



## RESEARCH PAPER

# Load Lightening in Southern Lapwings: Group-Living Mothers Lay Smaller Eggs than Pair-Living Mothers

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**Abstract**

Females of some cooperative-breeding species can decrease their egg investment without costs for their offspring because helpers-at-the-nest compensate for this reduction either by feeding more or by better protecting offspring from predation. We used the southern lapwing (*Vanellus chilensis*) to evaluate the effects of the presence of helpers on maternal investment. Southern lapwings are cooperative (some breeding pairs are aided by helpers), chick development is precocial, thus adults do not feed the chicks, and adults offer protection from predators through mobbing behaviors. We tested whether southern lapwing females reduced their reproductive investment (i.e. load-lightening [LL] hypothesis) or increased their investment (i.e. differential allocation hypothesis) when breeding in groups when compared with females that bred in pairs. We found that increased group size was associated with lower egg volume. A significant negative association between the combined egg nutritional investment (yolk, protein, and lipid mass) and group size was observed. Chicks that hatched from eggs laid in nests of groups were also smaller than chicks hatched in nests of pairs. However, there was no relationship between the body mass index of chicks, or clutch size and group size, which suggests that such eggs are, simply, proportionally smaller. Our results support the LL hypothesis even in a situation where adults do not feed the chicks, allowing females to reduce investment in eggs without incurring a cost to their offspring.

**Introduction**

In most avian species, the parental care required by chicks until they fledge and become independent is extremely costly to parents (Clutton-Brock 1991). For example, increments in annual fecundity (i.e. total chicks produced per year) and clutch size cause a significant decrease in annual survival rates of adults (Bennett & Owens 2002). It has also been shown that increases in reproductive effort (i.e. costs associated with reproductive activities such as finding mates or caring for offspring) often reduce immune response and future fecundity (Knowles et al. 2009). Thus, processes such as parasite infections and metabolism possibly mediate the trade-off between current and

future reproduction. For example, increased incubation effort has been shown to reduce future fecundity in female common eiders (Hanssen et al. 2005), and egg production has been shown to reduce survival of female great tits (*Parus major*; Visser & Lessells 2001). Furthermore, increases in reproductive effort (through experimental manipulation of brood or clutch size) have been shown to be positively associated with blood parasite infection levels in adult birds (Knowles et al. 2009). As a consequence of these mechanisms, individuals attempting to maximize lifetime reproductive success should reduce their reproductive efforts without negatively affecting their current offspring's chances of survival and breeding (Williams 1966; Bennett & Owens 2002).

Several studies of cooperative-breeding birds (reviewed in Koenig & Dickinson 2004; Hatchwell & Davies 1990; Hatchwell & Russell 1996; Hatchwell 1999; Wright & Dingemanse 1999; Russell et al. 2008) indicate that the assistance supplied by helpers-at-the-nest reduces the reproductive effort of the breeding pair, allowing them a higher lifetime reproductive success. Consequently, a parent can optimize its reproductive success while reducing reproductive effort, possibly avoiding negative effects for the chicks. With the reduction in investment, metabolic and immunological costs associated with breeding may also be lowered. This idea that helpers can reduce the effort of breeders in cooperative-breeding systems, thus allowing breeders to save resources that might improve survival, is known as the load-lightening hypothesis (LL; Brown & Brown 1981; see Russell & Lummaa 2009). Conversely, some studies have shown that females increase their investment when helper numbers are high (Wright 1998; Woxvold & Magrath 2005). This increase in investment with more help is known as the differential allocation hypothesis (DA; Burley 1986, 1988; Sheldon 2000; see Russell & Lummaa 2009).

The LL hypothesis predicts that females will reduce their investment when they expect more help. One way females can reduce their investments is by decreasing egg size and its contents when they expect compensation from helpers. For example, females of the cooperatively breeding superb fairy-wren (*Malurus cyaneus*) reduce their investment in eggs in the presence of helpers (Russell et al. 2007). Through feeding the offspring, helpers compensate the lower egg investment. Breeding females with helpers were able to reduce the costs associated with their investment in eggs, resulting in lower female annual mortality rate. With the reduction in annual mortality, breeding females can participate in future breeding attempts and maximize their reproductive success without sacrificing the quality and future success of their chicks (Russell et al. 2007). Another mechanism through which helpers can cause breeding females to reduce their investments is by protecting offspring against predation. For example, mothers of the cichlid *Neolamprologus pulcher* reduced their egg investments when group size was larger (Taborsky et al. 2007). *Neolamprologus pulcher* helpers participate in parental care by defending young from predators.

Plovers (families Charadriidae and Scolopacidae) are interesting study subjects to test hypotheses related to maternal investment in eggs because some species have precocial chicks that are cared for, but

not fed by adults (Reynolds & Székely 1997). We explored the possible effects of helpers on egg maternal investment in the southern lapwing (*Vanellus chilensis*, Charadriidae), a Neotropical plover with a flexible mating system (Saracura et al. 2008). Southern lapwings can be considered a cooperative species because of the presence of helpers that incubate eggs and defend the precocial offspring from predators during the breeding period (Saracura 2003; E. S. A. Santos, personal observation). Moreover, there is evidence of clutch-size variation in southern lapwings (range: 2–4 eggs; Walters 1982; Saracura 2003). Despite the observed variation in clutch size, there is no evidence for intra-specific brood parasitism (Saracura et al. 2008).

In this study, we tested whether southern lapwing females reduced their reproductive investment (i.e. LL hypothesis) or increased their investment (i.e. DA hypothesis) when breeding in groups when compared with females that bred in pairs. The LL hypothesis predicts that females should reduce their investment when the expected amount of help is high. On the other hand, the DA hypothesis predicts that females should increase their investment when the current reproduction value is higher than expected. If southern lapwing females behave according to the LL hypothesis, we predicted that: (1) clutch size would be smaller when breeding in groups than when breeding in pairs and (2) egg quality (measured as egg volume, and as the lipid and protein contents of the yolk) would be lower in group-living than in pair-living females. However, if southern lapwing females invest in agreement with the DA hypothesis, we predicted the opposite pattern: larger clutch size and higher egg quality for females in groups compared to those in pairs.

## Methods

### Study Species and Area

Two types of reproductive social units (RSUs) characterize the variable mating system of southern lapwings: secluded pairs that breed monogamously, and groups of three or more individuals (a pair and one or more helpers; Walters 1982; Saracura et al. 2008). Extra-pair paternity occurs only for breeding groups, and no cases of multiple females breeding within a group have been recorded (Saracura et al. 2008), although we cannot exclude this possibility in the current study because we did not conduct genetic analyses. It is unknown whether the

observed extra-pair chicks in groups are the result of mating within the social unit or with males from other social units, but all group members exhibit parental care (Saracura et al. 2008). Social partner fidelity is high in lapwings: 72% of social units are composed of the same individuals over repeated breeding seasons (Saracura 2003). Additionally, group composition is stable, and 92% of social units maintain the same number of individuals and return to the same breeding territory of previous years (Saracura 2003).

We monitored the activities of 74 RSUs (see Results for more details) in two neighboring urban areas (15°81'S 47°87'W and 15°91'S 47°94'W) in the city of Brasilia, Brazil. The areas have distinct landscapes, and their proximity to natural vegetation varies, but both present extensive lawns used by southern lapwings throughout the year for foraging and breeding.

#### General Field Procedures

We searched for and monitored nests during two field seasons (Aug. 3–Dec. 6, 2007 and Aug. 8–Oct. 16, 2008). We found all nests after laying had initiated, but before the clutch was completed, and these were visited in intervals of 2–4 d until the chicks fledged, or until breeding was interrupted by partial or total predation of the clutch, clutch desertion, or collection of the eggs for analyses (see below). Clutch size was determined as the maximum number of eggs in a nest during the incubation period, and RSU size by the maximum number of individuals counted during two consecutive nest visits. No RSU changed size between nest visits and during the study period.

#### Egg Quality Analyses

Egg volume was calculated by using the measured length ( $L$ ) and width ( $W$ ) of eggs (to nearest 0.01 mm) and applying Hoyt's (1979) formula:

$$V = 0.51 \times L \times W^2 \quad (1)$$

where 0.51 is the generalized volume coefficient. To avoid problems with lack of independence between data points, the mean egg volume for each nest was used in the statistical analyses.

We also quantified egg contents (Food Analysis Laboratory of the Universidade de Brasilia). We collected 10 clutches from secluded pairs (total = 28 eggs) and 10 clutches from groups (total = 29 eggs).

We standardized for egg development by using only those eggs that were at the very start of embryonic development, that is, those that remained at the bottom of the water column with angles  $<25^\circ$  in the flotation test (see Hays & LeCroy 1971 and Liebezeit et al. 2007). We measured egg mass and subsequently froze the eggs for further analyses. To avoid pseudoreplication, one egg from each nest was drawn for the analysis.

We defrosted 20 eggs (one per clutch) and removed the albumin to obtain the wet yolk mass, which is the primary energy source for embryos (Gill 2007). Yolks were oven-dried at 38°C for 96 h to obtain the dry yolk mass, after which we separated sub-samples of each yolk for quantification of lipid and protein mass, measured with an analytical scale (precision of 0.0001 g).

Protocol for quantification of the egg nutrients followed Russell et al. (2007), and we used the Soxhlet method (Horwitz et al. 2005) to quantify yolk lipids. Two sub-samples of 2 g were extracted with hexane from each dry yolk and placed within permeable cartridges that were used in the extraction tubes. The proportion of lipids ( $L$ ) in each 2 g sample ( $P$ ) was calculated with the formula:

$$L = \frac{N}{P} \quad (2)$$

where  $N$  is the mass of lipids extracted from each sample. The mean mass (g) of total lipids for each dry yolk was obtained by multiplying this proportion ( $L$ ) by the mass of each dry yolk.

We estimated the amount of protein in each dry yolk sample by determining the nitrogen content (Kjeldahl method; Horwitz et al. 2005). We extracted two samples of 0.3 g from each dry yolk and decomposed the organic matter to transform the existing nitrogen into ammonia. The amount of nitrogen in each sub-sample was determined by titration. The proportion of nitrogen (Pr) in each sub-sample of 0.3 g ( $P$ ) was calculated by the formula:

$$\text{Pr} = \frac{V \times N \times 14}{P \times 1000} \quad (3)$$

where  $V$  is the volume of hydrochloric acid used in the titration of each sub-sample,  $N$  is the normality of the acid ( $=0.1$ ), and 14 is the molecular weight of nitrogen. The total mass (g) of protein for each dry yolk was obtained by multiplying this proportion (Pr) by the conversion factor 6.25. All statistical analyses were conducted using the total masses of proteins and lipids.

### Chick Condition

We measured head and tarsus lengths, and body mass of all chicks. The ratio of mass to tarsus length was used to determine the body mass index (BMI) of the chicks. To control for chick development, we only used chicks measured on days 0 and 1 post-hatch. The head and tarsus lengths, body mass, and BMI of all chicks for each nest were used in linear mixed effects models (LMM) with nest ID as a random effect to account for repeated measures from the same nest.

### Statistical Analyses

We used a generalized linear model (GLM) with binomial error to evaluate the effect of RSU size on clutch size. We assumed that clutch size was binomially distributed (two possible values: 3 eggs = 0; 4 eggs = 1), because we did not use nests with one or two eggs in the analysis. This precaution was taken to avoid using partially predated clutches, because we could not distinguish between partial predation and naturally occurring smaller clutches. As a measure of sensitivity, we further analyzed the effect of RSU on clutch size without removing what we believed to be partially predated clutches from the dataset (one and two egg clutches). For the full clutch-size dataset, we fitted a GLM with quasipoisson error structure (see Results).

To evaluate the effect of RSU size on egg quality, we conducted unpaired *t*-tests for independent samples for each of the following variables: egg volume ( $n = 73$ ), wet yolk mass, dry yolk mass, protein mass, and lipid mass (all egg component variables:  $n = 19$ ). The effects of RSU size on chick head and tarsus lengths, mass, and BMI were evaluated using LMM (package 'lme4' in R, version 0.999375-35). The sample size for the chick condition analyses included 53 chicks from 19 nests. We calculated estimates of effect size (Pearson's correlation coefficient,  $r$ ) for all relationships between RSU size and the egg and chick variables. To avoid Type I error and the need for Bonferroni corrections because of multiple testing, we used the effect size and its associated confidence interval (CI) as this approach considers the magnitude of effect sizes in a continuous scale, unlike the conventional hypothesis test, which is based on significance level (Wilkinson and Task Force on Statistical Inference 1999, Thompson 2002; Nakagawa 2004; Garamszegi 2006). Furthermore, 95% CIs provide an estimate of the precision and repeatability of the analysis (Cumming & Finch 2001; Quinn & Keough 2002; Thompson 2002).

Subsequently, effect size estimates were converted into normally distributed  $Z$  values with Fisher's transformation ( $Z_r$ ; Sokal & Rohlf 1996) for use in the meta-analytical procedure (see below). All analyses were conducted using the software R (version 2.12.0, R Development Core Team 2010), and all data are presented as mean  $\pm$  SE, unless otherwise specified.

### Meta-Analytical Approach

We investigated the effect of RSU size on average maternal investment by adapting the flexible meta-analysis procedure (Nakagawa et al. 2007). This approach was applied because it addresses the problem of measuring several variables from the same study subjects. We used a weighted LMM to calculate an effect size estimate of the RSU size on mean maternal investment. A weighted model takes into consideration the differences in sample sizes of the input variables, i.e. larger sample sizes contributed more to the estimation of the effect on mean maternal investment than smaller samples. We used the restricted maximum likelihood method (REML) to estimate model parameters (package *nlme* in program R; Pinheiro & Bates 2000). To obtain the mean effect size,  $Z_{\text{mean}}$ , the model included only the intercept ( $Z_R \sim 1$ ). The LMM allowed us to use several estimates of effect size extracted from the same subjects by including a random grouping factor. A *t* value is presented to test whether the intercept of the LMM (mean effect size) is significantly larger than 0.

To determine whether the set of effect sizes is homogeneous, we estimated the heterogeneity in the model as the sum of the weighted squared residuals (more precisely  $Q_{\text{REML}}$ ) (Hedges & Olkin 1985; Nakagawa et al. 2007) and tested its significance against a chi-square distribution.  $Z_r$  values were back transformed into *r*-values for the presentation of the results. Effect sizes are accompanied by 95% CIs. The 95% CI of the overall meta-analytic mean was calculated using a composite variance component to deal with the combination of multiple outcomes from the same study in a meta-analysis, because these present some degree of correlation (Borenstein et al. 2009). The effect size estimates, 95% CIs, and the meta-analysis were calculated using standard equations (Nakagawa & Cuthill 2007; Nakagawa et al. 2007; Borenstein et al. 2009).

### Results

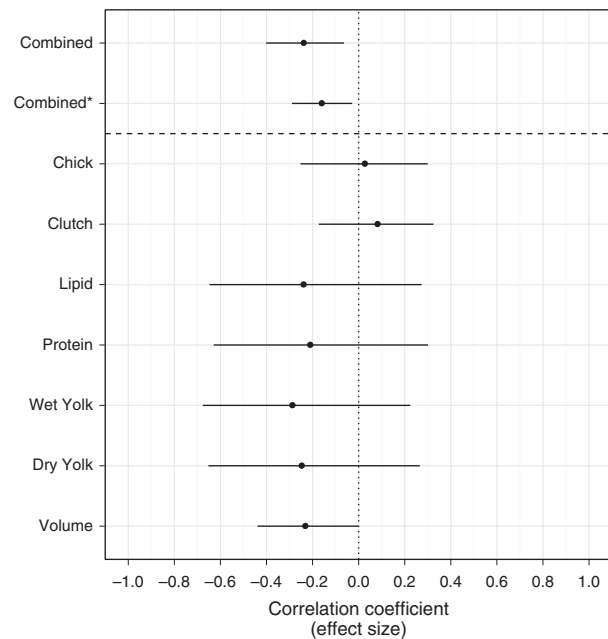
We found 74 nests in the two study sites: 42 (57%) in 2007 and 32 (43%) in 2008. Of these, 47 (63.5%)

were from pairs and 27 (36.5%) from pairs with helpers (group size [mean ± SD]: 3.2 ± 0.1 individuals). Clutch size varied from 1 to 4 eggs (mean ± SD: 3.2 ± 0.69 eggs). The variation in clutch size was not affected by the presence of helpers (binomial GLM including only clutches with three and four eggs:  $z = 0.65$ ,  $p = 0.52$ ; and quasipoisson GLM including all clutch sizes (1–4 eggs):  $\chi_1^2 = 0.15$ ,  $p = 0.31$ ; breeding pairs: 3.36 ± 0.08 eggs,  $n = 39$ ; groups: 3.44 ± 0.10 eggs,  $n = 25$ ). This small difference in mean clutch size between pairs and groups resulted in an effect size ( $r$ ) of 0.08 (95% CI: -0.17 to 0.32). As there was no effect of RSU on clutch size, the proportion of nests in each size class (three or four eggs) is reported independently of group size. Thus, 39 (61%) nests had three eggs and 25 (39%) had four eggs.

**Egg Quality**

Females breeding in groups with helpers laid smaller eggs than those females without helpers ( $t_{71} = 2.01$ ,  $p = 0.04$ ; groups: 23.31 ± 0.34 cm<sup>3</sup>,  $n = 26$ ; pairs: 24.06 ± 0.2 cm<sup>3</sup>,  $n = 47$ ). The mean difference of 0.75 cm<sup>3</sup> between eggs of females without helpers and those in groups with helpers resulted in an effect size ( $r$ ) of -0.23 (95% CI: -0.44 to -0.002). Despite this difference in egg volume between females with and without helpers, other maternal investment variables (wet and dry yolk mass, lipid mass, protein mass) did not present statistically significant differences (all  $p > 0.05$ ; Table 1). However, the effect sizes for these variables were smaller than  $r = -0.2$  (Table 1; Fig. 1), indicating a negative association between group size and the maternal investment variables.

We used the effect size for each maternal investment variable in a LMM to generate a mean effect of  $r = -0.24$  (95% CI: -0.401 to -0.06,  $n = 5$ ;



**Fig. 1:** Visual presentation of the results from the meta-analytical approach of the variables correlated with the size of the reproductive social unit (RSU) in southern lapwings (see Table 1 for details). Effect size (Pearson correlation coefficient) and 95% confidence intervals are presented for each result. The mean effect estimate represented as ‘Combined’ does not include ‘Clutch Size’ and ‘Chick BMI’. The mean effect estimate represented as ‘Combined\*’ includes all variables.

Table 1; Fig. 1). Thus, RSU size was negatively associated with mean maternal investment in the southern lapwing. The variables ‘Clutch Size’ and ‘Chick BMI’ were not included in this analysis because their effects were so close to 0 ( $r = 0.08$  and  $0.02$ , respectively) that they were considered unrelated to RSU size. Furthermore, the condition of the chicks would be a consequence of female investment in eggs, thus not a target of interest in the meta-analytical analysis. However, the inclusion of these variables in the model (Combined\*, Fig. 1) did not alter the

**Table 1:** Effect size estimates and results of the meta-analysis using linear mixed effects model with restricted maximum likelihood method (REML) for the effect of reproductive social unit (RSU) size on egg volume (Volume), dry yolk mass (Dry yolk), wet yolk mass (Wet yolk), yolk protein mass (Protein), yolk lipid mass (Lipid), and mean maternal investment (Mean effect) of southern lapwings. Statistically significant effect sizes (Volume and Mean effect) are in bold

Variable	<i>n</i>	Effect size <i>r</i>	95% CI for <i>r</i>	<i>t</i> value ( <i>p</i> , <i>df</i> )	Heterogeneity $Q_{REML}$ ( <i>p</i> , <i>df</i> )
Volume	73	<b>-0.23</b>	-0.44 to -0.002	2.01 (0.04, 72)	-
Dry yolk	19	-0.25	-0.65 to 0.26	1.05 (0.3, 18)	-
Wet yolk	19	-0.29	-0.67 to 0.22	1.24 (0.23, 18)	-
Protein	19	-0.21	-0.63 to 0.3	0.89 (0.38, 18)	-
Lipid	19	-0.24	-0.64 to 0.27	1.02 (0.32, 18)	-
Mean effect	5	<b>-0.24</b>	-0.40 to -0.06	22.36 (<0.0001, 4)	<0.0001 (1.0, 4)

interpretation of the meta-analysis result. The heterogeneity test between values of  $Z_R$  was not significant ( $Q_{REML} < 0.0001$ ,  $p = 1$ ,  $df = 4$ ), indicating that the variables contributed in a homogeneous way to the mean effect.

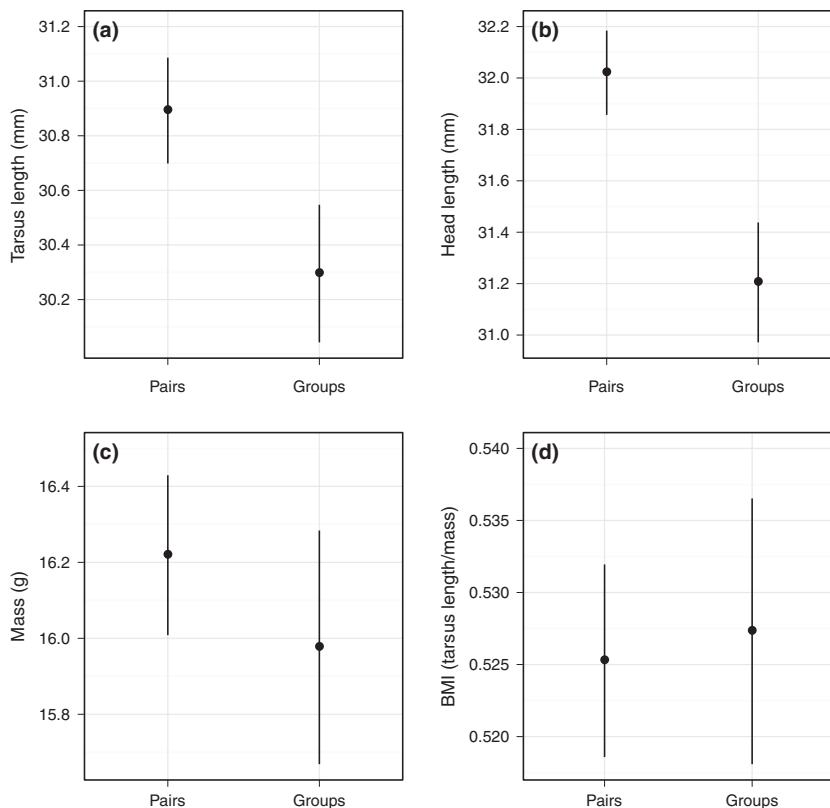
### Chick Condition

Chicks that hatched in groups with helpers were smaller than chicks that hatched from pairs (LMM tarsus length:  $t = -1.36$ ; groups:  $30.29 \pm 0.25$ ,  $n = 21$ ; pairs:  $30.89 \pm 0.19$ ,  $n = 32$ ; LMM head length:  $t = -2.16$ ; groups:  $31.20 \pm 0.23$ ,  $n = 21$ ; pairs:  $32.02 \pm 0.16$ ,  $n = 32$ ; Fig. 2a, b). The mean difference in tarsus length of 0.53 mm between chicks of females without helpers and those of females in groups with helpers resulted in an effect size ( $r$ ) of  $-0.25$  (95% CI:  $-0.49$  to  $0.02$ ). Furthermore, the mean difference in head length of 0.82 mm between chicks of pairs vs. those of groups resulted in an effect size ( $r$ ) of  $-0.38$  (95% CI:  $-0.59$  to  $-0.11$ ). Despite these differences, however, chicks from groups vs. those from pairs had similar weight (LMM body mass:  $t = 0$ ; groups:  $15.97 \pm 0.30$ ,  $n = 21$ ; pairs:  $16.21 \pm 0.21$ ,  $n = 32$ ; Fig. 2c). The BMI of chicks from females that had helpers was also similar to that of chicks

from females without helpers (LMM:  $t = 0.48$ ; groups:  $0.53 \pm 0.02$ ,  $n = 7$ ; pairs:  $0.52 \pm 0.01$ ,  $n = 12$ ; Fig. 2d). The mean BMI difference of 0.01 between chicks of females with and without helpers resulted in a small effect size of only  $r = 0.02$  (95% CI:  $-0.25$  to  $0.29$ ). We point out that our chick mass and BMI results seem contradictory (similar mass and BMI for group and pair chicks), given that chicks from groups were morphometrically smaller than chicks from pairs. We believe that this result is probably due to the high degree of variation in mass because measurements were taken from chicks over 24 h from hatching and not at their exact moment of hatching.

### Discussion

We found that southern lapwing females do not change clutch size, but reduce their maternal egg investment when breeding in cooperative groups, as egg quality was generally reduced in larger RSUs. Our clutch-size result was inconclusive for a group-size effect ( $r = 0.08$ ). However, our egg-investment results support the prediction from the LL hypothesis that in cooperative breeders, females reduce investment in eggs (Russell et al. 2007; Taborsky et al.



**Fig. 2:** Here, we show four parameters of southern lapwing chick condition for chicks that hatched in nests tended by pairs vs. groups. All parameters are shown as mean  $\pm$  SE. (a) Tarsus length. (b) Head length. (c) Mass. (d) Body mass index (BMI).

2007). Our results are even better explained by the refinement of this hypothesis, proposed by Taborsky et al. (2007), wherein females may reduce maternal egg investment because of helper contribution in the form of offspring protection from predators, even when helpers do not feed the offspring (Taborsky et al. 2007).

Our inconclusive clutch-size results do not suggest support to either the load lightening or the DA hypotheses. There is evidence in the literature supporting the DA hypothesis that females increase clutch size when they expect more investment from helpers (Davies 1992), or even because of mate quality (Petrie & Williams 1993). This hypothesis possibly would not apply to plovers (Charadriidae and Scolopacidae) because these birds generally exhibit a puzzling limitation in clutch size (see Lack 1947), usually laying an unvarying number of four eggs (Maclean 1972; Wallander & Andersson 2002). However, we can say that the southern lapwing is an exception to the clutch-size limitation rule, as there is no evidence of clutch-size limitation (61% of the clutches have three eggs and 39% have four eggs), thus validating the application of the initial question relative to clutch-size variation as a response to helper availability.

Our egg quality results imply that breeding in the presence of helpers-at-the-nest is advantageous to females even when helpers do not feed the offspring, as is the case of the southern lapwings, where chicks are precocial. Thus, helpers cannot increase chick quality by helping to feed them. Based upon the results of our study, we speculate that the helpers' positive effect may occur in other contexts. Despite the fact that females with helpers invest less into their eggs and these chicks are smaller at hatching, Saracura (2003) did not find a difference in survival rate of 1-mo-old southern lapwing chicks that were cared for by groups or pairs. Those results and the ones we present here suggest that helpers in a breeding group may compensate for lower maternal investment into eggs. Possibly, more adults in a group allow more frequent forays into food patches than in the absence of helpers, where parents may be limited in the time dedicated to tending the chicks during foraging. Despite not feeding their chicks, plovers present other forms of parental care, e.g. brooding, defense against predators, showing food by leading, and gathering young (Walters 1984; Reynolds & Székely 1997). Additionally, it is possible that chick body size is important for chick survival: mobility might be related to body size and thus, larger chicks have a better chance of avoiding predation.

With more adults in the breeding group, smaller, less mobile chicks from groups might have the same survival chances as larger, more mobile chicks from pairs, a mechanism similar to that reported for egg size reduction in *Neolamprologus pulcher* (Taborsky et al. 2007). Thus, our results further reinforce the generality of the negative relationship between maternal egg investment and helper number (Russell et al. 2007; Taborsky et al. 2007).

In conclusion, we found that breeding with the assistance of helpers was associated with a reduction of maternal reproductive effort in the southern lapwing, in the form of decreased egg volume and egg contents. Although several studies have demonstrated the benefits of group breeding (reviewed in Brown 1987; Koenig & Dickinson 2004), the Russell et al. (2007) study was the first to associate a reduction in maternal egg investment with group size. Our study upholds these findings for the first time in a unique context, for a cooperative species with precocial chick development. Lapwing helpers do not feed chicks, but instead provide protection from predators, or may be able to spend more time leading chicks to food patches, so that chicks may be able to compensate for the lower egg maternal investment. More importantly, our results fit the explanation proposed by Taborsky et al. (2007) that predator protection provided by helpers might be enough to allow breeding females to reduce their egg investments without a cost to the offspring. As far as we are aware, this is the first time that the concealed helper effect hypothesis (Koenig et al. 2009) has been shown to occur in birds through the mechanism proposed by Taborsky et al. (2007). We extend the concealed helper effect hypothesis by proposing that helpers compensate for reduced maternal investment not only by providing direct benefits to chicks through food provisioning, but also indirectly, possibly by defending larger foraging areas or investing more time in leading chicks in foraging forays. Future studies should attempt to measure territorial quality and time budgets of individual group members to determine whether indirect offspring care can account for reduced maternal investment.

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