Universidade de Brasília

Instituto de Ciências Biológicas

Programa de Pós-graduação em Ecologia

Geographical variation in reproductive investment of Tinamidae

Ana Paula Borges de Souza

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia do Instituto de Ciências Biológicas da Universidade de Brasília, como requisito parcial para a obtenção do título de Mestre em Ecologia.

Orientador: Prof. Dr. Miguel Ângelo Marini

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Este trabalho é dedicado aos meus avós Zélia e Danilo Borges.

"Às vezes, a verdadeira vitória não se pode mostrar, nem a verdadeira coragem é tão visível ou evidente quanto se pensa."

Ernest Hemingway

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SUMÁRIO

1 **ABSTRACT**

2   Tinamidae is a Neotropical family of gallinaceous-looking birds that occurs from

3 Mexico to Argentina and is composed by nine genera and 46 species. They are precocial birds,

4 which means that female investment is focused primarily on egg laying rather than on post

5 hatch parental care. Our objective was to analyze the geographic variation and the reproductive

6 investment of Tinamidae by testing two hypotheses: a) that egg size varies with body mass

7 (allometry) and b) that larger individuals and eggs should occur at higher latitudes and at colder

8 climates (Bergmann's Rule). We measured 839 eggs of nine species and six genera

9 photographed at 29 museums. Female body masses were obtained in the literature and in

10 scientific collections. We analyzed the relationships between 1) egg volume and estimated

11 female body mass; 2) estimated female body mass and latitude; 3) egg volume and latitude.

12 We made Linear Models (LM) at the species and genus level and Linear Mixed Effects Model

13 (LMER) for family level at the first two analyses and a PGLS and GLS were made to analyze

14 reproductive investment in the last one. Overall, changes in the two species traits analyzed, egg

15 volume and female body mass, varied differently across multiple taxonomic levels. All

16 analyses at family level showed significant results, but for the sole genus analyzed,

17 *Crypturellus,* only egg volume changed significantly with latitude. At species level, results

18 were highly mixed, with partial support for both the allometric relationship and Bergmann's

19 Rule. Only analyses with *R. rufescens* supported both hypotheses with significant positive

20 effects in all three analyses. The results of the relationship between egg volume and body mass

21 were the most contradictory, with three species showing a positive relationship, two a negative

22 relationship and four non-significant relationships. Only two species had significant positive

23 relationships between body mass and latitude, whereas for five species, including all four

24 *Crypturellus*, egg volume increased with latitude. In conclusion, we found partial support for

25 both hypotheses tested. Allometric rules cannot be widely applied to the relationship of egg

1 volume and female body mass in Tinamidae, since there was both positive, negative and lack

2 of correlations. Also, Bergmann's Rule cannot be widely applied in Tinamidae to explain

3 changes in female body mass across a latitudinal gradient, since only two species showed a

4 significant relationship. However, the best support for Bergmann's rule came from the increase

5 in egg volume with latitude in 64% (n = 11) of the comparisons made. Nonetheless, when

6 considering all analyses, we showed a wide variation among species and across taxonomic

7 levels, with no clear pattern, except for one species, *R. rufescens*. Overall, our results show that

8 since rules cannot be generalized, and to have more accurate and interpretable results, it would

9 be wise to break down analyses to the species level in future studies.

10

11 **Key words:** oology; allometry; latitudinal patterns; reproductive investment; neotropical

12 birds; Bergmann's rule.

13

14 **Palavras-chave:** Oologia; alometria; padrão latitudinal; investimento reprodutivo; aves

15 neotropicais; Regra de Bergmann**.**

INTRODUCTION

The search for patterns and explanations of geographical variation in species' traits, including reproductive ones, has been the one of the aims of ecologists for a long time. In birds, latitudinal gradients in reproductive investment exist with larger clutch sizes at higher latitudes (Moreau 1944; Koenig 1986; Ricklefs 2000). Also, southern and tropical species have longer periods of parental care and delayed dispersal (Russell 2000; Russell et al. 2004), supporting the idea that parental care and north-south asymmetry in survival rates may be due to differing climatic conditions between latitudes (Scholer et al. 2020). Seasonality of resources, nest predation and length of breeding period are some factors that might explain smaller clutch sizes in the tropics in relation to temperate areas (Griebeler et al. 2010). Therefore, tropical species are expected to have smaller clutch size and higher adult survival (Scholer et al. 2020). Also, it is expected that birds change their investment in egg quality, and thus egg size, at higher latitudes and colder climates. Parental incubation behavior often determines egg size in tropical species. Larger eggs may reflect compensation for increased energy requirements from cold egg temperatures and long embryonic periods that were the result of reduced parental attendance (Martin 2008).

One geographical pattern, Bergmann's Rule (Bergmann 1847), states that species of animals living in colder climates should be larger than phylogenetically close relatives living in warmer climates (Boyer et al. 2010; Blackburn et al. 2019). Later, Bergmann's rule was by redefined as warm-blooded animals living in colder climates are generally larger than those living in warmer regions (Rensch 1938). So larger animals would be in advantage when in cooler climates since the surface area to volume ratio is lower for them. However, even after this reformulation the definition and applications of Bergmann's rule are still widely discussed (Blackburn et al. 1999).

1   Despite its widespread use, Bergman's rule has limitations. It predicts that as heat is lost

2   from the body surface larger animals will have advantages due to their larger size and volume

3   ratio. However, the difference between individuals from higher and lower latitudes is not large

4   enough for this to be seen in nature (Blackburn et al. 1999; Meiri & Dayan 2003). Despite

5   criticisms, the rule is well supported for several taxa (Blackburn et al. 2019). Ray (1960)

6   compiled a series of studies and concluded that the rule was valid for 75% of the species. More

7   recently, Meiri & Dayan (2003) concluded that in birds and mammals Bergman's rule is valid

8   and that sedentary birds are more likely to follow the rule than migratory ones since migratory

9   species do not encounter severe climates as often as sedentary ones.

10   Allometry is the correlation between morphological dimensions of body parts and overall

11   size and describes differences in proportions of specific parts of an organism (Gould 1966;

12   LaBarbera 1989; Birchard & Deeming 2015). There are at least four different types of

13   allometry according to Gayon (2000): 1) ontogenetic allometry, which refers to the relative

14   increase in individuals; 2) phylogenetic allometry, which refers to the constant increase among

15   lineages; 3) intraspecific allometry, which refers to adult individuals of a species or population;

16   and 4) interspecific allometry, which refers to a phenomenon between species that are related.

17   In this work we will use the concepts of interspecific allometry according to Gould (1966)

18   which refers "*Allometry among species of a single genus (genera of a family, etc.) at the same*

19   *growth stage (usually the adult), but of different sizes*" and intraspecific allometry according

20   to Gould (1966) "*Allometry among races or subspecies of a single species at the same growth*

21   *stage (usually the adult), but of different sizes*". Since the relationship between egg size and

22   body mass in animals is allometric (Rahn et al. 1975; Ar et al. 1979), it is also of interest to

23   understand variations among species.

24   Tinamous are gallinaceous-looking birds which occur in the Neotropical region, from

25   Mexico (avg temperature 21 ºC – 34 ºC) to Patagonia (avg temperature 10 ºC – 25 ºC), with

1   nine genera - *Nothocercus, Tinamus, Crypturellus, Taoniscus, Nothura, Nothoprocta,*

2   *Rhynchotus, Tinamotis* and *Eudromia* - and 46 species (Bertelli & Porzecanski 2004).

3   Tinamidae species are sedentary and mostly do not inhabit regions with cold temperatures. The

4   genera vary considerably in size, with *Tinamus* being the largest – with a body mass of up to

5   2,000 g, and *Nothura* the smallest - with ca. 200 g. *Crypturellus* in turn exhibits a large variation

6   in body mass among species, as it is the largest genus, with species weighing from 200 to 650

7   g (Sick 2001; Dema et al. 2020; Gomes 2020). The family lacks sexual dimorphism in plumage

8   pattern, but females are regularly larger than males (Sick 2001). They eat fruits, leaves,

9   preferentially seeds, and eventually mollusks and arthropods.

10   Tinamidae nests are shallow openings and scrapes on the ground and offspring are

11   precocious. Female reproductive investment is primarily focused on laying the eggs, with low

12   investment in post hatch parental care if compared to altricial species (Blackburn 1991;

13   Brennan 2010). Males are sole caretakers of the nest and are responsible for incubation and

14   parental care of fledglings (Weeks 1973). Most interestingly, egg laying behavior varies

15   considerably among the species. For example, *Tinamus solitarius* females lay on average six

16   eggs in one single nest that is cared for by one male (Handford & Mares 1985; Sick 2001). On

17   the other hand, *Tinamus tao* also lays six eggs on average but divides the clutch in two different

18   nests, laying three eggs for one male to incubate and three for a second male to incubate

19   simultaneously (Sick 2001). Another interesting behavior occurs in *Crypturellus variegatus*

20   which also divides its clutch but this time in four nests from four different males (Sick 2001).

21   Tinamidae clutch size is highly variable, especially considering that some species, such as

22   *Crypturellus boucardi*, *Nothoprocta cinerascens*, *Eudromia elegans*, nest communally (Sick

23   2001), with more than one female laying eggs in the same nest. Besides these differences in

24   egg laying and clutch size, some behaviors change with age (Sick 2001). For example,

1 *Nothocercus* sp. when young are monogamous but when older change their reproductive

2 strategy to polygamy (Handford & Mares 1985; Sic 2001).

3   Tinamidae's eggs are commonly large in comparison to female body mass and vary

4 widely in size, shape and color among species. *Tinamus tao* have proportionally smaller eggs

5 than smaller species such as *Nothocercus bonapartei* (Sick 2001). Eggs may be more oval or

6 elliptical in smaller species of *Crypturellus* and become more spherical in *Tinamus*. The eggs

7 are very colorful and shiny, looking polished and enameled. There is a wide range of egg colors

8 within the family. From more bluish tones in *Tinamus* and *Nothocercus*, to brown tones

9 sometimes pinkish or burgundy as in *Crypturellus* and *Rhynchotus* (Hanley et al. 2013;

10 Hamchand et al. 2020). It is still unclear why all this color variation exists, but current studies

11 suggested as a possibility that signaling of nest location as Tinamidae nests are placed on the

12 ground and eggs are usually quite conspicuous (e.g. Hanley et al. 2013).

13   Given this high variation in reproductive traits among Tinamidae species, the general

14 purpose of this study is to analyze geographical variation in reproductive investment (egg

15 volume) in the species, genus and family levels. To achieve this, we first evaluated the

16 relationship between female body mass and egg volume. We expected that egg volume would

17 change with body mass, proportionally increasing or decreasing with body mass. Second, we

18 assessed how geographic variation along the latitudinal gradient affects body mass and

19 reproductive investment (egg volume) at the family, genus and species levels. Based on

20 Bergmann's rule, we expect that larger individuals and eggs should occur at higher

21 latitudes/colder climate areas.

22

23 **METHODS**

24 *Data collection*

1   We used the database of the Laboratório de Ecologia e Conservação de Aves to select

2   egg sets deposited at 29 South American, European and North American scientific collections.

3   The eggs were photographed to enable measurements (see below). Egg sets in scientific

4   collections are labelled with the name of the species, date and place of collection, among other

5   information. We measured 839 eggs, after we applied filters to exclude egg sets with

6   incomplete locality (country, state/department and city), and from captive birds. Nine species

7   of six genera had enough material for analysis, at least 29 eggs per species. All eggs with

8   complete locality had their latitudes estimated using the R program (R Core Team 2021) and

9   the ggmap package (Wickham 2016).

10

11   *Taxonomic resolution*

12   Considering that many scientific egg collections have outdated taxonomy, we reviewed

13   the taxonomic classifications of each egg set employing as sources the following catalogues,

14   according to the collection date: Salvadori (1895), Peters (1931), and Hellmayr & Conover

15   (1942). Lastly, we updated the scientific name according to Clements et al. (2019). As part of

16   the validation process of the records, we checked if the collecting location described in the

17   museum label was within, or very close to the species breeding range (Appendix 1), as shown

18   at the Handbook of the Birds of the World (HBW 2020). Egg sets that could not be validated

19   were discarded.

20

21   *Female body masses*

22   To allow analysis of latitudinal effects on egg size we need to control for the confounding

23   effects of changes in body mass with latitude. However, since we did not have body masses of

24   the laying females for any of the egg sets, we estimated average female body mass for each

25   latitude based on available body masses for each species (see details below). To accomplish

this, we searched for reports of female body masses in published records and at museums from the online database Arctos. We complemented the dataset with information from specimens deposited at the Coleção Ornitológica Marcelo Bagno, Brasília, Brazil (COMB) (Appendix 2). Since we needed approximate latitudinal coordinates, only body masses with localities with traceable latitudes were used. Also, we rounded coordinates to full degrees to improve sample sizes of localities with broad descriptions, but never extending more than one degree. Details of the collecting location can be found in the respective reference list in Appendix 2. A few studies reported average values of birds from the same locality, and we excluded body masses of males and immatures, island, and captive birds. To avoid adding records of misidentified or undernourished individuals, and of individuals that were found dead, we excluded body masses with outlier values.

Egg measurements

Egg measurements were made from the digital photographs using *ImageJ* software (https://imagej.nih.gov/ij/), with the support of the plugin "*EggTools*" (http://www.jolyon.co.uk/research/eggs/) (Troscianko 2014).

Statistical analyses

<u>*Egg size x Body mass*</u>

To determine the allometric relationship between reproductive effort and female body size we analyzed in egg size at species, genus and family levels, controlling for their body mass using linear models. All the models were constructed with egg size (egg volume; cm³) as a response variable and the estimated female mass, corresponding to the latitude of the clutch collection site, as the independent variable. At the family and genus level analyses, we fitted linear mixed effects models (LMER) using the R packages "lme4" (Bates et al. 2015) and

1 "lmerTest (Kuznetsova et al. 2017) where we used "genus + species" and "species" as a random

2 effect, respectively.

3   To define the body size for each female for the egg sets gathered from egg collections,

4 the latitude from each egg set was taken as a predictor of body mass. To achieve this, the

5 estimated female mass from each egg set was inferred through the linear model constructed for

6 the model "body mass X latitude". We based on the equation $\hat{y}_i = \hat{\beta}_0 + \hat{\beta}_1 x_i + \hat{\varepsilon}_i,$ where $\hat{\beta}_0$

7 is the intercept of regression, $\hat{\beta}_1$ is the angular coefficient about the explanatory variable x_i,

8 which was replaced with latitude from the egg set, and $\hat{\varepsilon}_i$ represents the residual errors, which

9 were randomly determined in the interval standard error. Then, the predicted value $\hat{y}_i$, was set

10 as potential mass for the female from the egg set.

11

12 *Body mass x Latitude*

13   The potential response of female body mass along the latitudinal gradient was analyzed

14 with the Linear Models (LM) method for each species. The Linear Mixed Effects Models

15 (LMER) approach was applied to test this response for all the Tinamidae family dataset and

16 for each isolated genus dataset (Zuur et al. 2009). We used body mass values as response

17 variables while the latitude values, extracted from the centroid of each respective location, were

18 taken as independent variables. For the family model, including all our Tinamidae dataset, we

19 took "genus" and "species" as random effects. We took "species" as a random effect when

20 analyzing each genus, indicating the hierarchical grouping from the data based on biological

21 similarity within taxonomic groups. All the LMER were performed using the "lme4" package

22 (Bates et al. 2015).

23

24 *Egg size x Latitude*

1   We used a Phylogenetic Generalized Least-Squares (PGLS) method approach, through

2   the "nlme" package (Pinheiro et al. 2020), to evaluate the relationship between latitude and egg

3   size at the family level. For this, we used the phylogenetic tree from the complete phylogeny

4   provided by Jetz et al. (2012) at the Bird Tree website (birdtree.org) (Figure 1). we selected the

5   species included in this study, then we extracted 1,000 tree versions using the Hackett's

6   backbone distribution. The consensus tree was produced after 1,000 randomizations using the

7   "ape" package (Paradis & Schliep 2019). To determine the relevance of the phylogenetic

8   correlation in the dependent variable, we estimated Pagel's lambda (λ) (Pagel 1999). Pagel's

9   lambda value allows us to understand, at a range between 0 and 1, how correlated are the tree

10   components, and therefore how much evolutionary history is shared by them. we still checked

11   the robustness of the PGLS model by maximum likelihood, comparing it to models fitted with

12   generalized least squares approach, by combining phylogenetic correlation and estimated

13   female body mass as a fixed variable or with the "weight" function of the "nlme" package.

14   Then, we proceeded with the model with the highest maximum likelihood value. For the genus

15   approach, we fitted linear mixed effects models with "species" as a random effect. The analysis

16   at the species level was constructed based on the linear model approach (LM).

17   Respecting the principles of homoscedasticity, independence, and normality, we checked

18   the distribution of all variables, tested their correlation using Spearman's index, and

19   subsequently tested the distribution of the residuals of the models. To avoid model convergence

20   errors, all the variables used in the analyses were standardized to a mean of zero and a standard

21   deviation of one.
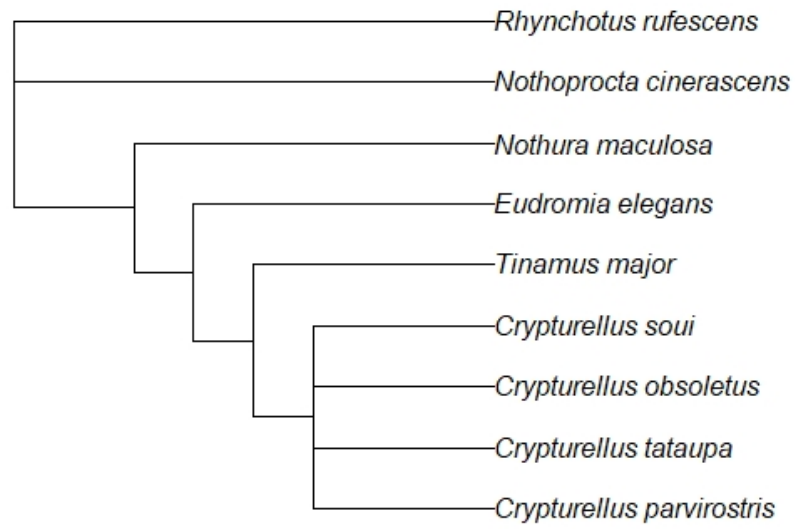
1

2 **Figure 1** Phylogenetic tree of the species of Tinamidae used in this study based on Jetz et al.

3 (2012).

4

1 **RESULTS**

2   We measured a total of 839 eggs, from 6 genera and nine species from the Tinamidae

3 family, with egg volume ranging from 1.7 cm^3 for *Crypturellus parvirostris* to 6.5 cm^3 for

4 *Tinamus major* (Table 1). We assembled 118 female body masses, which varied from 171 g

5 for *C. parvirostris* to 1,090 g for *T. major* (Table 1). The proportional investment in individual

6 eggs was low for all species ranging from ~ 0.6 to 1.0 % of female body masses, with species

7 ≥ 500 g investing less (0.59-0.68 %) and the lighter species investing more (0.85-1.00 %).

8

9 **Table 1** Egg volume (cm^3) and female body mass (g) and investment in eggs (% = the

10 proportion between egg volume and female body mass) of Tinamidae species. N = sample

11 sizes.

| Species	Egg		Female body mass		
	N	Volume (cm^3)	N	Body mass (g)	Investment (%)
Tinamus major	113	6.47 ± 0.89	23	1,090 ± 149.5	0.59
Rhynchotus rufescens	86	6.03 ± 1.05	12	873 ± 53.4	0.69
Eudromia elegans	91	4.20 ± 0.40	16	693 ± 74.1	0.61
Nothoprocta cinerascens	75	3.40 ± 0.45	8	498 ± 61.0	0.68
Crypturellus obsoletus	29	3.77 ± 0.62	13	409 ± 62.9	0.92
Nothura maculosa	188	2.29 ± 0.40	12	269 ± 23.7	0.85
Crypturellus soui	77	2.24 ± 0.39	16	223 ± 43.9	1.00
Crypturellus tataupa	124	2.08 ± 0.33	12	222 ± 26.3	0.94
Crypturellus parvirostris	56	1.70 ± 0.20	6	171 ± 14.8	0.99

1

Egg volume x Female body mass

The relation between egg volume and female body mass varied differently across multiple taxonomic levels. Egg volume increased with female body mass at the family level, but not for the *Crypturellus* genus (Table 2, Figure 2). When we analyze each species individually, for five species egg volume changed significantly with female body mass, though results were contradictory. For three species (*C. obsoletus, N. cinerascens* and *R. rufescens*) egg volume increased with an increase of female body mass, but for two species (*C. soui,* and *C. tataupa*) the relationship was inverse, with egg volume decreasing with an increase of body mass (Table 2, Figure 3).

Female body mass x Latitude

Similarly to the results of egg volume and body mass, the response of female body mass with latitude also varied differently across multiple taxonomic levels. Body mass increased with latitude at the family level, but not for the *Crypturellus* genus (Table 3, Figure 2). At the species level, only two of the nine species showed an increase in body mass with latitude (Table 3, Figure 3).
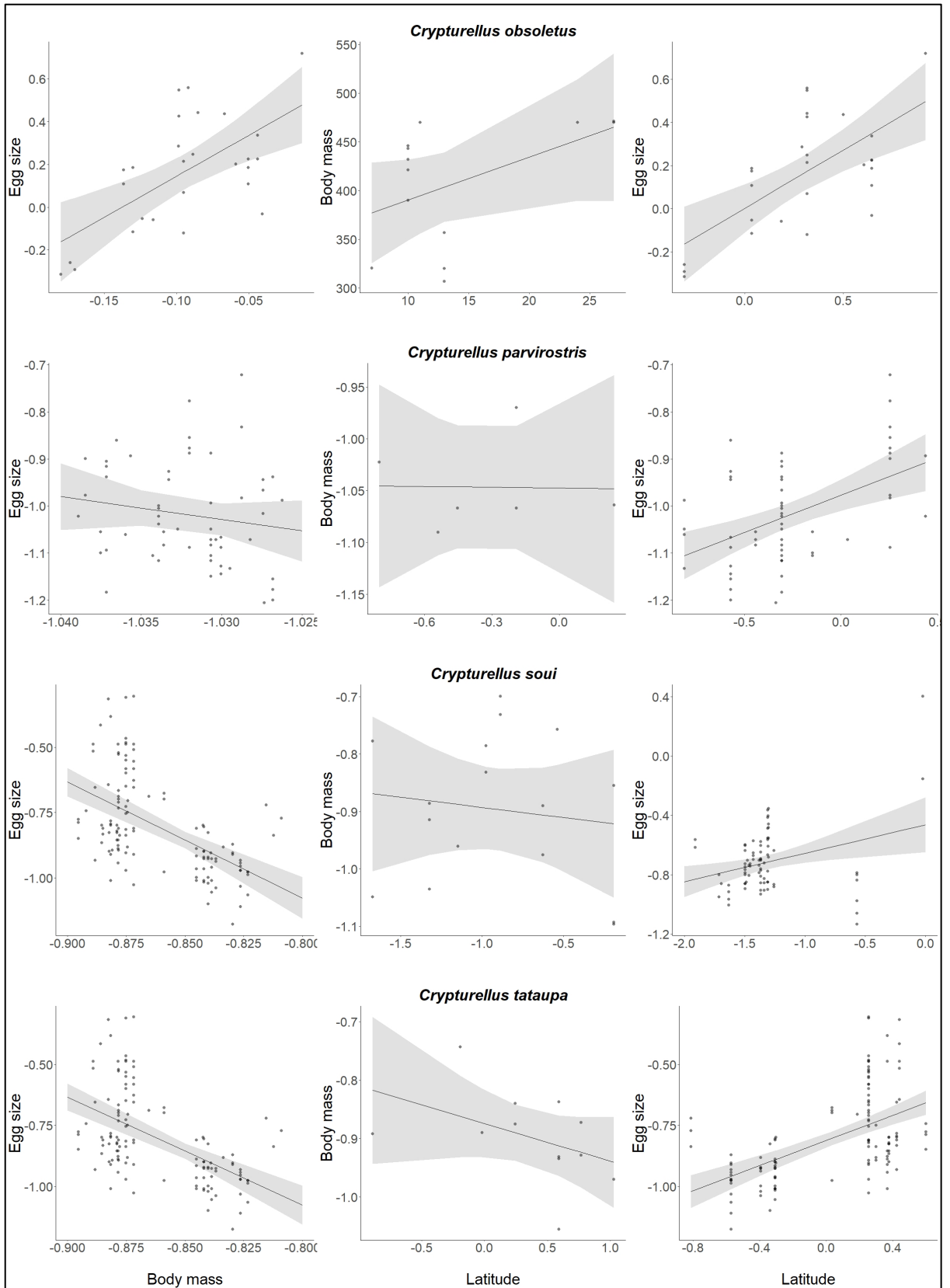
Egg volume x Latitude

Again, as in the two analyses above, egg volume changed with latitude, but varied differently across multiple taxonomic levels. Egg volume varied with latitude at the family level and was significant for the genus *Crypturellus* (Table 4, Figure 2). At the species level, all four *Crypturellus* species and *R. rufescens* showed a significant positive relationship between egg volume and latitude (Table 4, Figure 3).
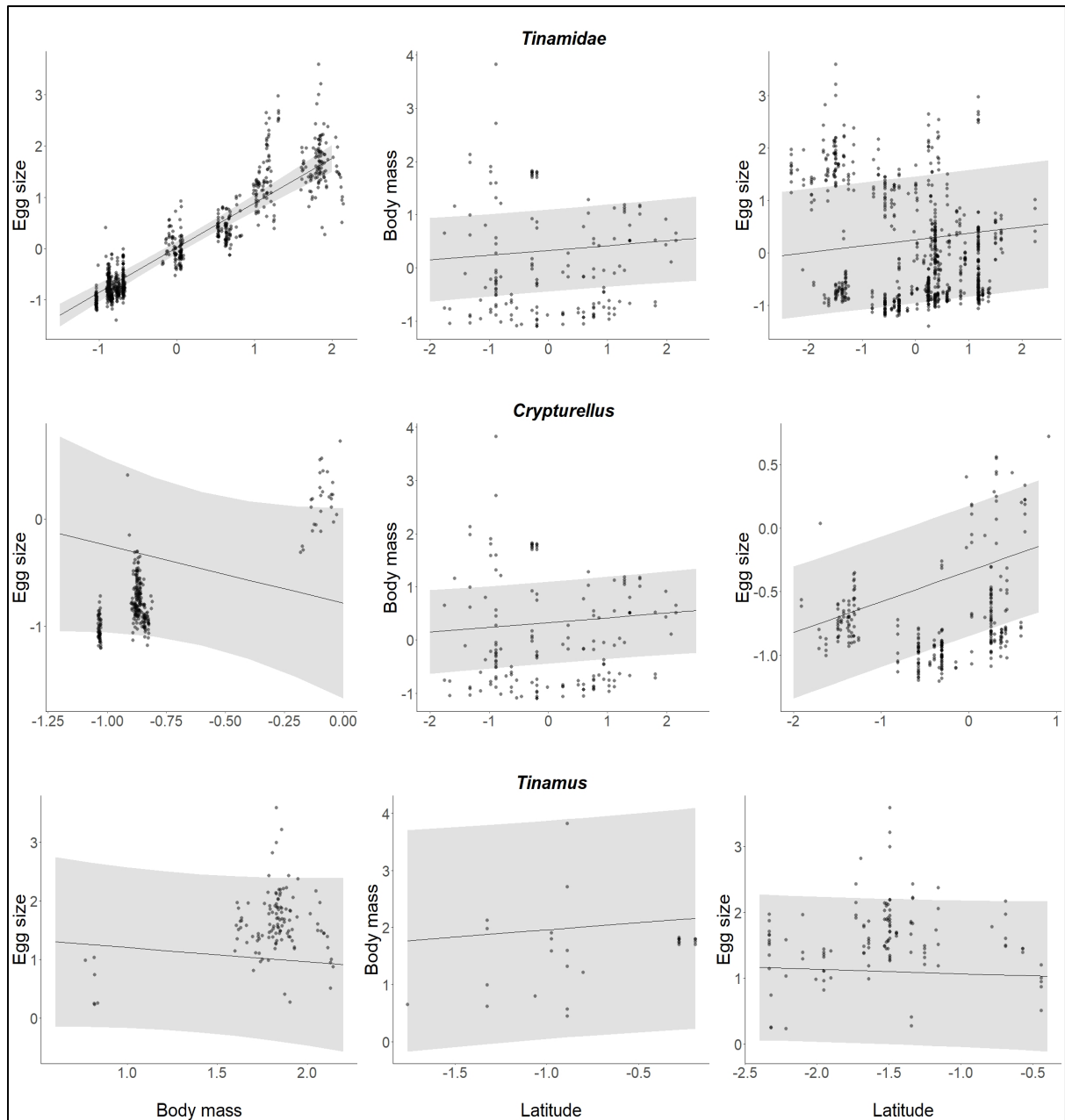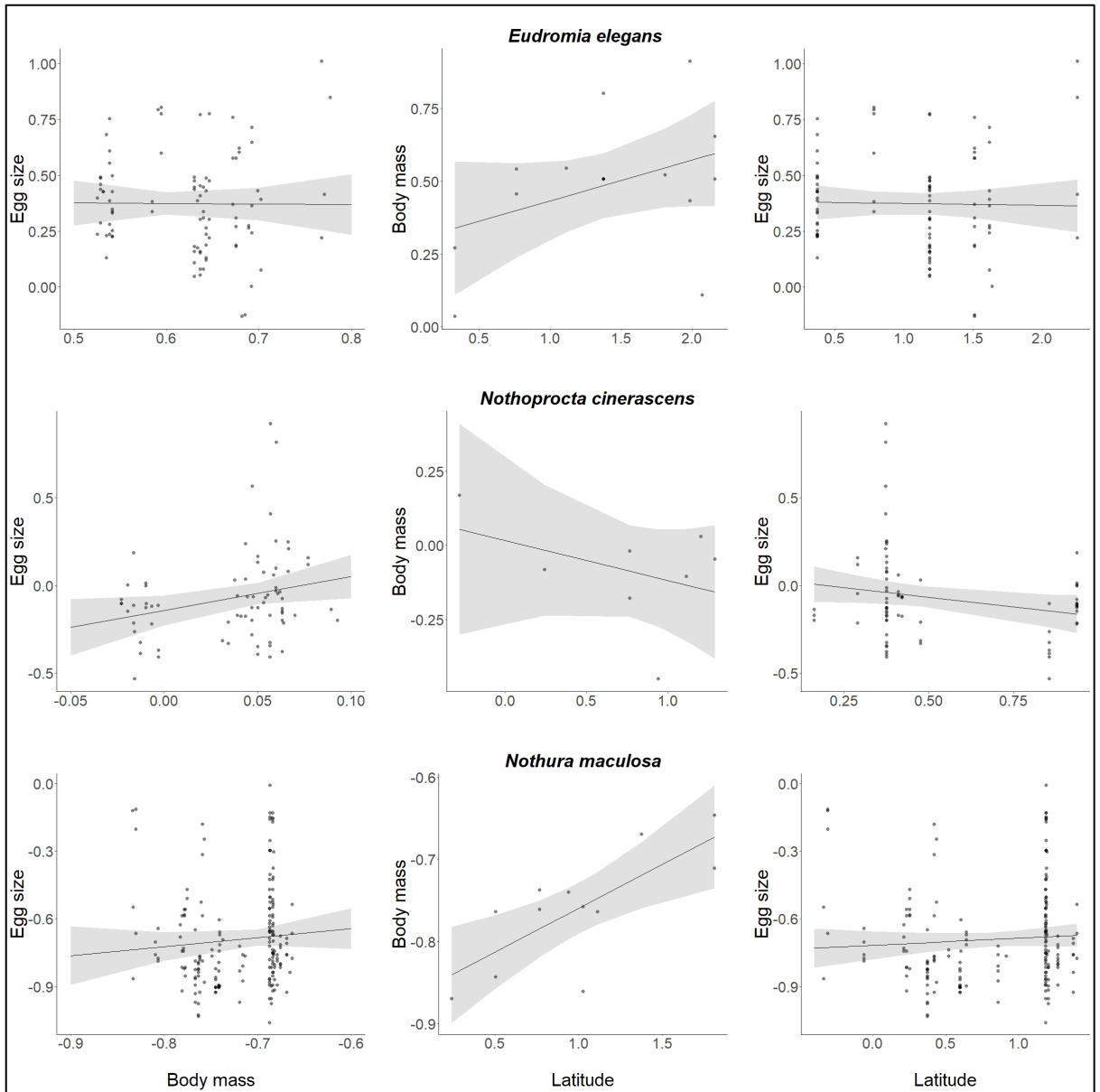
Figure 2 Relationships between egg volume and female body mass, female body mass and latitude, and egg volume and latitude for the Tinamidae family and *Crypturellus* genera. The scales were resized to avoid model convergence errors (mean = 0, standard deviation = 1). For estimates, see tables 2, 3 and 4.

Crypturellus obsoletus

Crypturellus parvirostris

Crypturellus soui

Crypturellus tataupa

Body mass

Latitude

Latitude

1
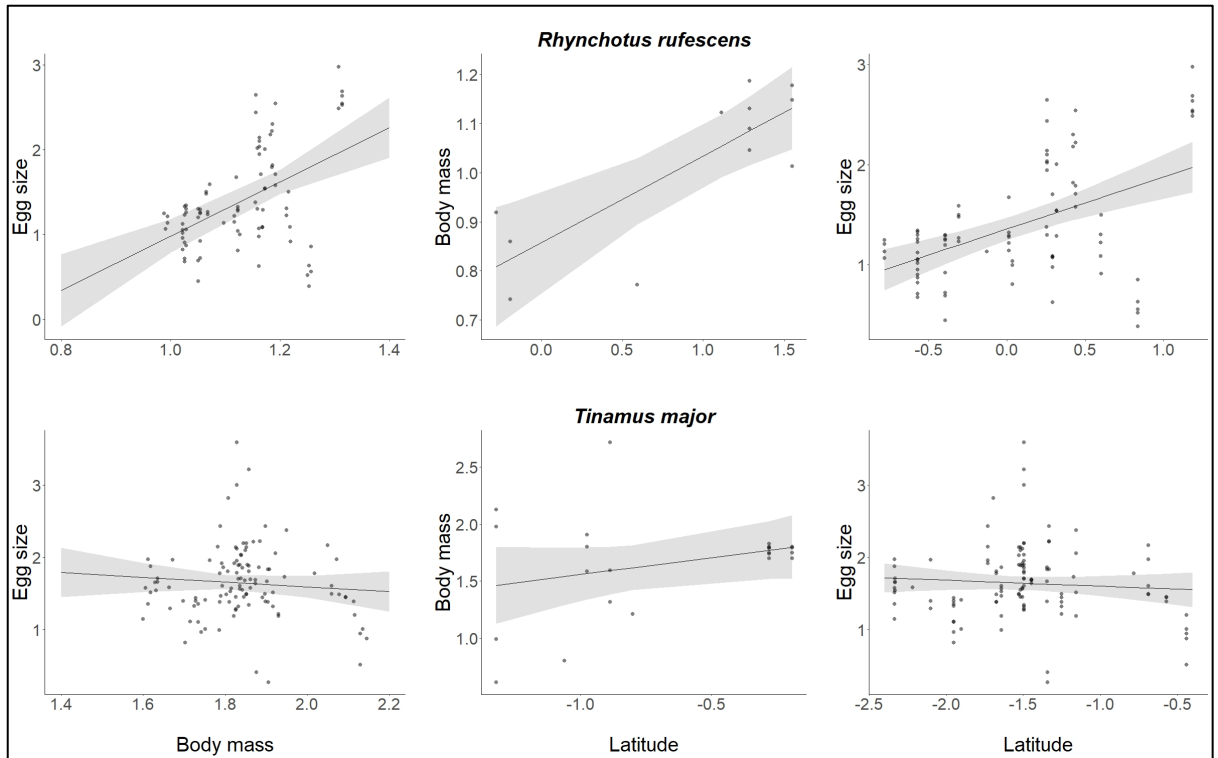
Figure 3 Egg volume by female body mass; female body mass by latitude; and egg volume by latitude for nine species of Tinamidae. The scales were resized to avoid model convergence errors (mean = 0, standard deviation = 1). For estimates see tables 2, 3 and 4.

1 **Table 2** Egg volume x female body mass LMER for family and genera levels and LM for

2 species level of Tinamidae, Spearman's index was used to test the correlation. Significant

3 results are highlighted in bold.

	N	intercept	β	Std. error	T-value	p-value
Tinamidae	**839**	**0.013**	**0.868**	**0.061**	**14.337**	**<0.001**
Crypturellus spp.	284	-0.787	-0.538	0.455	-1.181	0.25
Crypturellus obsoletus	**27**	**0.529**	**3.834**	**0.942**	**4.068**	**<0.001**
Crypturellus parvirostris	56	-6.026	-4.852	4.076	-1.19	0.239
Crypturellus soui	**77**	**-4.612**	**-4.494**	**1.933**	**-2.325**	**0.023**
Crypturellus tataupa	**124**	**-4.627**	**-4.436**	**0.62**	**-7.16**	**<0.001**
Eudromia elegans	91	0.39	-0.026	0.362	-0.072	0.943
Nothoprocta cinerascens	**75**	**-0.142**	**1.929**	**0.868**	**2.224**	**0.029**
Nothura maculosa	188	-0.402	0.401	0.354	1.132	0.259
Rhynchotus rufescens	**86**	**-2.216**	**3.197**	**0.629**	**5.08**	**<0.001**
Tinamus major	113	2.247	-0.328	0.373	-0.881	0.38

4

5

1　**Table 3** Female body mass x latitude LMER for family and genera levels and LM for species

2　level of Tinamidae, Spearman's index was used to test the correlation. Significant results are

3　highlighted in bold.

	N	intercept	β	Std. error	T-value	p-value
Tinamidae	**162**	**0.329**	**0.09**	**0.039**	**2.29**	**0.024**
Crypturellus spp.	66	-0.396	0.032	0.036	0.89	0.378
Crypturellus obsoletus	14	-0.272	0.148	0.081	1.84	0.093
Crypturellus parvirostris	6	-1.048	-0.003	0.061	-0.042	0.968
Crypturellus soui	16	-0.928	-0.035	0.07	-0.503	0.623
Crypturellus tataupa	13	-0.874	-0.064	0.042	-1.532	0.157
Eudromia elegans	17	0.293	0.14	0.087	1.606	0.131
Nothoprocta cinerascens	8	0.017	-0.135	0.126	-1.068	0.327
Nothura maculosa	**12**	**-0.866**	**0.107**	**0.03**	**3.594**	**0.005**
Rhynchotus rufescens	**12**	**0.858**	**0.177**	**0.04**	**4.443**	**0.001**
Tinamus major	23	1.853	0.294	0.208	1.416	0.171

4

5

Table 4 Egg volume x latitude WPGLS for family and genera levels and GLS for species level, Spearman's index was used to test the correlation. Significant results are highlighted in bold.

	intercept	β	Std. error	T-value	p-value
Tinamidae	**0.253**	**0.120**	**0.025**	**4.837**	**0.000**
***Crypturellus* spp.**	**-0.337**	**0.242**	**0.028**	**8.631**	**<0.001**
Crypturellus obsoletus	**0.004**	**0.533**	**0.125**	**4.258**	**<0.001**
Crypturellus parvirostris	**-0.977**	**0.159**	**0.039**	**4.079**	**<0.001**
Crypturellus soui	**-0.471**	**0.186**	**0.070**	**2.674**	**0.009**
Crypturellus tataupa	**-0.812**	**0.259**	**0.036**	**7.154**	**<0.001**
Eudromia elegans	0.378	-0.005	0.045	-0.102	0.919
Nothoprocta cinerascens	0.042	-0.218	0.115	-1.897	0.062
Nothura maculosa	-0.723	0.039	0.035	1.111	0.268
Rhynchotus rufescens	**1.359**	**0.519**	**0.103**	**5.057**	**<0.001**
Tinamus major	1.519	-0.081	0.101	-0.807	0.422

DISCUSSION

The geographical variation in species' traits was evaluated here by testing two hypotheses, the allometric relationship of egg volume with an increase in female body mass, and Bergmann's Rule which proposes that body mass and egg volume increase with increasing latitude. Overall, changes in the two species traits analyzed, egg volume and female body mass, varied differently across multiple taxonomic levels (Table 5). All analyses at family level showed significant results, but for the sole genus analyzed, *Crypturellus,* only egg volume changed significantly with latitude. At the species level, results were highly mixed, with partial

1 support for both the allometric relationship and Bergmann's Rule. Only *R. rufescens* supported

2 both hypotheses with significant positive effects in all three analyses. The results of the

3 relationship between egg volume and body mass were the most contradictory, with three

4 species showing a positive relationship, two a negative relationship and four with non-

5 significant relationships. Only two species had significant positive relationships between body

6 mass and latitude, whereas for five species, including all four *Crypturellus*, egg volume

7 increased with latitude.

8

9 **Table 5** Summary of the results of the correlations between egg volume x body mass, body

10 mass x latitude and egg volume x latitude, with species ordered by female body mass. NS =

11 non-significant, (+) = significant positive correlation, and (–) = significant negative correlation.

Taxonomic level	Body mass (g)	Egg volume x Body mass	Body mass x latitude	Egg volume x latitude
Tinamidae	----	+	+	+
Crypturellus spp.	----	NS	NS	+
Tinamus major	1,090	NS	NS	NS
Rhynchotus rufescens	873	+	+	+
Eudromia elegans	693	NS	NS	NS
Nothoprocta cinerascens	498	+	NS	NS
Crypturellus obsoletus	409	+	NS	+
Nothura maculosa	269	NS	+	NS
Crypturellus soui	223	–	NS	+
Crypturellus tataupa	222	–	NS	+
Crypturellus parvirostris	171	NS	NS	+

12

1   *Egg volume x Female body mass*

2   Our results demonstrate that egg volume relative to female body mass varies

3   considerably across multiple taxonomic levels. The expected increase in egg volume in relation

4   to female body mass (Rahn et al. 1975; Olsen & Cockburn 1993; Deeming 2007) was

5   corroborated at the family level but had contradictory results at the species level. While three

6   species showed the expected positive allometry (*C. obsoletus, N. cinerascens* and *R. rufescens*)

7   this relationship, contrary to expectations, was negative for *C. soui* and *C. tataupa* which

8   suggests a negative allometric relationship between egg volume and body mass. Negative

9   allometry occurs when egg volume and female body mass increase occur in different

10   proportions (Meiri et al. 2015). In this case, larger females lay smaller eggs, which means that

11   egg volume is not increasing in the same proportion as female body mass (Meiri et al. 2015;

12   Mytiai et al. 2021). To further complicate the scenario, for both species egg volume increased

13   with latitude, whereas female body mass did not.

14   Lastly, species with smaller females invested proportionally more in individual eggs than

15   larger females. Intuitively, one would interpret this result proposing a negative relationship

16   between egg size and clutch size, with smaller species laying smaller clutches and vice-versa.

17   However, since female egg laying behavior and mating systems in the Tinamidae family are

18   highly variable and still partially undescribed (Handford & Mares 1985; Sick 2001), any

19   current interpretation seems premature. Experiments in controlled laboratory conditions might

20   help explain this pattern, by individually marking females, by following egg laying and

21   measuring eggs.

22

23   *Female body mass x Latitude*

24   The correlations of estimated female body mass with latitude varied across taxonomic

25   levels and showed complex results. Body mass increased significantly with latitude only at the

1 family level and for two species, thus weakly supporting Bergmann's rule (Blackburn et al.

2 2019). Since most species showed no effect, there is a limitation of widely applying

3 Bergmann's rule to Tinamidae species.

4   Possible limitations of Bergmann's rule (Blackburn et al. 1999) could provide some

5 explanations for the partial support of this hypothesis in the group. Smaller body sized species

6 need to develop behavioral and physiological adaptations to survive/evolve in colder

7 environments. Species which cannot adapt to cooler climates would probably be replaced by

8 other species more adapted to such climates. Also, individuals can reproduce in higher latitudes

9 and spend the winter in lower latitudes or in hibernation (Blackburn et al. 1999). Small species

10 are less represented at higher latitudes, have lower dispersal ability and even migratory birds

11 tend to show larger body mass as latitudes increase (Blackburn et al. 1999; Meiri & Dayan

12 2003). Larger sized animals increase resistance to starvation, which would be an advantage in

13 high latitudes because of resource shortage (Meiri & Dayan 2003). However, there are other

14 strategies to acquire, store, and save energy, including hibernation, storage of energetic

15 reserves (fat), food stocking, and the use of microclimate refuges like burrows or nests

16 (Blackburn et al. 1999; Meiri & Dayan 2003).

17

18 *Egg volume x Latitude*

19   The pattern that was most supported by our data was the increase in egg volume with

20 latitude, with significant consistent results in seven of the 11 analyses, but still with some

21 variation among species. Egg volume increased with latitude at the family level, for the

22 *Crypturellus* genus, for all four *Crypturellus* species and for *R. rufescens.*

23   As mentioned before, for two species of *Crypturellus* (*C. soui* and *C. tataupa*) we found

24 a negative relationship between egg volume and body mass and a positive relationship between

25 egg volume and latitude, but no change in body mass with latitude. Though these results are

counterintuitive, they allow us to provide two explanations. First, that egg volume does not necessarily have to increase in the same proportion as body mass. Thus, probably some intrinsic characteristic of these two species might explain the change to lower investment in individual eggs with larger body sizes. Second, that there is a decoupling of latitudinal effects on birds` traits. This decoupling was evident for all four species of *Crypturellus* as well as for *Nothura maculosa* which increased body mass, but not egg volume with an increase in latitude. Overall, our results show that species traits are probably evolving independently and suffering different selective pressures and should, thus, be interpreted on a species-by-species basis.

The lack of a broad pattern across all nine species of Tinamidae for all three comparisons (egg volume x body mass, body mass x latitude and egg volume x latitude), might have several explanations. First, species might have intrinsic independent ecological, behavioral and physiological characteristics. For example, life history patterns such as incubation period, parental care behavior, clutch size and hatchling mass also influence egg volume (Martin et al. 2006; Rotenberry & Balasubramaniam 2020). The incubation period often increases with egg volume thus the decrease in egg volume could also be due to location, latitude and possible predators and risk factors that could not allow for longer incubation (Rotenberry & Balasubramaniam 2020; Scholer et al. 2020). Second, sample sizes for body masses were low (6 to 23 females), and the estimation we used to infer female body masses by latitude need to be improved. However, this sample size explanation should not apply to egg volume analyses since sample sizes were medium to large (27-188 eggs). Lastly, at least for some species, such as *Eudromia elegans* and *Nothoprocta cinerascens*, latitudinal ranges are inherently small (Figure 1), which might explain the lack of latitudinal effect on species traits. This explanation, however, loses support, since *Crypturellus obsoletus* also has a narrow range, but showed an increase in egg volume with latitude. Using the same rationale, a small range of variation in

female body masses of *Crypturellus parvirostris* (-11º to -23º S) would make it difficult to detect any allometric relationship between egg volume and body mass.

The limited availability of body masses of most Tinamidae shows that, contrary to Vuilleumier (1999) studies reporting body masses only with sexed birds and geographical coordinates are still necessary, even for common species. Also, our study shows the importance and potential use of scientific egg collections to test hypotheses (Marini et al. 2020), with data seldom available in the published literature. Despite that potential, even these egg collections still lack large sample sizes to analyze most species.

CONCLUSIONS

In conclusion, we found partial support for both hypotheses tested. Allometric rules cannot be widely applied to the relationship of egg volume and female body mass in Tinamidae, since there was both positive, negative and lack of correlations. Also, Bergmann's Rule cannot be widely applied in Tinamidae to explain changes in female body mass across a latitudinal gradient, since only two species showed a significant relationship. However, the best support for Bergmann's rule came from the increase in egg volume with latitude in 64% (n = 11). Overall, when considering all analyses, we showed a wide variation among species and across taxonomic levels, with no clear pattern, except for one species, *R. rufescens*. Our results show that since rules cannot be generalized, and to have more accurate and interpretable results, it would be wise to break down analyses to the species levels in future studies. For future studies, it would be interesting to perform analyzes with clutches and collect more body masses to have more robust results and perform analyzes with more species.

REFERENCES

Ar, A., H. Rahn, & C. V. Paganelli (1979). The avian egg: Mass and strength. *The Condor,* 81,

1   331.

2   Bates, D., M. Mächler, B. Bolker, & S. Walker (2015). Fitting linear mixed-effects models

3   using lme4. *Journal of Statistical Software,* 67, 1–48.

4   Bergmann, C. (1847). Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse.

5   *Göttinger Studien*, 1, 1, 595-708.

6   Bertelli, S., & A. L. Porzecanski. (2004). Tinamou (Tinamidae) systematics: a preliminary

7   combined analysis of morphology and molecules. *Ornitologia Neotropical*, 15, 293–299.

8   Blackburn, T. M. (1991). An interspecific relationship between egg size and clutch size in

9   birds. *The Auk*, 108, 973–977.

10   Blackburn, T. M., Gaston, K. J., & Loder, N. (1999). Geographic gradients in body size: A

11   clarification of Bergmann's rule. *Diversity and Distributions,* 5, 165–174.

12   Blackburn, T. M., Redding, D. W., & Dyer, E. E. (2019). Bergmann's rule in alien birds.

13   *Ecography* 42(1), 102–110.

14   Boyer, A. G., Cartron, J. L. E., & Brown, J. H. (2010). Interspecific pairwise relationships

15   among body size, clutch size and latitude: Deconstructing a macroecological triangle in

16   birds. *Journal of Biogeography*, 37(1), 47–56.

17   Brennan, P. L. R. (2004). Techniques for studying the behavioral ecology of forest-dwelling

18   tinamous (Tinamidae). *Ornitologia Neotropical*, *15*(suppl.), 329–337.

19   Brennan, P. L. R. (2010). Clutch predation in great tinamous *Tinamus major* and implications

20   for the evolution of egg color. *Journal of Avian Biology*, 41(4), 419–426.

21   Deeming, D. C. (2007). Effects of phylogeny and hatchling maturity on allometric relationships

22   between female body mass and the mass and composition of bird eggs. *Avian and Poultry*

23   *Biology Reviews*, 18, 21–37.

24   Deeming, D. & Birchard, G. (2015). Egg allometry: influences of phylogeny and the altricial

25   precocial continuum. Oxford University Press. Oxford.

Gayon, J. (2000). History of the concept of allometry. *American Zoologist*, 40(5), 748–758.

Gould, S. J. (1966). Allometry and size in ontogeny and phylogeny. *Biological Reviews of the Cambridge Philosophical Society*, 41(4), 587–640.

Griebeler, E. M., Caprano, T., & Bo, K. (2010). Evolution of avian clutch size along latitudinal gradients: do seasonality, nest predation or breeding season length matter? *Journal of Evolutionary Biology,* 23, 888–901.

Hamchand, R., Hanley, D., Prum, R. O., & Brückner, C. (2020). Expanding the eggshell colour gamut: uroerythrin and bilirubin from tinamou (Tinamidae) eggshells. *Scientific Reports*, 10(1), 1–9.

Handford, P. & Mares, M.A. (1985) The mating system of ratites and tinamous: an evolutionary perspective. *Biological Journal of the Linnean Society*, 25, 77-104.

Hanley, D., Stoddard, M. C., Cassey, P., & Brennan, P. L. R. (2013). Eggshell conspicuousness in ground nesting birds: Do conspicuous eggshells signal nest location to conspecifics? *Avian Biology Research*, 6(2), 147–156.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. 2012. The global diversity of birds in space and time. *Nature,* 49(1), 444–448.

Koenig, W. D. (1986). Geographical ecology of clutch size variation North American woodpeckers. *The Condor*, 88, 499–504.

LaBarbera, M. (1989). Analyzing body size as a factor in ecology and evolution. *Annual Review of Ecology, Evolution, and Systematics*, (20), 97–117.

Marini, M.Â., L. Hall, D. Russell, J. Bates, R. McGowan, L. F. Silveira, S. K. Robinson, S. Frahnert, A. Gamauf, S. Córdoba-Córdoba, P. R. Sweet, F. R. Steinheimer, D. A. Lijtmaer, P. Tubaro, H. F. Greeney, R. Corado & Heming, N.M. 2020. The five million bird eggs in the world's museum collections are an invaluable and underused resource. *Ornithological Advances,* 137(4), 1-7.

Martin, T. E. (2008). Egg size variation among tropical and temperate songbirds an embryonic temperature hypothesis. *Proceedings of the National Academy of Sciences,* 105, 9268–9271.

Martin, T. E., R. D. Bassar, S. K. Bassar, J. J. Fontaine, P. Lloyd, H. A. Mathewson, A. M. Niklison, & A. Chalfoun (2006). Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. *Evolution*, 60, 390–398.

Meiri, S., & Dayan, T. (2003). On the validity of Bergmann's rule. *Journal of Biogeography*, 30, 331–351.

Meiri, S., Feldman, A., & Kratochvíl, L. (2015). Squamate hatchling size and the evolutionary causes of negative offspring size allometry. *Journal of Evolutionary Biology*, 28(2), 438–446.

Moreau, R. E. (1944). Clutch-size: A comparative study, with special reference to African birds. *Ibis,* 86, 286–347.

Mytiai, I. S., Shatkovska, O. V., & Ghazali, M. (2021). Allometry of Egg Size as a Factor Influencing Egg Shape in Birds. *Acta Ornithologica*, 56(1), 69–78.

Olsen, P. D., & Cockburn, A. (1993). Do large females lay small eggs? Sexual dimorphism and the allometry of egg and clutch volume. *Oikos,* 66(3), 447-453.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature,* 401, 877–884.

Paradis, E., & K. Schliep (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics,* 35, 526–528.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2022). *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-155, https://CRAN.R-project.org/package=nlme.

R Core Team (2021). R: A Language and Environment for Statistical Computing. [Online.] Available at https://www.r-project.org/.

Ray, C. (1960) The application of Bergmann's and Allen's rules to the poikilotherms. *Journal of Morphology,* 106, 85–108.

Rensch, B. (1938) Some problems of geographical variation and species formation. *Proceedings of the Linnean Society of London*, 150, 275–285.

Ricklefs, R. E. (2000). Lack, Skutch, and Moreau: The early development of life-history thinking. *The Condor,* 102, 3–8.

Rotenberry, J. T., & Balasubramaniam, P. (2020). Estimating egg mass-body mass relationships in birds. *The Auk*, 137(3), 1–11.

Scholer, M. N., Strimas-Mackey, M., & Jankowski, J. E. (2020). A meta-analysis of global avian survival across species and latitude. *Ecology Letters*, 23(10), 1537–1549.

Sibly, R. M., C. C. Witt, N. A. Wright, C. Venditti, W. Jetz, & J. H. Brown (2012). Energetics, lifestyle, and reproduction in birds. *Proceedings of the National Academy of Sciences*, 109, 10937–10941.

Sick, H. 2001. Ornitologia brasileira. Second Edition. Nova Fronteira, Rio de Janeiro, Brazil.

Symonds, M. R. E., & Tattersall, G. J. (2010). Geographical variation in bill size across bird species provides evidence for Allen's rule. *American Naturalist*, 176(2), 188–197.

Vuilleumier, F. (1999) The weights of Neotropical birds. Ornitologia Neotropical 10: 207-209.

Weeks, S.E. (1973) Behavior of red-winged tinamou, *Rhynchotus rufescens*. *Zoologica*, 58, 13-40.

Wickham, H (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. https://ggplot2.tidyverse.org.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, & G. M. Smith (2009). Mixed effects models and extensions in ecology with R. Springer, New York, New York.

1   **Appendix 1** Distribution maps of 9 species of Tinamidae. The gray area represents the

2   distribution range of each species, and the colored points represent localities where egg

3   sets were collected.
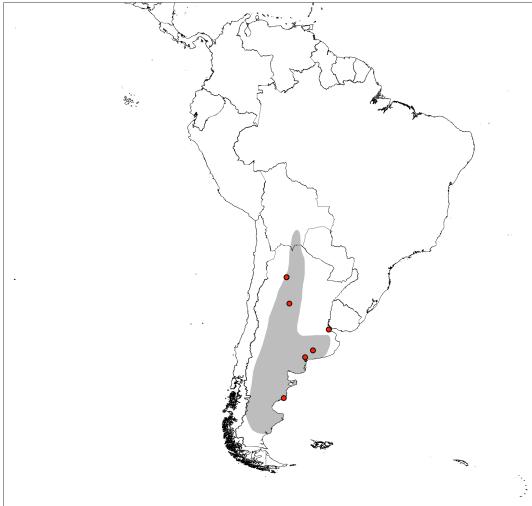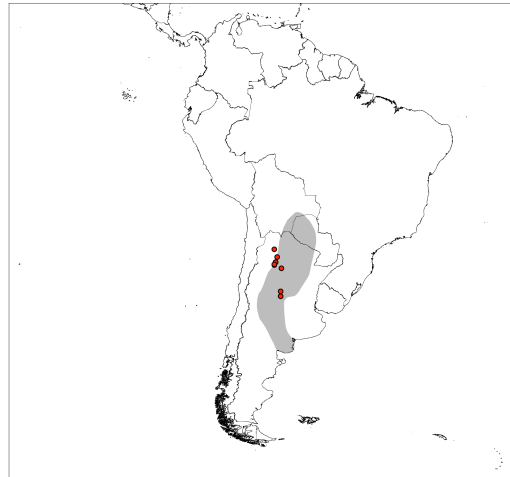

4

5

Eudromia elegans

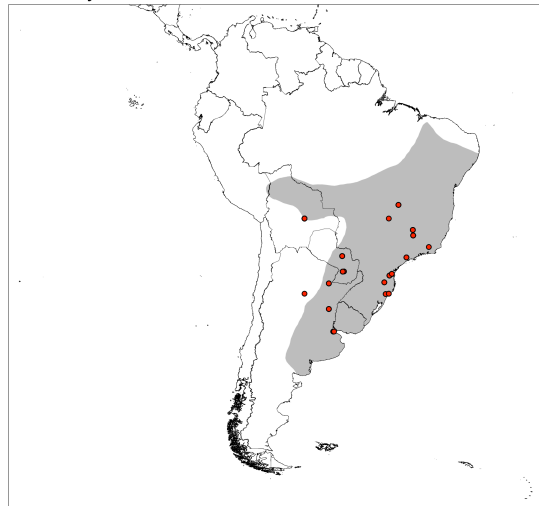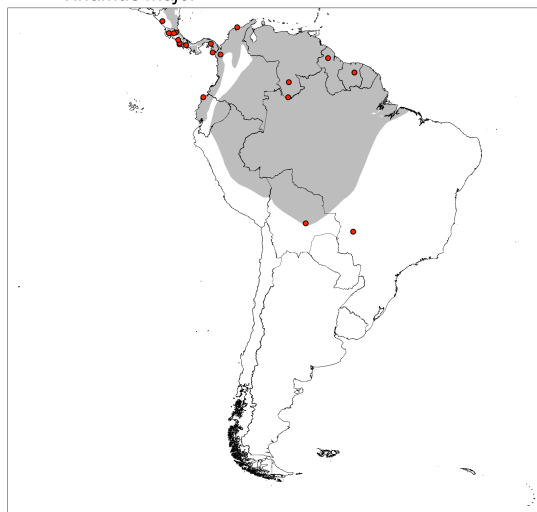*Nothoprocta cinerascens*

1

Nothura maculosa

Rhynchotus rufescens

2

Tinamus major

3

4

1   **APPENDIX 2** Body masses of species of Tinamidae with locality, latitude and source.

Species	Body mass (g)	Country	State/Province	Latitude	Source[1]
Crypturellus obsoletus	320.3	Peru	Amazonas	-7	FMNH 473928
Crypturellus obsoletus	390.2	Brazil	Mato Grosso	-10	Novaes & Lima 1991
Crypturellus obsoletus	421	Brazil	Mato Grosso	-10	Novaes & Lima 1991
Crypturellus obsoletus	432	Brazil	Mato Grosso	-10	Novaes & Lima 1991
Crypturellus obsoletus	443	Brazil	Mato Grosso	-10	Novaes & Lima 1991
Crypturellus obsoletus	446	Brazil	Mato Grosso	-10	Novaes & Lima 1991
Crypturellus obsoletus	470	Brazil	Rondônia	-11	FMNH 389674
Crypturellus obsoletus	307	Peru	Cusco	-13	KU 126012
Crypturellus obsoletus	320	Peru	Cusco	-13	KU 125946
Crypturellus obsoletus	357	Peru	Cusco	-13	FMNH 311160
Crypturellus obsoletus	470	Paraguay	Canindeyu	-24	UMMZ 201945
Crypturellus obsoletus	471	Paraguay	Itapua	-27	KU 91381
Crypturellus obsoletus	470	Brazil	Santa Catarina	-27	COMB 1403
Crypturellus parvirostris	180	Brazil	Bahia	-11	COMB 1531
Crypturellus parvirostris	157	Brazil	Mato Grosso	-14	Cavalcanti & Marini 1993
Crypturellus parvirostris	165	Brazil	Distrito Federal	-15	Cavalcanti & Marini 1993
Crypturellus parvirostris	165	Bolivia	Santa Cruz	-18	FMNH 425478
Crypturellus parvirostris	198	Bolivia	Santa Cruz	-18	FMNH 425447
Crypturellus parvirostris	166	Paraguay	Concepción	-23	KU 129520
Crypturellus soui	156	Belize	Belize District	18	ROM 104060
Crypturellus soui	237	Belize	Belize District	18	ROM 104059
Crypturellus soui	270.4	Nicaragua		14	UCLA 34702
Crypturellus soui	260.5	Panama	Cana Zone	9	Strauch 1977
Crypturellus soui	245*	Panama	Panama	9	Hartman 1961
Crypturellus soui	175.8	Colombia	Chocó	5	Ocampo et al. 2021
Crypturellus soui	216.8	Colombia	Chocó	5	Ocampo et al. 2021

Crypturellus soui	226.4	Colombia	Chocó	5	Ocampo et al. 2021
Crypturellus soui	263.4	Ecuador	Los Ríos	-1	FMNH 370476
Crypturellus soui	171	Ecuador	Manabi	-1	WFVZ 45000
Crypturellus soui	201	Peru	San Martín	-7	MSB Bird 42743
Crypturellus soui	196	Peru	Cusco	-13	FMNH 320356
Crypturellus soui	225	Peru	Cusco	-13	FMNH 320357
Crypturellus soui	155	Bolivia	Santa Cruz	-18	LACM 110165
Crypturellus tataupa	224.5	Brazil	Mato Grosso	-10	Novaes & Lima 1991
Crypturellus tataupa	275	Bolivia	Santa Cruz	-18	YPM ORN 136992
Crypturellus tataupa	225	Bolivia	Santa Cruz	-20	Kratter et al. 1993
Crypturellus tataupa	230	Paraguay	Amanbay	-23	Ericson & Sosa 2020
Crypturellus tataupa	242	Argentina	Jujuy	-23	SS 46670
Crypturellus tataupa	168.8	Argentina	Chaco	-27	Contreras 1983 - II
Crypturellus tataupa	210	Argentina	Chaco	-27	Contreras 1983 - II
Crypturellus tataupa	211	Argentina	Chaco	-27	Contreras 1983 - II
Crypturellus tataupa	243	Paraguay	Itapua	-27	MVZ 190299
Crypturellus tataupa	212	Argentina	Catamarca	-29	Salvador & Di Giacomo 2014
Crypturellus tataupa	231	Argentina	Santiago del Estero	-29	Salvador & Di Giacomo 2014
Crypturellus tataupa	198	Argentina	Córdoba	-32	Pagano & Salvador 2017
Eudromia elegans	540	Argentina	Salta	-24	FMNH 422372
Eudromia elegans	620	Argentina	Salta	-24	FMNH 422374
Eudromia elegans	683	Argentina	Santiago del Estero	-29	Salvador & Di Giacomo 2014
Eudromia elegans	712	Argentina	Santiago del Estero	-29	Salvador & Di Giacomo 2014
Eudromia elegans	713*	Argentina	Córdoba	-33	Salvador 2014
Eudromia elegans	700	Argentina	Buenos Aires	-36	KU 78065
Eudromia elegans	700	Argentina	Buenos Aires	-36	KU 78091
Eudromia elegans	700	Argentina	Buenos Aires	-36	KU 78142
Eudromia elegans	700	Argentina	Buenos Aires	-36	KU 107927
Eudromia elegans	800	Argentina	Buenos Aires	-36	KU 78028

Eudromia elegans	705	Argentina	Rio Negro	-41	KU 98424
Eudromia elegans	675	Argentina	Chubut	-43	ROM 127724
Eudromia elegans	837.6	Argentina	Chubut	-43	ROM 128925
Eudromia elegans	565	Argentina	Chubut	-44	KU 81555
Eudromia elegans	700	Argentina	Chubut	-45	KU 108030
Eudromia elegans	750	Argentina	Chubut	-45	KU 108027
Nothoprocta cinerascens	585	Bolivia	La Paz	-17	Cabot 1997
Nothoprocta cinerascens	500	Argentina	Jujuy	-23	SS 36974
Nothoprocta cinerascens	467	Argentina	Catamarca	-29	Salvador & Di Giacomo 2014
Nothoprocta cinerascens	521	Argentina	Catamarca	-29	Salvador & Di Giacomo 2014
Nothoprocta cinerascens	375	Argentina	San Juan	-31	Pagano & Salvador 2017
Nothoprocta cinerascens	492*	Argentina	Córdoba	-33	Salvador 2014
Nothoprocta cinerascens	538	Argentina	La Pampa	-34	Pagano & Salvador 2017
Nothoprocta cinerascens	512	Argentina	La Pampa	-35	Pagano & Salvador 2017
Nothura maculosa	232	Paraguay	Concepción	-23	Ericson & Sosa 2020
Nothura maculosa	268	Argentina	Formosa	-26	Pagano & Salvador 2017
Nothura maculosa	241	Paraguay	Caazapa	-26	KU 88413
Nothura maculosa	269	Argentina	Santiago del Estero	-29	Salvador & Di Giacomo 2014
Nothura maculosa	277	Argentina	Santiago del Estero	-29	Salvador & Di Giacomo 2014
Nothura maculosa	276*	Brazil	Rio Grande do Sul	-31	Silveira & Menegheti 1981
Nothura maculosa	235	Argentina	Entre Ríos	-32	LACM 104662
Nothura maculosa	270	Argentina	Entre Ríos	-32	LACM 104644
Nothura maculosa	268*	Argentina	Córdoba	-33	Salvador 2014
Nothura maculosa	300	Argentina	Buenos Aires	-36	KU 77978
Nothura maculosa	286	Argentina	Río Negro	-41	Pagano & Salvador 2017
Nothura maculosa	308	Argentina	Río Negro	-41	Pagano & Salvador 2017
Rhynchotus rufescens	840	Bolivia	Santa Cruz	-17	YPM ORN 136979
Rhynchotus rufescens	780	Bolivia	Santa Cruz	-18	YPM ORN 136981
Rhynchotus rufescens	820	Bolivia	Santa Cruz	-18	YPM ORN 136985

Rhynchotus rufescens	790	Paraguay	Itapua	-27	KU 91382
Rhynchotus rufescens	909*	Argentina	Córdoba	-33	Salvador 2014
Rhynchotus rufescens	883	Argentina	Córdoba	-35	Salvador 1988
Rhynchotus rufescens	898	Argentina	Córdoba	-35	Salvador & Di Giacomo 2014
Rhynchotus rufescens	912	Argentina	Córdoba	-35	Salvador & Di Giacomo 2014
Rhynchotus rufescens	931	Argentina	Córdoba	-35	Salvador 1988
Rhynchotus rufescens	872	Argentina	Buenos Aires	-38	Pagano & Salvador 2017
Rhynchotus rufescens	928	Argentina	Buenos Aires	-38	Pagano & Salvador 2017
Rhynchotus rufescens	918	Argentina	Buenos Aires	-38	UMMZ 156963
Tinamus major	1106	Guatemala	Petén	18	Van Tyne 1935
Tinamus major	1122	Guatemala	Petén	18	Van Tyne 1935
Tinamus major	1136	Guatemala	Petén	18	Van Tyne 1935
Tinamus major	1106	Guatemala	Petén	17	UMMZ 70018
Tinamus major	1122	Guatemala	Petén	17	UMMZ 70015
Tinamus major	1135.2	Guatemala	Petén	17	MCZ 342774
Tinamus major	1136	Guatemala	Petén	17	UMMZ 70016
Tinamus major	1118	Mexico	Chiapas	17	MVZ 97928
Tinamus major	1148	Mexico	Chiapas	17	MVZ 97930
Tinamus major	1450	Costa Rica	Alajuela	10	WFVZ 36853
Tinamus major	1066	Costa Rica	Puntarenas	9	SS 19753
Tinamus major	1140	Panama	Panama	9	Hartman 1955
Tinamus major	1175	Panama	Panama	9	Hartman 1961
Tinamus major	736.5	Colombia	Chocó	5	Ocampo et al. 2021
Tinamus major	865	Colombia	Chocó	5	Ocampo et al. 2021
Tinamus major	1200	Colombia	Chocó	5	Ocampo et al. 2021
Tinamus major	1250	Colombia	Chocó	5	Ocampo et al. 2021
Tinamus major	800	Brazil	Amazonas	-8	Novaes 1976
Tinamus major	975	Brazil	Mato Grosso	-10	Novaes & Lima 1991
Tinamus major	1070*	Brazil	Mato Grosso	-10	Novaes & Lima 1991

Tinamus major	940	Brazil	Mato Grosso	-11	Novaes 1976
Tinamus major	1140	Bolivia	Santa Cruz	-17	YPM ORN 136996
Tinamus major	1140	Bolivia	Santa Cruz	-18	YPM ORN 136995

[1] Museum acronyms: COMB (Coleção Ornitológica Marcelo Bagno, Brasília, Brazil), FMNH (Field Museum of Natural History, Chicago, USA), KU, LACM, MSB, MCZ (Museum of Comparative Zoology, Cambridge, USA), MVZ (Museum of Vertebrate Zoology, Berkeley, USA), ROM (Royal Ontario Museum, Toronto, Canada), SS, UCLA, UMMZ (University of Michigan Museum of Zoology, Ann Arbor, USA), WFVZ (Western Foundation of Vertebrate Zoology, Camarillo, USA), YPM.

* Average values.

REFERENCES OF BODY MASSES

Cabot, J. 1997. Dos nuevas subspecies de Nothoprocta ornate y sobre la distribuición de N. ornate rostrata (Aves, Tinamidae). Iheringia, Série Zoologia 82: 119-125.

Cavalcanti, R. B. & Marini, M. Â. 1993. Body masses of birds of the *cerrado* region, Brazil. Bulletin British Ornithologists' Club 113: 209-212.

Contreras, J. R. 1983. Notas sobre el peso de aves argentinas. II. Historia Natural 3: 39-40.

Ericson, P. G. P. & Sosa, W. 2020. Birds collected and captured during the PROVEPA ornithological fieldwork in Paraguay 1993-1999. Report from the Swedish Museum of Natural History 2020:1. Naturhistoriska riksmuseets småskriftserie.

Hartman, F. A. 1955. Heart weight in birds. The Condor 57(4): 221-238.

Hartman, F. A. 1961. Locomotor mechanisms of birds. Smithsonian Miscellaneous Collections 143(1): 1-91.

Kratter, A. W., Sillett, T. S., Chesser, R. T., O'Neill, J. P., Parker III, T. A. & Castillo, A. 1993. Avifauna of a Chaco Locality in Bolivia. The Wilson Bulletin 105(1): 114-141.

Novaes, F. C. 1976. As aves do rio Aripuanã, Estados de Mato Grosso e Amazonas. Acta Amazônica 6(4): 61-85, Supl.

Novaes, F. C. & Lima, M. F. C. 1991. As aves do Rio Peixoto de Azevedo, Mato Grosso, Brasil. Revista Brasileira de Zoologia 7(3): 351-381.

1   Ocampo, D., K. G. Borja-Acosta, J. Lozano-Flórez, S. Cifuentes-Acevedo, E. Arbeláez-

2   Cortés, N. J. Bayly, Á. Caguazango, B. Coral-Jaramillo, D. Cueva, F. Forero, J. P.

3   Gómez, C. Gómez, M. A. Loaiza-Muñoz, G. A. Londoño, S. Losada-Prado, S. Pérez-

4   Peña, H. E. Ramirez-Chaves, M. E. Rodríguez-Posada, J. Sanabria-Mejía, M. Sánchez-

5   Martínez, V. Hugo Serrano-Cardozo, M. D. S. Sierra-Buitrago, J. Soto-Patiño & O.

6   Acevedo-Charry. 2021. Body mass data set for 1317 bird and 270 mammal species

7   from Colombia. Ecology 102(3): e03273. 10.1002/ecy.3273

8   Pagano, L. G. & Salvador, S. A. 2017. Datos de pesos de aves argentinas. Parte 4. Historia

9   Natural 7(1): 21-43.

10   Salvador, S. A. 1988. Datos de peso de aves argentinas. El Hornero 13: 78–83.

11   Salvador, S. A. 2014. Peso de las aves del Departamento General San Martín, Provincia de

12   Córdoba, Argentina. Revista Biológica 17: 48-57.

13   Salvador, S. A. & Di Giacomo, A.G. 2014. Datos de pesos de aves argentinas. Parte 3.

14   Historia Natural (Tercera serie) 4: 63-88.

15   Silveira, C. F. B. & Menegheti, J. O. 1981. Estudo sobre a relação peso e sexo em Nothura

16   maculosa (TEMMINCK, 1815) (Aves, Tinamiformes, Tinamidae). Iheringia, Série

17   Zoologia 58:7-16.

18   Strauch, Jr., J. G. 1977. Further bird weights from Panama. Bulletin of the British

19   Ornithologists` Club 97: 61-65.

20   Van Tyne, J. 1935. The birds of northern Petén, Guatemala. Miscellaneous Publications of

21   the Museum of Zoology University of Michigan 27: 1-46.