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Article

Egg investment in response to helper presence in cooperatively breeding Tibetan ground tits

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Life-history theory predicts a trade-off between current and future reproduction to maximize lifetime fitness. In cooperatively breeding species, where offspring care is shared between breeders and helpers, helper presence may influence the female breeders' egg investment, and consequently, survival and future reproductive success. For example, female breeders may reduce egg investment in response to helper presence if this reduction is compensated by helpers during provisioning. Alternatively, female breeders may increase egg investment in response to helper presence if helpers allow the breeders to raise more or higher quality offspring successfully. In the facultatively cooperative-breeding Tibetan ground tit *Pseudopodoces humilis*, previous studies found that helpers improve total nestling provisioning rates and fledgling recruitment, but have no apparent effects on the number and body mass of fledglings produced, while breeders with helpers show reduced provisioning rates and higher survival. Here, we investigated whether some of these effects may be explained by female breeders reducing their investment in eggs in response to helper presence. In addition, we investigated whether egg investment is associated with the female breeder's future fitness. Our results showed that helper presence had no effect on the female breeders' egg investment, and that egg investment was not associated with breeder survival and reproductive success. Our findings suggest that the responses of breeders to helping should be investigated throughout the breeding cycle, because the conclusions regarding the breeders' adjustment of reproductive investment in response to being helped may depend on which stage of the breeding cycle is considered.

Keywords: clutch size, clutch volume, cooperative breeding, egg size, maternal investment, reproductive success, survival

Introduction

Parental investment may vary greatly throughout the different stages of the avian breeding cycle. It has generally been assumed that the major reproductive costs mainly occur during offspring provisioning, while evidence for costs incurred during egg production is more limited (Martin 1987, Lessells 1991, Roff 1992, Stearns 1992). However, an

increasing number of studies have shown that egg production and incubation may be costly for female breeders (Visser and Lessells 2001, Nager 2006). Egg-removal experiments indicate that parents that invested more in egg production may show reduced offspring provisioning, which may result in lower offspring survival (Heaney and Monaghan 1995, Monaghan et al. 1998). Moreover, the current investment in eggs may also affect a female's future reproductive success. Increased egg investment could lead to poorer maternal body condition, reduced maternal survival, a lower number of future breeding attempts, longer re-breeding intervals and poorer reproductive performance in following breeding seasons (reviewed in Nager 2006, Bowers et al. 2012).

In birds, a positive relationship between egg size and offspring fitness has been widely reported across species (reviewed in Williams 1994, Christians 2002, Krist 2011). Williams (1994) and Christians (2002) suggested egg size effects to be most important at hatching and during early stages of the nestling-rearing period and a meta-analysis showed that egg size is positively related to offspring fitness during all life cycle stages through improved hatching success, body mass, body condition, growth rates and survival (Krist 2011).

In many avian cooperatively breeding species, helpers may assist the dominant breeding pair during reproduction, for example through their help with nest building, incubation, predator deterrence and provisioning (Stacey and Koenig 1990, Koenig and Dickinson 2004, 2016, Komdeur et al. 2017). The presence of helpers may induce different investment strategies for breeders. The load-lightening hypothesis argues that breeders should reduce their investment into current reproduction in response to helper presence, to save energy to improve their survival and future reproductive success (Crick 1992, Hatchwell 1999, Heinsohn 2004). The differential allocation hypothesis (Burley 1986, 1988, Sheldon 2000, Harris and Uller 2009) argues that breeders should not reduce investment in response to helper presence, but invest more to maximize their current reproduction when the conditions for successful reproduction are favourable, such as when helpers are present (Valencia et al. 2006, Carranza et al. 2008). Both hypotheses may also apply with respect to the investment in eggs. Female breeders could reduce their investment in response to the presence of helpers, as this may increase their own survival, while the decline in egg investment may be compensated by the higher provisioning provided by helpers (Russell et al. 2007). However, female breeders may also invest more in eggs in the presence of helpers to maximize their current reproductive success, which may lead to lower survival of the female breeder (reviewed in Russell and Lummaa 2009).

So far, several studies have investigated the factors underlying maternal investment in eggs in cooperatively breeding birds, but the results from these studies differ. In some studies, a load-lightening strategy has been shown in response to helper presence (Russell et al. 2007, Canestrari et al. 2011, Santos and Macedo 2011). In contrast, other studies have shown that females may increase their investment in eggs when they are assisted by helpers (Woxvold and Magrath 2005, Russell and Lummaa 2009, Liebl et al. 2016, Lejeune et al. 2016, Valencia et al. 2017) or show no response (Koenig et al. 2009). Although a change in egg investment in relation to helper presence is expected to affect survival and reproductive success, few studies have investigated this (Russell et al. 2007).

Here, we investigate the association between helper presence and female investment in eggs at the level of individual egg and the whole clutch, and the association between egg investment and survival and reproductive success in the Tibetan ground tit *Pseudopodoces humilis*. The ground tit is a facultatively cooperative-breeding passerine that inhabits the Tibetan plateau. In this species, helpers are always sexually mature males and stay with the breeders throughout the breeding period and help with nest building, territory defence and provisioning nestlings (Du and Lu 2009, Lu et al. 2011). A previous study on ground tits showed that during the nestling provisioning stage, the total amount of food delivered to the nestlings was higher in broods with helpers than in broods without helpers, while parents with helpers invested less in provisioning than parents without helpers (Lu et al. 2011). Additionally, a study in another ground tit population found no effect of helper presence on the number of offspring that fledged, and detected no difference in body mass of fledglings between broods raised with and without helpers (Li et al. 2015). However, in this population, the presence of helpers improved annual survival of breeders of both sexes and the first-year recruitment of male fledglings (Li et al. 2015). Based on these findings, we predict that the observed improved annual survival and future reproductive success of female breeders with helpers may be, at least partly, due to lower investment in eggs.

Material and methods

Study sites and population

Fieldwork was carried out on two high-altitude populations of ground tits: in Damxung county of Lhasa (30°28′N, 91°05′E; 4300 m a.s.l.) and in Tianjun county of Qinghai (37°17′N, 99°06′E; 3400 m a.s.l.) during the breeding seasons (May–July) in 2006–2009 and 2009–2013, respectively. Annual average temperature (Damxung: 1.3°C; Tianjun: −1.1°C) and annual precipitation (Damxung: 529 mm; Tianjun: 345 mm) in both study sites are very low, indicating an extremely harsh environment relative to that in tropical areas where most cooperatively breeding bird species occur (Rubenstein and Lovette 2007). The breeding season starts from early May and lasts until the middle of July. Tibetan ground tits breed in burrows that are excavated at the beginning of each breeding season (Ke and Lu 2009). 27.2% (Damxung) – 47.1% (Tianjun) of breeding pairs have one or more helpers. Breeding pairs with helpers have one (85.4%), two (13.1%) or three (1.5%) male helpers, who are

mainly yearlings (83.0%). Helping is kin-directed; in 83.3% of cases, helpers assist breeding pairs of which at least one member is the helper's parent (Tang et al. 2017). Helpers, which are always males, join the breeding pairs before egg laying and subsequently assist with nest building, nestling provisioning and territory defence (Ke and Lu 2009, Li et al. 2015, Tang et al. 2017). Females lay one egg each day until the clutch is completed (average clutch size = 6 eggs, range: 4–9; Tang et al. 2017). Incubation is performed by the female breeder for ca 15 d. Nestlings are fed by both breeders and helpers for ca 25 d. Usually, each breeding group can only raise a single brood in each year (Tang et al. 2017). Fledglings receive extended parental care for at least 20 d after fledging, after which they start to disperse. Fledgling dispersal is sex-biased; surviving male offspring (average annual survival rate = 0.2) remain in the study population whereas female offspring usually leave the study population (Tang et al. 2017).

In both populations, all nests produced during each breeding season were observed from the nest building stage until the nestlings fledged. Adults (breeders and helpers) and nestling were captured during the nestling period and, if not yet (colour-) banded before, marked with a unique combination of colour rings and one numbered metal ring. Most focal nests that were detected before egg laying commenced were checked daily until the day the last egg was laid. Some nests that were found after the onset of incubation were checked on the day they were found. During the egg laying period, each egg was marked and egg sizes were measured (length and width, to the nearest 0.1 mm using callipers) on the day the egg was laid. We averaged egg length and width of all eggs present in each nest and egg volume was calculated according to Hoyt's formula ($0.51 \times \text{length} \times \text{width}^2$; Hoyt 1979), and we multiplied clutch size by egg volume to obtain a single value for clutch volume for each nest.

Statistical analyses

To test whether clutch size, egg volume and clutch volume were associated with the presence of helpers, we performed (generalized) linear mixed models ((G)LMMs), with a Poisson distribution and a logit link function (for the analyses with clutch size as the dependent variable) or a Gaussian distribution and an identity link function (for egg volume and clutch volume). Although there was no significant correlation between egg volume and clutch size ($r = -0.1$, $p = 0.355$, $n = 92$), there was a significant positive correlation between clutch size and clutch volume ($r = 0.9$, $p < 0.001$, $n = 92$), and also a small positive correlation between egg volume and clutch volume ($r = 0.3$, $p = 0.006$, $n = 92$). While clutch size and clutch volume were tightly correlated, we analyzed both clutch size and clutch volume separately as the total clutch volume is a better estimate of the total investment in the clutch as it includes both egg size and clutch size. Only investigating egg volume and clutch size may be an incomplete representation of the total maternal investment and its consequences for female fitness, since subtle changes in egg size or clutch size may lead to a significant difference in the total clutch volume investment. In these models, fixed terms included helper presence (yes or no; since only 11% (four out of 38) of nests with helpers had more than one helper, we considered helper presence as a binary variable in the analyses), female breeder's age (young: one-year old, old: > one-year old; since female ground tits start breeding at one year of age, yearling females may invest less due to the lack of reproductive experience), study population (Damxung population, Tianjun population), and the incubation start date (number of days from the 1st of April to the start of incubation; this variable was included to control for a potential seasonal decline in reproduction; for four nests, the incubation start dates were unknown, reducing the sample size to 88 in these analyses). As egg volume may depend on clutch size (e.g. smaller eggs when clutches are larger (Lack 1954, Smith and Fretwell 1974, Tuomi 1990)), we also included clutch size as a continuous predictor variable in the analysis of egg volume. Furthermore, to test whether the impact of helpers on maternal egg investment depends on maternal age, we included the two-way interaction between female breeder age and helper presence. To test whether the impact of helpers on clutch size, egg volume and clutch volume differed between the two populations, we included a two-way interaction between helper presence and population. Female identity and year were included as separate random terms to account for repeated observations of the same females in different years and to account for 'year effects', such as annual variation in food availability or weather conditions.

We then investigated whether egg volume and clutch size were related to 1) female breeder survival until the next breeding season, 2) fledgling number, 3) fledging success (number of fledged nestlings versus number of nestlings that failed to fledge) and 4) male fledgling recruitment in the next breeding season (only recruitment of male fledgling was monitored because they always remain in the study population whereas female offspring generally disperse). For this, we conducted generalized linear mixed models (GLMMs) with a Poisson distribution for fledgling number and a binomial distribution for the other dependent variables. Egg volume, clutch size and their interaction with helper presence, female breeder's age, and study population were included in all models as predictors. Female identity and year were included as separate random terms in all models, while for the model investigating male fledgling recruitment, we also included family identity into the random part to account for the fact that several offspring originate from the same nest. In our dataset there was only one case where a female produced the second brood after the first breeding attempt failed, thus we did not include the re-nesting attempt into analyses.

All analyses were conducted in R ver. 3.3.2 (R Development Core Team), using package lme4 ver. 1.1.12 (Bates et al. 2016). Models were selected by eliminating non-significant (i.e. p > 0.05) fixed terms, in order of least significance and

starting with the interactions, until a final model was reached containing only significant predictors. All p values were calculated using likelihood ratio tests and the p value of each term was reported when it was removed from the model.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.7d028rp> (Zhao et al. 2019).

Results

Helpers and egg volume

In total, egg investment was measured in 88 nests, of which 37 were nests with helpers. Egg volume varied from 2583 mm³ to 3513 mm³ and clutch size varied from 4 to 9.

On average, females with and without helpers produced eggs of similar volume (mean ± SE egg volume with helpers: 3105 ± 31 mm³, n = 37; without helpers: 3054 ± 27 mm³, n = 51; Table 1a, Fig. 1a). Young and older females produced eggs of similar volume (mean ± SE egg volume of young females: 3050 ± 25 mm³, n = 53; older females: 3114 ± 35 mm³, n = 35; Table 1a). The interaction between helper presence and the female breeder's age was non-significant (Table 1a). Population, clutch size and incubation start date were not significantly related to egg volume (Table 1a).

Helpers and clutch size

Clutch size did not differ between female breeders with or without helpers (mean ± SE clutch size without helpers: 6.31 ± 0.12, n = 51; with helpers: 6.68 ± 0.19, n = 37; Table 1b, Fig. 1b). We found no effect of the female breeder's age, population, and the interaction between the female breeder's age and helper presence was not significant (Table 1b). Clutch size tended to decline during the breeding season, but this decline was non-significant (p = 0.052, Table 1b).

Helpers and clutch volume

Clutch volume was not associated with helper presence (Fig. 1c) or population, but clutch volume of older females was significantly larger than that of young females (mean ± SE clutch volume of young females: 18 984 ± 421 mm³, n = 53; older females: 21 213 ± 521 mm³, n = 35; Table 1c). Female investment in clutch volume significantly decreased during the breeding season (Table 1c).

Egg investment and female breeder survival and reproductive success

Annual survival probability of female breeders was not associated with egg volume, but it decreased significantly with increasing clutch size (Table 2a, Fig. 2a). Helper presence was positively associated with female survival (Fig. 2b;

Table 1. The impact of helper presence on (a) egg volume (mm³), (b) clutch size and (c) clutch volume (egg volume × clutch size; mm³) in female Tibetan ground tits. Results are from general(ized) linear mixed models (see Material and methods, n = 88 nests of 72 female breeders from 7 yr). Significant variables are indicated in bold.

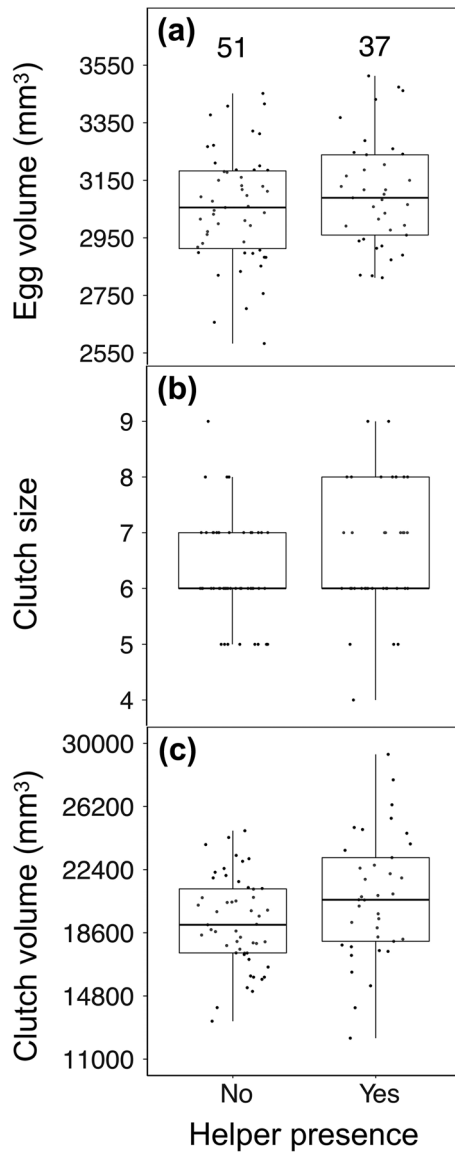|	(a) Egg volume				(b) Clutch size				(c) Clutch volume			
	Estimate	SE	t	p	Estimate	SE	z	p	Estimate	SE	t	p
Helper presence (Y/N)	48.9	35.9	1.4	0.181	0.0	0.1	0.0	0.983	402.6	628.4	0.6	0.524
Female breeder age (old)	40.5	37.9	1.1	0.293	0.1	0.1	0.9	0.379	**1783.5**	**635.2**	**2.8**	**0.006**
Incubation start date	45.3	38.3	1.2	0.242	−0.2	0.1	−1.9	0.052	**−1974.2**	**698.6**	**−2.8**	**0.006**
Population (Tianjun)	4.3	72.0	0.1	0.954	0.1	0.1	0.9	0.384	1789.1	830.7	2.2	0.078
Clutch size	71.9	39.9	1.8	0.082	–	–	–	–	–	–	–	–
Helper × female breeder age (old)	106.0	79.8	1.3	0.189	0.0	0.2	−0.2	0.872	533.6	1297.5	0.4	0.682
Helper × population (Tianjun)	−130.6	70.4	−1.9	0.072	0.1	0.2	0.3	0.756	342.1	1234.3	0.3	0.782

Figure 1. (a) Egg volume, (b) clutch size and (c) clutch volume in relation to helper presence in Tibetan ground tits. Data points are raw data, the box and whisker plots show the median, interquartile range and 1.5 × interquartile range. Numbers are sample sizes. For statistical analyses, see Table 1.

annual survival with helper: 0.55 without helper: 0.39), but the effect of helping on survival was independent of egg volume or clutch size (Table 2a). Population and the age of the female breeder were not significantly related to the female breeder's survival (Table 2a). Repeating the analysis using clutch volume instead of egg volume and clutch size, showed that greater clutch volume was associated with lower female survival, although this was marginally non-significant (estimate ± SE = −0.92 ± 0.47, z = −1.96, p = 0.050). As for clutch size, this effect did not depend on helper presence (Supplementary material Appendix 1 Table 1a).

Table 2. The impact of helper presence, egg volume and clutch size on (a) female breeder survival, (b) number of fledglings produced, (c) fledging success (number of fledglings vs. brood size) and (d) male fledgling recruitment in Tibetan ground tits. Results are from generalized linear mixed models (see methods, n = 92 nests of 75 female breeders from 7 yr). Significant variables are indicated in bold.

|	(a) Female breeder survival				(b) Number of fledglings				(c) Fledging success				(d) Male fledgling recruitment			
	Estimate	SE	z	p	Estimate	SE	z	p	Estimate	SE	z	p	Estimate	SE	z	p
Helper presence (Y/N)	**1.0**	**0.5**	**2.1**	**0.034**	0.0	0.1	0.1	0.958	0.2	0.3	0.6	0.535	0.3	0.4	0.8	0.442
Egg volume	0.8	0.5	1.6	0.108	0.1	0.1	0.9	0.355	0.3	0.4	0.8	0.418	0.2	0.4	0.4	0.714
Clutch size	**−1.3**	**0.5**	**−2.7**	**0.007**	**0.4**	**0.1**	**4.0**	**< 0.001**	0.3	0.3	1.0	0.310	−0.6	0.4	−1.4	0.178
Population (Tianjun)	0.0	0.5	−0.1	0.936	0.1	0.1	0.7	0.468	0.2	0.4	0.4	0.662	0.3	0.8	0.4	0.694
Female breeder age (Old)	−0.1	0.5	−0.1	0.893	0.1	0.1	0.7	0.489	−0.3	0.3	−0.9	0.364	−0.1	0.4	−0.1	0.894
Helper × egg volume	−0.8	1.0	−0.7	0.469	0.2	0.2	0.8	0.451	−0.1	0.7	−0.1	0.885	−0.5	0.9	−0.6	0.562
Helper × clutch size	−1.0	1.0	−1.0	0.342	0.2	0.2	0.8	0.430	1.2	0.7	1.7	0.084	0.1	0.9	0.1	0.899
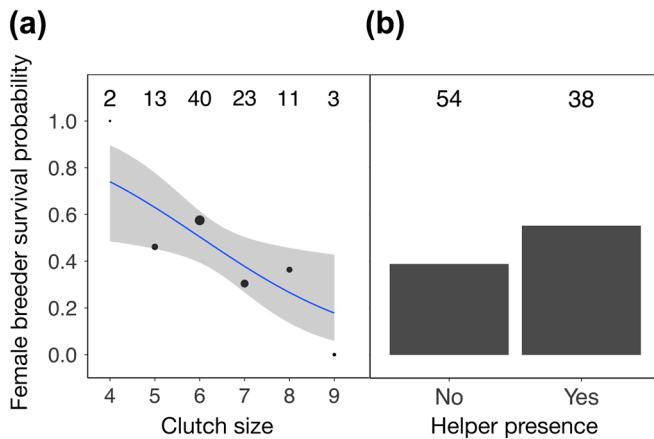
Figure 2. Annual survival of female breeders in relation to (a) clutch size and (b) helper presence (Y/N). Points are means for each clutch size and the size of the points is proportional to sample size. Lines and shaded areas are predictions and 95% confidence intervals. The numbers are sample sizes. For statistical analyses, see Table 2a.

The number of fledglings produced per breeding attempt was positively correlated with clutch size and clutch volume, but not related to helper presence or egg volume (Table 2b, Supplementary material Appendix 1 Table 1b). We found no effect of helper presence and egg volume, clutch size, or female breeder age on fledging success and male fledgling recruitment (Table 2c–d).

Discussion

We found that female breeders in the facultatively cooperative-breeding ground tit do not adjust their egg investment to the presence of helpers, but female breeder survival was higher when they had helpers. We also found that females that produced a larger clutch had lower survival, but this effect was similar for females with and without helpers.

Influence of helpers on maternal egg investment

The way females adjust maternal investment in response to helper presence varies between species. For example, in superb fairy-wrens *Malurus cyaneus* and in southern lapwings *Vanellus chilensis*, female breeders with helpers lay smaller but a similar number of eggs compared to females without helpers (Russell et al. 2007, Santos and Macedo 2011). Similarly, in carrion crows *Corvus corone* female breeders decrease egg size but not clutch size with an increasing number of helpers in their group (Canestrari et al. 2011). In contrast, female red-winged fairy-wrens *Malurus elegans* produce larger clutches but do not adjust egg size (Lejeune et al. 2016). Female apostlebirds *Struthidea cinerea* and chestnut-crowned babblers *Pomatostomus ruficeps* also increase clutch size with helper assistance, but whether they adjust egg size is not known (Woxvold and Magrath 2005, Russell and Lummaa 2009, Liebl et al. 2016). Finally, female Iberian magpie *Cyanopica*

cooki do not adjust their clutch size but produce larger eggs in response to helper presence (Valencia et al. 2017). Similar to what was found in the acorn woodpecker *Melanerpes formicivorus*, both egg size and clutch size were not associated with helper presence in female ground tits (Koenig et al. 2009).

In our study, females did not adjust the size of their eggs based on the presence of helpers. Therefore, the improved recruitment of male fledglings from territories with helpers that was found in a previous study (Li et al. 2015; but not in our study, Table 2d) is likely a result of higher nestling provisioning, as a consequence of the presence of helpers (Lu et al. 2011), and not of an increase in egg size when helpers were present.

The presence of helpers was also not associated with clutch size, despite that helper's assistance may give the female the ability to raise additional offspring. The reason for this could be that females are limited in their ability to produce additional offspring because of energetic costs, irrespective of the presence of helpers (Savage et al. 2012). Ground tits inhabit areas located between 2500 and 5500 m a.s.l. on the Tibetan Plateau, where low temperature and persistent snow cover in spring provide extremely harsh environmental conditions for ground-nesting birds (Hendricks 2003). For example, egg production and offspring feeding are costly in terms of higher energy demand and expenditure at higher elevation (Monaghan et al. 1998, Stevenson and Bryant 2000). The large energy requirement for egg formation could be limited by resource availability. Supplementary feeding experiments during the egg laying period have shown that food supplemented birds have reduced laying intervals (Nilsson and Svensson 1993), advanced laying dates and increased clutch and egg sizes (reviewed in Price 1998, Christians 2002). For insectivorous ground tits, food availability during the pre-laying stage is extremely limited due to the high altitude, the low amount of precipitation and scarcity of vegetation, and varies between territories. Some female breeders were observed receiving food from their partner during the egg laying period (pers. obs.). Helpers seldom feed the female breeder, and if so, only during incubation (unpubl.). Variation in territory quality and the amount of food received from the partner might explain the substantial variation we find in egg volume and clutch size.

Influence of maternal investment on reproductive success and female breeder survival

Egg size is often positively correlated with offspring fitness (Clutton-Brock 1991, Williams 1994). For example, a larger egg volume may result in increased hatching success, and nestlings hatching from larger eggs are often heavier, grow faster, fledge earlier and survive better (Parsons 1970, Williams 1994, Krist 2011). However, this was not the case in ground tits as we found no evidence that egg size influences offspring fitness in terms of fledging success and male fledgling recruitment. However, it should be noted that egg size may also benefit offspring in other ways (e.g. hatchability, growth rate) than those we considered here.

Russell et al. (2007) found that female superb fairy wrens *Malurus cyaneus* with helpers reduced their investment in individual eggs, and that the presence of helpers was associated with higher female breeder survival. However, whether this relationship is directly caused by reduction in egg investment is not known, as this study did not directly relate reduced egg investment to female survival.

Our results showed that clutch size was negatively associated with female breeder annual survival. Such an effect could be explained by higher reproductive investment leading to higher mortality, or by females investing more during their terminal reproductive attempt. Interestingly, the positive impact of helper presence on the female breeder's survival was independent of clutch size, suggesting that, contrary to our expectation, the helper's helping effort does not fully compensate for the female's energetic costs of reproduction. The production of larger clutch may require higher investment in later breeding stages, such as higher incubation and provisioning investment. This might also provide an explanation for why female ground tits did not increase clutch size in response to helper presence, as predicted by the 'differential allocation' hypothesis. Lu et al. (2011) showed that in the Damxung population of ground tits, one of our studied populations, helpers allowed the breeders to reduce their provisioning effort, which suggests that the positive association between helper presence and female breeder survival in ground tits may be achieved through a decreased investment during the provisioning period rather than during the egg laying stage.

To conclude, our study suggests that female ground tits do not adjust their investment in eggs in response to helper presence, while previous studies have shown that they adopt a load-lightening strategy during the nestling provisioning stage. Our results highlight that in order to understand the reproductive strategies of breeders in response to receiving help in cooperative breeding species, it is important to study the responses of breeders during different phases of breeding period.

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