for many bird species (Sydeman and Emslie 1992, Weimerskirch 1992), and decreased as the breeding season progressed. Weather conditions may also affect mother expenditure in the current clutch (e.g. acorn woodpecker *Melanerpes formicivorus*; Koenig et al. 2009). In our case, clutches were smaller in years with more winter rainfall, but this negative effect of the environmental conditions disappeared when there were predictable (FO) helpers. Heavy winter rainfall may have been detrimental in our study area because it delays the start of breeding (Valencia et al. 2002), so that the last period of the chicks' development may take place under conditions of low resource availability at the beginning of the hot and dry summer of southern Iberia (Herrera 1978). The assistance of helpers has been reported to buffer the negative effect of unfavourable environmental conditions on fledgling success in many species (Blackmore and Heinsohn 2007, Covas et al. 2008), including the Iberian magpie (Valencia et al. 2003). Clutch size has been found to increase with the presence of helpers in a number of species; for example, apostlebird females *Struthidea cinerea* produced 0.67 more eggs for each additional group member (Woxvold and Magrath 2005), and Koenig et al. (2009) found for the acorn woodpecker *Melanerpes formicivorus* that females laid more eggs when they counted on helpers. We found no general effect of the presence of helpers on clutch size although, interestingly, the presence of helpers did not make mothers reduce the size of clutches under conditions of greater winter rainfall.

The size of individual eggs was unaffected by environmental conditions such as temperature or winter rainfall, and was higher for adult mothers compared to juveniles. Egg volume also varied greatly among individual mothers, a pattern that did not differ from that commonly found for many bird species (Saether 1990, Christians 2002, Ramirez et al. 2015). Juvenile females increased egg volume when eggs were laid late in the season. Although we do not have an explanation for this trend, one possibility is that the offspring of young mothers might need a better head start when they are produced late in the season, since food availability will quickly decrease during their development if it takes place well within the summer season. This explanation is in agreement with our finding that clutch size tended to decrease in late clutches, which may result from adjusted solutions to the propagule size vs number trade-off.

In conclusion, Iberian magpie mothers do not reduce expenditure in individual eggs when they have helpers, as predicted by Russell et al. (2007) and actually found for some species (see above). On the contrary, a rare pattern emerges of an association between higher expenditure in individual eggs and the presence of predictable (FO)

helpers, in agreement with previous findings at the nestling stage (Valencia et al. 2006); this is probably related to higher reproductive value of the brood (Carranza et al. 2008).

Provisioning and antipredatory defence are very different types of parental care with contrasting effects both for carers and receivers (generally referred as depreciable and nondepreciable care; Clutton-Brock 1991). However, in the context of the load-lightening hypothesis, benefits to helpers related to antipredatory defence are not straightforward. Taborsky et al. (2007) proposed that mothers may reduce investment in eggs even if helpers have an antipredatory effect but do not feed the offspring. However, the protective effect of helpers may influence offspring access to food patches. Santos and Macedo (2011) found that southern lapwings reduce egg volume in the presence of helpers, despite the fact that helpers do not feed the chicks but only defend them, and they discuss that helpers might indirectly provide food for chicks by defending larger foraging areas or investing more time in leading chicks on foraging forays. Future work should consider in detail the different effects of predatory protection and providing food for offspring, as well as the differences between both stages, i.e. egg laying and feeding the brood, either because the incorporation of helpers may not be equally predictable at both stages or because the cost-benefit balance for mothers is unequal when investing in eggs or the brood.

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