

BETWEEN AND WITHIN CLUTCH VARIATION OF EGG SIZE IN GREATER RHEAS

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ABSTRACT.—We describe egg characteristics, and analyze between and within clutch variation in egg size and mass in a natural population of Greater Rheas (*Rhea americana*). We assess the effect of this variation on nesting success and egg success. Yolk represented 29.5% of egg mass whereas albumen was 63.9%. Yolk mass increased with egg width but not with egg length, while mass of albumen increased mainly with egg length. The largest and smallest eggs were 10.3% larger and 25.3% smaller, respectively than mean intra-clutch values. The widest egg was 11.9% wider while the narrowest egg was 20.5% narrower than mean intra-clutch values. There was a significant decrease in egg size between clutches during the breeding season as a result of a decrease in egg length. There was no effect of laying order on intra-clutch variation in egg size, but we detected an increase in the variation of egg length within clutches with clutch size. We did not detect a relationship between egg size and nesting success, and between egg size and egg success. The relatively low intra-clutch variation in egg size and lack of effect of egg size on hatching success do not support the hypothesis that females invest in eggs according to expected chick fitness. Received 23 November 2007. Accepted 15 April 2008.

Intraspecific egg size variation is relatively common in birds (Slagsvold et al. 1984, Williams et al. 1993, Christians 2002). Most variation is among rather than within clutches and it is generally accepted this variation is the result of a strong genetic component of egg size (Christians 2002, Stryrsky et al. 2002, Valkama et al. 2002). However, variation among or within clutches laid by the same female should be attributed to phenotypic or environmental-mediated variation (Nager et al. 2006). Nutrient or energetic constraints could be responsible for egg size variation in some bird species (O'Connor 1979, Pierotti and Bellrose 1986). Egg size could also vary with parental age or experience with eggs laid by older and experienced females larger than those laid by younger females (Davis 1975, Blomqvist et al. 1997, Hipfner et al. 1997). Alternatively, egg size variation could respond to an adaptive investment of females, thereby influencing offspring quality. Larger eggs may contain more water and nutrients, which may benefit hatchlings by increasing their hatching success, growth rate, and survival (Parsons 1970, Reid and Boersma 1990, Magrath 1992, Williams 1994, Smith and Bruun 1998, Pelayo and Clark 2003). Egg size in some species

decreases with laying order (e.g., Nisbet 1978, Shaw 1985, Custer and Frederick 1990). This decrease could be interpreted as an adaptive strategy because the reduction in size of last laid eggs could be a mechanism for shortening incubation period and favoring synchronous hatching (e.g., Birkhead and Nettleship 1982, Perrins 1996, Kennamer et al. 1997).

Maternal investment in eggs also could be related to mate quality or prospects of success. Some studies have found that females mated with non-preferred males produced fewer and smaller eggs than females mated with the males they chose (Yamamoto et al. 1989, Cunningham and Russell 2000).

Most studies of egg size variation were conducted on species where the clutch is laid by a unique female. In species with communal egg laying (where more than one female laid eggs into a single nest), differences in egg investment by females could have more important consequences for offspring fitness. For example, larger eggs in Guira Cuckoo (*Guira guira*) produce heavier and larger chicks that may out compete smaller and lighter nest companions (Macedo et al. 2004). As a consequence, larger communal clutches in this species had eggs with more nutrients than in smaller clutches. Females of species with communal laying could manipulate the nutrient investment in their eggs depending upon social condition to enhance individual fitness (Macedo et al. 2004).

We analyzed inter- and intra-clutch varia-

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tion of egg size in a natural population of Greater Rheas (*Rhea americana*). Greater Rheas are communal nesters where two to 10 or more females lay eggs into a single nest that a male incubates. We analyzed the effect of season and clutch sizes (total number of eggs in the nest) on both inter- and intra-clutch variation of egg size to assess if egg size was associated with hatching success. The relationship between egg size and nesting success was analyzed because it is possible females reduce their investment in eggs laid for low quality males (i.e., young inexperienced or in poor physical condition) that are prone to desert the nest. We also analyzed the relationship between egg components (yolk and albumen) and egg size. We expected a positive relationship between egg size and yolk content, and between egg size and nest success, and hatching success.

METHODS

Study Site.—Data were collected during the 1992 and 1993 breeding seasons of Greater Rheas (Fernández and Reboreda 1998, 2003). We searched for Greater Rhea nests in three contiguous cattle ranches of ~3,500, 3,000, and 800 ha, near the town of General Lavalle in Buenos Aires Province, Argentina (36° 25' S, 56° 56' W). Numbers of rheas on these ranches were ~250, 100, and 150, respectively. The area is flat, low, and marshy with little of the land rising more than 10 m above sea level. Native vegetation is short grass with scattered patches of woodland in the higher areas (Fernández and Reboreda 1998).

Data Collection.—Greater Rhea nesting occurred from September to December, but most attempts were in November (Fernández and Reboreda 1998). We found 99 nests, 41 in 1992, and 58 in 1993. We used data from a sample of 53 active nests where we measured all eggs (30 nests in 1992, 23 in 1993). We individually numbered the eggs in each nest with water proof ink and recorded clutch size (number of eggs in the nest). Nests were visited (<20 min/visit) between 0900–1700 hrs every 2–3 days until the eggs hatched or the nest failed. We estimated the date at which laying started either directly (we knew the date of laying of the first egg) or indirectly by the color of the eggs (light yellow when laid but white in ~5 days) or by backdating (start

of laying was estimated as date of hatching minus 40 days).

We measured length and width of the eggs with calipers (± 0.1 mm) and mass with a 1-kg Pesola spring scale (± 5 g). Egg mass varies during incubation (Grant et al. 1982) and we corrected it using the relationship between fresh egg weight and egg volume (length \times width²; Hoyt 1979) estimated from a subsample of 24 eggs found before onset of incubation. This relationship was highly significant ($F_{1,22} = 955.2$, $P < 0.0001$) and the model equation was:

$$\begin{aligned} \text{fresh mass (g)} \\ &= 11.8 + 0.55 \times (\text{length} \times \text{width}^2) \\ & (R^2 = 0.98). \end{aligned}$$

Egg volume was estimated using the water displacement for 39 fresh eggs collected from early deserted nests. We measured the volume displaced when the egg was immersed in water after its air cell was filled with water. The relationship between the product of L \times W² (length \times width²) and the measured volume for these eggs was highly significant (simple regression analysis, $F_{1,37} = 101.6$, $P < 0.001$). The equation was:

$$\begin{aligned} \text{volume (cm}^3\text{)} \\ &= -47.18 + 0.56 \times (\text{L} \times \text{W}^2) \\ & (R^2 = 0.73). \end{aligned}$$

We collected fresh eggs from nests deserted before the onset of incubation to study egg composition. We took one egg from four nests and two eggs from another four nests (total = 12 eggs) to minimize pseudoreplication. Eggs were measured, weighed, and boiled for ~30 min to solidify the content (Carey 1996). We manually separated shell plus membranes, albumen, and yolk and recorded their wet mass with a Pesola spring scale (± 5 g).

Statistical Analyses.—We estimated the variance component of differences in egg size (width and length) within and between clutches. We performed a one-way ANOVA, with egg measurements as dependent variables and nests as a random factor.

We assessed the relationship between laying sequence and egg size using simple regression analyses with transformed data. We standardized egg length and width dividing

each by the mean clutch value to correct for differences among clutches (Kennamer et al. 1997). We only included eggs laid up to 12 days after the start of laying.

We estimated intra-clutch variation in egg size by calculating the variation coefficients (CV) for each nest. We assessed variation of CVs with clutch size and season using general linear models (GLMs) with egg length and width as response variables, and season, clutch, and its interaction, as explanatory variables. We assigned nests to the date at which laying started and divided the breeding season into periods: 1–15 October; 16–31 October; 1–15 November; 16–30 November; 1–15 December; and 16–31 December. We did not observe laying after 31 December. We assumed a normal distribution of response variables, and checked it using residual and normal plots. We selected the final model after dropping all non-significant terms and checking for changes in deviance (Crawley 1993).

We used linear mixed models to test seasonal variation of egg size with egg length, width, and mass as response variables; year, clutch size, time of the season, and their second term interactions were explanatory variables. Nest identity was incorporated as a random factor to solve the problem of measuring eggs produced by the same female. We used residual and normal probability plots to check model assumptions. We selected the final model by sequentially dropping non-significant interactions and the non-significant main effects until only significant terms remained, and any additional factor deletion generated a significant change in the model. We assumed a normal distribution of residuals and used an identity link function for the analysis.

The wet mass of egg components (albumen, yolk, shell, and membranes) was related to egg total mass, volume, length, and width using simple regression analyses. Shell-free egg mass was estimated as the weight of the fresh egg minus the weight of the shell plus membranes. Yolk and albumen mass were expressed as the percentage of shell-free egg mass, whereas mass of shell and membranes was expressed as percentage of total weight of the fresh egg (including shell and membranes).

We evaluated differences in size and weight among eggs in successful and deserted nests using a generalized linear model (GLM) in-

cluding year, season, clutch size, and mean egg volume as explanatory variables, and nest fate (successful or deserted) as the response variable. We assumed a binomial distribution of residuals for the response variable and a logit link function for this analysis. We used residual and normal probability plots to check model assumptions. We selected a final model by sequentially dropping non-significant interactions and then non-significant main effects until only significant terms remained (Crawley 1993). The effect of egg characteristics on probability of hatching was tested using a logit regression with a binary response (hatched-non-hatched) and egg length, egg width, and season as independent variables. Egg length and width were standardized to the mean value of each nest. Hatching success can vary with egg size in a non-linear form (Deeming 1995), and we included the quadratic terms for egg width and length as predictor variables in an alternative model. We used Genstat DE2 (Release 4.2, VSN International Ltd., UK) to fit the models and perform all statistical analyses. All statistics presented are two-tailed and measures are mean \pm SD.

RESULTS

Egg Size Variation.—We measured 1,226 Greater Rhea eggs from 53 nests. Egg volume varied from 255.4 to 788.0 cm³ and egg mass from 275 to 825 g (Table 1). Egg length was more variable than egg width (Table 1). The largest egg was 10.3% larger while the smallest egg was 25.3% smaller than mean values. The widest egg was 11.9% wider while the narrowest egg was 20.5% narrower than mean values. Within clutch variation of egg width was higher than between clutch variation, while variation of egg length was similar within and between clutches. The variance in egg width explained by within clutch variation was 80.8%, whereas variance explained by between-clutches variation was 19.2%. Similarly, variation in egg length explained by within clutch variation was 88.7%, while between clutches variation only explained 11.3% of the variance.

Variation in egg length within clutches was related to clutch size (variance ratio $VR_{1,48} = 2.18$, $P = 0.04$) but was independent from time of the season ($\Delta D = 5.43$, $df = 4$, $P = 0.02$ for clutch size; and $P > 0.05$ for time of

TABLE 1. Morphological characteristics of Greater Rhea eggs from 53 nests (mean clutch size = 22.6 eggs, SD = 10, range = 7–56 eggs), Buenos Aires Province, Argentina.

	Mean	SD	Range	n
Length (cm)	13.3	0.55	9.9–14.6	1,226
Width (cm)	9.3	0.38	7.39–10.4	1,225
Mass (g)	618.7	65.1	275–825	1,113
Volume (cm ³)	595.4	66.5	255.4–788.0	1,125
Density (g/cm ³) ^a	1.0	0.06	0.75–1.3	1,107
Area (cm ²) ^b	340.3	24.0	199.2–412.2	1,113
Shell density (g/cm ³) ^c	2.1	0.003	2.1–2.1	1,113

^a Density = $1.038 \times \text{weight}^{0.006}$ (Paganelli et al. 1974).

^b Area = $4.835 \times \text{weight}^{0.662}$ (Paganelli et al. 1974).

^c Shell density = $1.945 \times \text{weight}^{0.014}$ (Paganelli et al. 1974).

the season and the interaction term). The coefficient of variation in egg length increased with clutch size. In contrast, within-clutch variation in egg width did not vary with clutch size or season (variance ratio $VR_{11,48} = 0.67$, $P = 0.75$).

Egg Composition.—Yolk mass represented $29.5 \pm 3.5\%$ ($n = 11$, range = 24.1–35.6%) of egg mass and $34.7 \pm 3.4\%$ (range = 29.5–42.5%) of shell-free egg mass. Mean yolk mass was 170 ± 18.1 g and varied linearly with egg mass ($F_{1,10} = 10.9$, $P = 0.01$, $R^2 = 0.58$), and egg volume ($F_{1,10} = 13.2$, $P = 0.04$, $R^2 = 0.34$; Fig. 1). Yolk mass increased with egg width (regression analysis, $F_{1,10} = 13.2$, $P = 0.005$, $R^2 = 0.57$), but was independent of egg length (regression analysis, $F_{1,10} = 0.135$, $P = 0.72$).

Albumen mass represented $63.9 \pm 3.5\%$ ($n = 10$, range = 51.7–70.5%) of egg mass and $66 \pm 2.4\%$ (range = 61.3–70.5%) of shell-free egg mass. Mean albumen mass was 330.5 ± 28.3 g and increased with egg length, width, mass, and volume (regression analyses; $F_{1,8} = 7.23$, $P = 0.03$, $R^2 = 0.47$; $F_{1,8} = 5.31$, $P = 0.05$, $R^2 = 0.32$; $F_{1,8} = 18.7$, $P = 0.002$, $R^2 = 0.64$; and $F_{1,8} = 37.9$, $P < 0.01$, $R^2 = 0.83$, respectively; Fig. 1). We did not detect a relationship between albumen and yolk mass (Pearson product-moment correlation, $r = 0.42$, $P > 0.05$).

Mean mass of shell and membranes was 84.0 ± 15.1 g and represented $14.5 \pm 2.4\%$ of egg mass (range = 11.8–19.6%). We did not find any relationship among mass of shell plus membranes and egg mass, volume, length or width (regression analyses, $P > 0.05$).

Effect of Laying Order and Time of Breeding on Egg Characteristics.—We found no ef-

fect of laying order on egg length ($F_{1,136} = 1.54$, $P = 0.22$), egg width ($F_{1,136} = 0.13$, $P = 0.72$), and egg mass ($F_{1,136} = 0.81$, $P = 0.37$). Similarly, egg characteristics were not affected by clutch size ($F_{1,35} = 1.45$, $P = 0.24$ for length; $F_{1,35} = 0.74$, $P = 0.39$ for breadth; $F_{1,35} = 0.05$, $P = 0.82$ for mass).

The minimal model for explaining between-clutch variation of egg length included season and the interaction between year and season ($Wald/df = 3.74$, $df = 5$, $P = 0.002$, and $Wald/df = 2.67$, $df = 4$, $P = 0.03$, respectively). Egg length decreased towards the end of the breeding season (Dec), but this decrease was most important during 1992 (Fig. 2A). We did not detect any effect of season, clutch size, and year on egg width (Fig. 2B). Egg mass had a significant decrease with time of breeding, and the interaction between year and time of breeding ($Wald/df = 2.80$, $df = 5$, $P = 0.02$, and $Wald/df = 3.31$, $df = 3$, $P = 0.02$, respectively). Egg mass also decreased towards the end of the breeding season and the decrease was most prominent during 1992.

Effect of Egg Size on Nest Fate and Hatching success.—Mean egg size, clutch size, and season did not affect nest fate (*Deviance ratio* = 0.84, $df_{\text{reg}} = 8$, $df_{\text{res}} = 29$, $P = 0.57$). Successful and deserted nests had similar mean egg sizes (*t*-test, *a posteriori*, $t_{37} = -0.05$, $P = 0.96$). Hatching success was not affected by egg size ($\Delta D = 0.77$, $df = 1$, $P = 0.39$) but was affected by season ($\Delta D = 5.43$, $df = 4$, $P = 0.01$) although it does not vary in a predictable manner (simple regression, $F_{1,20} = 0.015$, $P = 0.90$).

DISCUSSION

Egg Size Variation.—Eggs of Greater Rheas varied considerably in size, differing in

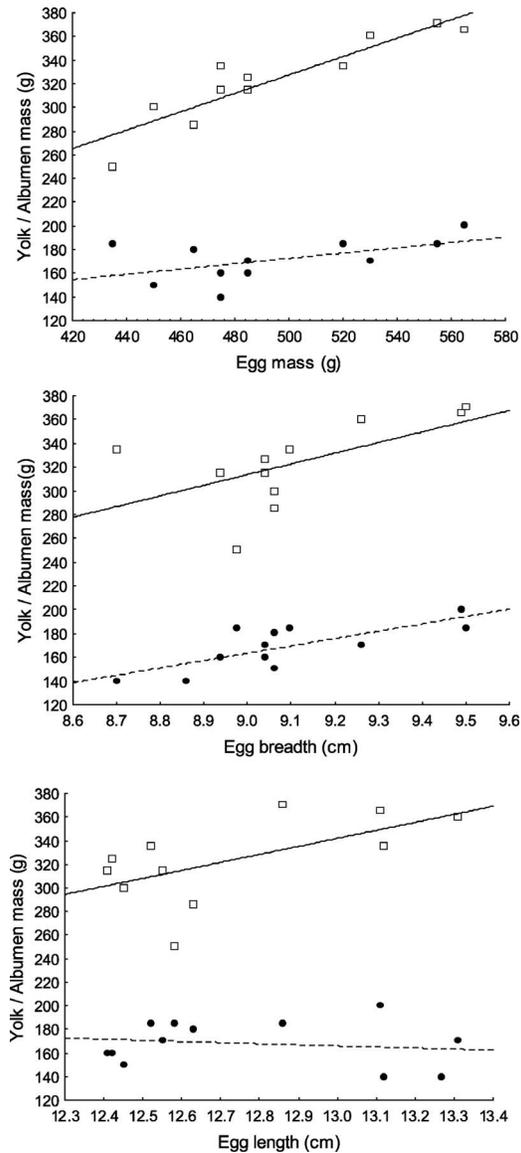


FIG. 1. Variation of yolk and albumen mass with egg mass, egg length, and egg width. Full lines represent adjusted functions for albumen mass variation with these independent variables, whereas broken lines represent the adjusted functions for variation in yolk mass.

mass by up to 550 g. Egg length and width also varied, as the largest rhea egg was 148% larger than the smallest, while the widest egg was 140% wider than the most narrow one.

We detected differences in egg size between clutches associated with date of egg laying.

There was a significant reduction in egg length but not in egg width during the breeding season. Other authors also found a negative association between egg size and laying date (i.e., Coulson and White 1958, Furness 1983, but see Perrins 1996). The reduction in egg size could affect embryo development and hatching success (Dzialowski and Sothlerland 2004) or post-fledgling survival (Dow and Fredga 1984, Newton and Marquiss 1984, Dzus and Clark 1998, but see Blomqvist et al. 1997 and Massaro et al. 2002). We did not detect differences in a previous study in short-term survival between chicks hatched early (Nov-Dec) and late in the breeding seasons (Jan-Feb) (Fernández and Reboreda 2003). The lack of differences in egg size between successful and failed nests, and the absence of effects of egg size on the probability of hatching appear to indicate that seasonal reduction in egg size in Greater Rheas does not affect female fitness.

The decline in egg size could be the consequence of female differences in age and/or experience. Some authors have reported the ability of females to produce eggs improves with age, resulting in older females laying earlier and larger eggs (Hipfner et al. 1997, Massaro et al. 2002). Similarly, eggs laid by young Greater Rhea females in captivity are smaller than those laid by older, experienced females (Flieg 1973, Guittin 1985, Gunski 1992). Besides, nesting success increases during the breeding season (Fernández and Reboreda 1998). Therefore, young females would be expected to have higher fitness than older hens if the differences in egg size we found were age related.

Another hypothesis for explaining seasonal variation in egg size postulates that females are constrained by laying late in the season (Lack 1968). Food supply, nutrient availability, or body reserves late in the season could affect the capability of females for laying (Williams 1994, 2005). In a related species, Emu (*Dromaius novaehollandiae*), clutch size appears to vary with amount of food available before laying (Davies 2002). Polyandry in rheas could similarly increase female demand for nutrients as the breeding season advances, limiting female capability for egg synthesis. Constraints in food quality or supply could af-

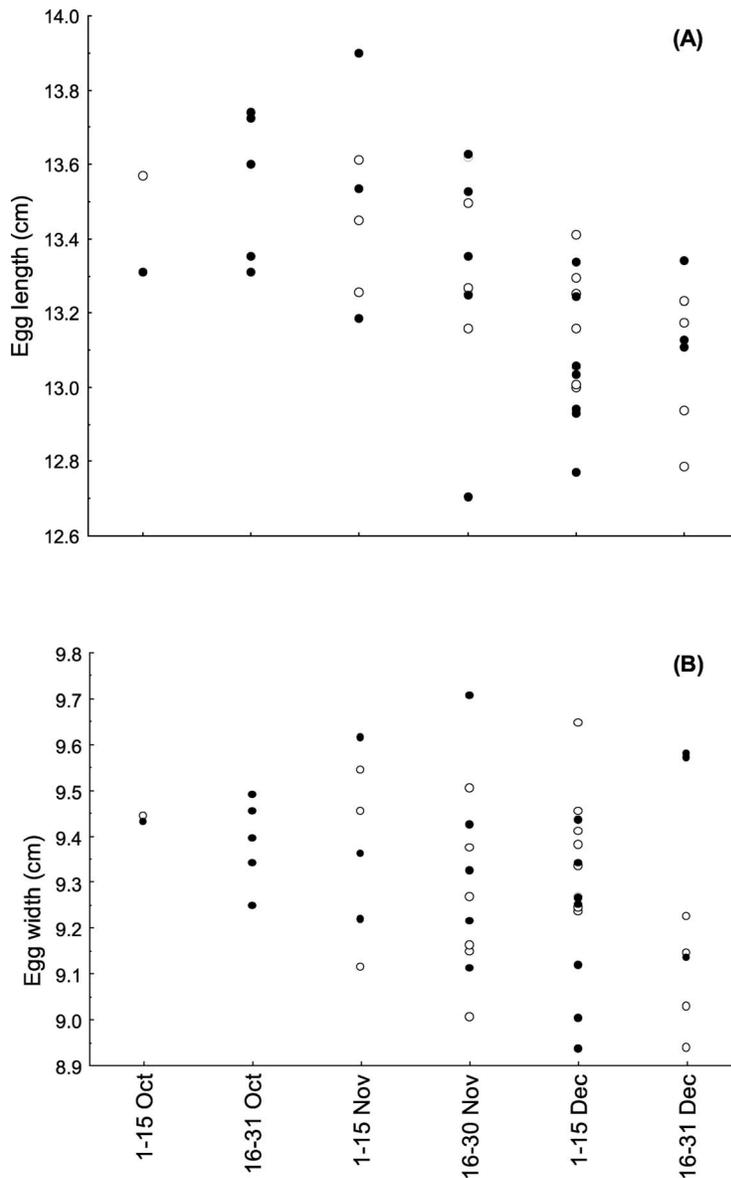


FIG. 2. Seasonal variation in egg length (A), and width (B) in Greater Rheas. Open and black dots correspond to egg mean values for clutches measured during 1992 and 1993, respectively.

fect egg size without affecting hatching success and chick survival.

We found that intra-clutch variation of egg size increased with clutch size. This variation could reflect the mating system of rheas. In this species, males defend a group of females that lay their eggs communally in a single nest. Thus, the variation detected may be the consequence of a larger number of different

females laying their eggs in the same nest, as larger clutches are the result of larger harems laying in the same nest (Fernández and Reboresda 1998).

Egg Content and Egg Size Variation.—Yolk mass represented ~35% of egg content. This value was slightly smaller than predicted (39.1) for precocial eggs using the equation of Sotherland and Rahn (1987). It was similar to

that measured in Common Ostrich (*Struthio camelus*, 37.8%; Sotherland and Rahn 1987), but smaller than that of Southern Cassowary (*Casuarius casuarius*, 42%; Sotherland and Rahn 1987), Emu (47%; Dzialowski and Sotherland 2004), and Southern Brown Kiwi (*Apteryx australis*, 61%; Calder et al. 1978). The smaller content of yolk mass in rhea eggs is associated with a shorter incubation period (40 days) compared to other ratites (Emu: 56 days; Cassowary: 50–52 days; Kiwi: 70–90 days; Davis 2002) but similar to that of ostriches (40–45 days). The percentage of yolk mass of rheas that we measured was similar to that obtained in a previous study with eggs collected in captive and wild populations (Navarro et al. 2001). That study found that wet yolk represented ~34–36% of shell-free egg mass.

Seasonal reduction in egg length and the increase in egg size differences within clutches as clutch size increases were not associated with changes in yolk content, but likely with albumen mass, as the latter was associated with egg length. Females under nutritional constraints may reduce investment by reducing albumen content, while keeping yolk content constant. If natural selection favors reduction in variation of egg characteristics that affect chick fitness (Jover et al. 1993), females with nutritional constraints could vary investment in egg components other than yolk content (Carey et al. 1980). Thus, it would be expected that lower seasonal variation in egg width (which is associated with yolk content) than in egg length (which is associated with albumin content) would produce no effect on egg size on hatching success. Additional support is provided by the absence of an association between variation in egg width and clutch size, which could reflect the high constancy of yolk contained within eggs.

Variation of egg size in Greater Rheas was not associated with a decrease in hatching success or nesting success. Thus, there are no apparent benefits from laying larger eggs, as reported for other precocial species (i.e., Hepp et al. 1989). Seasonal variation of egg size in Greater Rheas would be the result of environmental constraints (nutrients or food quality or availability) and/or variation in quality, age or experience of laying females, rather than an adaptive strategy of females to maximize

hatching success and chick survival. Further data about nutritional constraints and female investment in eggs are necessary to confirm this hypothesis.

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