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# Sexual size dimorphism and testis size allometry in tuco-tucos (Rodentia: Ctenomyidae)

**Abstract:** We studied sexual size dimorphism (SSD) and testes size allometry in 97 natural populations, including 39 nominal species and 19 unnamed or undescribed forms, of tuco-tucos (*Ctenomys*) from Argentina, Bolivia, Chile, Paraguay, and Uruguay in order to gain insight on the existence of sperm competition in these solitary, territorial, and possibly polygynic subterranean rodents. Our results indicated that sex-biased SSD occurs within the genus and also within lower taxa. SSD conforms to Rensch's rule. Testes size showed a strong negative allometry when compared with male body mass both across and within species, clearly suggesting the operation of sperm competition in this genus. Thus, within a *Ctenomys* population, small males would invest more than larger males in testes growth and thus in ejaculate quality, which would counterbalance their presumably lower chances of accessing females due to their smaller body size.

**Keywords:** Rensch's rule; sexual selection; sexual size dimorphism; testis/body size allometry; tuco-tucos.

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## Introduction

Sexual size dimorphism (SSD), the existence of conspicuous differences in body size between males and females, is very common in animals (Andersson 1994, Blanckenhorn et al. 2007a, b, Kupfer 2007, Lindenfors et al. 2007, Székely et al. 2007). In mammals, it is usually male-biased (MSSD) although many female-biased cases of SSD (FSSD) are known (Ralls 1976, Andersson 1994, Schulte-Hostedde et al. 2002, Lindenfors et al. 2007, Schulte-Hostedde 2007). Ever since Darwin (1871), SSD has been considered a result of sexual selection, although other explanations such as natural selection for different ecological roles or niche utilization in males and females have been put forward for special cases (Selander 1966, Andersson 1994, Butler et al. 2000, Mysterud 2000).

Rensch's rule (Rensch 1950, 1960) states that the degree of SSD tends to increase with increasing average body size in taxa in which males are the larger sex, and decreases with body size in those where females are larger (Abouheif and Fairbairn 1997, Blanckenhorn et al. 2007a). Although these two patterns seem to conflict, it has been suggested that they may be part of the same trend (Fairbairn and Preziosi 1994, Fairbairn 1997) that involves greater evolutionary change in males and strong covariation of size between the sexes because of genetic correlations (Lindenfors 2002). That trend has been well documented across species; however, it also occurs within species of vertebrates and invertebrates (Fairbairn 2005, Bidau and Martí 2007, 2008a,b).

The size of testes in mammals and other organisms is revealing of reproductive strategies; thus, the study of the allometric relation between testes size or mass, and body size is relevant within the context of evolutionary biology and sexual selection theory (Møller 1989, Heske and Ostfeld 1990, Stockley and Purvis 1993, Hosken 1998, Breed and Taylor 2000, Gage and Freckleton 2003, Schulte-Hostedde et al. 2003, 2005, Schulte-Hostedde and Millar 2004). In mammals, an allometric relation between testes mass and body mass has been demonstrated, although the range of relative testes size is large, especially for small mammals (Kenagy and Trombulak 1986). Furthermore, intraspecific size variation in testes mass has been observed in a number of mammals, usually associated to sperm competition (SC) and a series of morphological and life history characteristics (Breed and Taylor 2000, Schulte-Hostedde et al. 2003, 2005, Schulte-Hostedde and Millar 2004).

Tuco-tucos (genus *Ctenomys* de Blainville, 1826) constitute an excellent model to test predictions about SSD and sexual selection. First, the genus includes >60 Linnean species, showing a wide variation in body size and, a large geographic distribution spanning across 45°

of southern latitude (from ca. -10° in the Peruvian highlands to almost -55° in Tierra del Fuego). Species can be found between 0 and >5000 m above sea level from the Pacific to the Atlantic oceans (Contreras and Bidau 1999, Bidau 2006, 2012, Parada et al. 2011). Second, these rodents are fully subterranean and spend >95% of their lives underground (Nevo 1999), and it is possible that reproductive strategies and thus, the operation of sexual selection, might differ from those of surface-dwelling rodent species. Third, although *Ctenomys* includes ca. 63 named extant species (Bidau 2006, 2012), these are morphologically homogeneous and show the same adaptations for living underground but vary greatly in body size (Medina et al. 2007).

Finally, tuco-tucos inhabit an enormous variety of habitats and climates and although localized populations may be subjected to intense environmental selection resulting from differences in soil texture and depth, available food plants, intensity of predation, etc., their burrows maintain fairly constant temperature and humidity independently of geographic location (Reig et al. 1990, Nevo 1999, Busch et al. 2000, Bidau 2006, Medina et al. 2007). This characteristic probably isolates them quite effectively from the external environment.

The main objectives of this study were (1) to analyze the extent and direction of SSD in tuco-tucos at the inter- and intraspecific levels; (2) to verify the application of Rensch's rule to this genus; (3) to study the allometric relation between testes size and body size; and (4) to investigate the possible relation between SSD, testes allometry, and geographic body size variation in *Ctenomys*.

# Materials and methods

## Study species and characters

This study is based on 611 specimens of *Ctenomys* belonging to 97 natural populations, including 39 nominal species and 19 unnamed or undescribed forms from Argentina, Bolivia, Chile, Paraguay, and Uruguay sampled by the authors and collaborators (Medina et al. 2007) or obtained from the literature (Appendix). Sources of data were Thomas and St. Leger (1926), Osgood (1943, 1946), Barlow (1965), Pine et al. (1979), Lessa and Langguth (1983), Pearson (1984), Pearson and Christie (1985), Kelt and Gallardo (1994), and Anderson (1997).

External measurements of all specimens included total body (TBL) and head plus body (HBL) lengths. Tail (TL), hind foot (HFL), and ear (EL) lengths were also recorded for specimens of the *Ctenomys perrensi* Thomas, 1896 superspecies (see below). In most individuals, body mass (BM) was also measured or obtained from the literature (Appendix).

Length and width of both testes were measured in all male individuals captured by us. We estimated testicular volume by the formula for a prolate spheroid (Hoyt 1979): testis volume=$0.51\times(\text{width})^2\times(\text{length})$. Testis density is nearly 1.0; thus, testis volume was equaled to testis weight (França and Godinho 2003, França et al. 2006).

## Statistical methods

SSD was calculated for each population as the ratio between the arithmetic mean of each measured character of males, and the corresponding mean of females (Smith 1999). The scaling of SSD with body size was described by regressing $\log_{10}$ (male size) on $\log_{10}$ (female size) for all studied characters (Fairbairn and Preziosi 1994, Abouheif and Fairbairn 1997, Fairbairn 1997, 2005). Rensch's rule is said to occur when the slope of the regression line is >1.0, while slopes significantly smaller than 1.0 signal its reversion (Fairbairn 1997). Ordinary least-squares regression (OLS) is not adequate for these analyses because x (in this case, female body size) is not fixed and estimated with error; thus, the slope b, and its confidence interval, are estimated with error (Fairbairn 1997). In these cases, type II regression has been recommended (Sokal and Rohlf 1995). We used reduced major axis (RMA) regression to estimate slopes for the relation between $\log_{10}$ (male size) and $\log_{10}$ (female size), using the software of Bohonak and van der Linde (2004) (Java version). Clarke's T statistic with adjusted degrees of freedom (df) was used for testing the null hypothesis that $b_{RMA}=1.0$ (Clarke 1980).

Testes allometry in males was also investigated by regressing the trait (volume/mass of both testes) on body length or body mass using the same statistical procedures described above. Testes asymmetry was calculated as directional asymmetry (DA) [DA=$\log_{10}$ left testis volume (LTV)-$\log_{10}$ right testis volume (RTV)] and relative asymmetry (RA) [RA=$\log_{10}$ LTV-$\log_{10}$ RTV/0.5($\log_{10}$ LTV+$\log_{10}$ RTV)] (Graves 2004). OLS was employed for the analysis of testicular allometry on an individual basis using SPSS v.13.

All $\log_{10}$-transformed variables were tested for normality using the Kolmogorov-Smirnov one-sample test with the Liliefors correction. Coefficients of variation for each analyzed trait were calculated as CV=$s\times100/\bar{x}$ (Zar 1999).

Research on live animals followed the American Society of Mammalogists guidelines (Gannon et al. 2007) and was approved by local faunal authorities.

# Results

## Variation of size and SSD in *Ctenomys*

*Ctenomys* shows a wide variation in body size. Among the populations studied by us, adult body mass ranged between 43 g in a female *Ctenomys* sp. 29 from Puerto Madryn (Argentina) and 1200 g in a male *Ctenomys conoveri* Osgood, 1946 from Carandayti (Bolivia). The total length ranged from 146 mm in a female *Ctenomys* sp. 12 from Pago Alegre (Argentina) to 680 mm in the same *C. conoveri* male. Females were consistently smaller than males in all species, and their respective size ranges were as follows: females, body weight, 43–420 g; total length, 146–374 mm; males, body weight, 49–1200 g; total length, 149–680 mm. Male body size showed, on the whole, a higher variability than that of females. The coefficients of variation of head and body length for the whole sample were 20.58 for males and 14.53 for females. In the case of body mass, the values were 67.99 and 50.73, respectively, and for total body length, 18.22 and 13.99, respectively (Medina et al. 2007). The Appendix shows the amount of SSD for the studied characters in all population samples.

## Rensch's rule in *Ctenomys*

SSD in body mass was analyzed in 58 populations of tucotucos by means of RMA regression. Male and female mean weights were highly significantly correlated across species and populations (Table 1). The calculated RMA slope was significantly different from 1.0, showing an increase of SSD with increasing general body size (Table 1). Similar results were obtained from the analyses of three linear measurements (TBL, HBL, and TL) of *Ctenomys* populations (Table 1).

## Rensch's rule within the *Ctenomys perrensi* superspecies

We studied the trends in SSD of six morphological traits of 24 populations of the *Ctenomys perrensi* superspecies (Table 2). In this group of populations, Rensch's rule was verified for BM, TBL, and TL, while the RMA slope was not significantly different from 1.0 for other linear measurements such as HBL (marginal significance), E, and HF. Highly significant correlations were, however, obtained for all analyzed characters.

## Testes volume/mass allometry in *Ctenomys*

Testes mass as inferred from testes volume (see Materials and methods) was regressed against TBL, HBL, and weight (Wt) using the RMA procedure. The results of the statistical tests are shown in Table 3. Although positive allometry was observed when testes mass was regressed against TBL, and a similar non-significant relation was observed with HBL, a highly significant negative allometric trend was observed when the independent variable was body mass (Table 3).

## Testes volume/mass allometry in the *Ctenomys perrensi* superspecies

Within this group of populations, a comparable allometric trend in testes mass was observed as in the general sample (Table 4). However, in this case, highly significant

| | Correlation coefficient | | | | RMA slope | | | | | RMA intercept | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Trait | r | t | df | p-Value | β (SE) | T | df[1] | p-Value | 95% CI | a (SE) | 95% CI |
| TBL | 0.762 | 11.28 | 92 | $<10^{-6}$ | 1.217 (0.082) | 3.23 | 74.09 | 0.0018 | 1.054–1.380 | -0.497 (0.196) | -0.885–-0.108 |
| HBL | 0.769 | 11.48 | 91 | $<10^{-6}$ | 1.223 (0.082) | 3.33 | 73.02 | 0.0014 | 1.061–1.386 | -0.477 (0.182) | -0.840–-0.115 |
| TL | 0.665 | 8.50 | 95 | $<10^{-6}$ | 1.164 (0.089) | 2.15 | 80.62 | 0.0341 | 0.986–1.341 | -0.286 (0.165) | -0.614–0.042 |
| BM | 0.832 | 11.22 | 56 | $<10^{-6}$ | 1.184 (0.088) | 2.50 | 44.35 | 0.0162 | 1.007–1.360 | -0.335 (0.195) | -0.728–0.057 |

**Table 1** Results of RMA regression of log (male size) on log (female size) for population means of four morphometric traits from *Ctenomys* populations.
For abbreviations of traits, see Materials and methods. r=Pearson's correlation coefficient; t=Student's t statistic; β=slope of the RMA regression line; T=Clarke's T statistic; df=degrees of freedom; [1]df=Clarke's adjusted degrees of freedom for T; a=intercept of the RMA regression line; 95% CI=95% confidence interval; SE=standard error; p=probability.

| | Correlation coefficient | | | | RMA slope | | | | | RMA intercept | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Trait | r | t | df | p-Value | β (SE) | T | df[1] | p-Value | 95% CI | a (SE) | 95% CI |
| TBL | 0.446 | 2.34 | 22 | 0.0288 | 1.438 (0.274) | 2.35 | 22.91 | 0.0278 | 0.869–2.007 | -1.031 (0.659) | -2.3978–0.3350 |
| HBL | 0.476 | 2.54 | 22 | 0.0187 | 1.320 (0.247) | 1.75 | 22.66 | 0.0944 | 0.807–1.833 | -0.699 (0.555) | -1.8509–0.4522 |
| TL | 0.602 | 3.54 | 22 | 0.0018 | 1.450 (0.247) | 2.70 | 21.48 | 0.0132 | 0.938–1.963 | -0.826 (0.465) | -1.7899–0.1374 |
| HFL | 0.577 | 3.31 | 22 | 0.0032 | 1.095 (0.191) | 0.56 | 21.72 | 0.5812 | 0.699–1.490 | -0.121 (0.285) | -0.7117–0.4699 |
| E | 0.572 | 3.27 | 22 | 0.0035 | 1.182 (0.207) | 1.06 | 21.77 | 0.3008 | 0.753–1.610 | -0.144 (0.183) | -0.5221–0.2347 |
| BM | 0.561 | 3.18 | 22 | 0.0044 | 2.780 (0.491) | 10.31 | 21.87 | $<10^{-6}$ | 1.762–3.797 | -3.967 (1.109) | -6.267–-1.666 |

**Table 2** Results of RMA regression of log (male size) on log (female size) for population means of six morphometric traits from the *Ctenomys perrensi* complex populations from Corrientes Province.
For abbreviations of traits, see Materials and methods. r=Pearson's correlation coefficient; t=Student's t statistic; β=slope of the RMA regression line; T=Clarke's T statistic; df=degrees of freedom; [1]df=Clarke's adjusted degrees of freedom for T; a=intercept of the RMA regression line; 95% CI=95% confidence interval; SE=standard error; p=probability.

RMA slopes were obtained for linear measurements (TBL and HBL), while the negative allometric trend with respect to body size was not as statistically significant as for the whole *Ctenomys* sample (Table 4).

## Testicular asymmetry

Testicular asymmetry was initially studied on an individual basis, independent of species or population. Testicular volume varied widely within left and right testis in our sample: mean LTV=168.19±97.1 $mm^3$, range=11.36–572.35 $mm^3$; mean RTV=168.86±105.4 $mm^3$, range=8.87–571.69 $mm^3$. However, a paired-samples t-test revealed no significant difference between left and right testis (t=0.91; df=140; p=0.365). Mean values of asymmetry variables were as follows: DA=-0.0093 and RA=-0.0064. Both were strongly positively correlated (Spearman's ρ=0.996; $p<10^{-6}$), and the regression of LTV on RTV produced a linear relation with a positive slope close to 1.0 ($\log_{10}$ LTV=-0.0104+1.0005×$\log_{10}$ RTV; F=871.42, df=1.139, $p<10^{-6}$; $R^2$=0.862).

| | Correlation coefficient | | | | RMA slope | | | | | RMA intercept | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Trait | r | t | df | p-Value | β (SE) | T | df[1] | p-Value | 95% CI | a (SE) | 95% CI |
| TBL | 0.459 | 4.23 | 67 | 0.0001 | 1.252 (0.136) | 2.34 | 63.51 | 0.0224 | 0.980–1.523 | -2.375 (0.326) | -3.0270–1.7230 |
| HBL | 0.435 | 3.96 | 67 | 0.0002 | 1.197 (0.132) | 1.80 | 64.13 | 0.0766 | 0.934–1.461 | -2.060 (0.296) | -2.6520 –-1.4680 |
| BM | 0.414 | 3.25 | 51 | 0.0020 | 0.349 (0.045) | 5.15 | 49.09 | $5\times10^{-6}$ | 0.260–0.439 | -0.157 (0.101) | -0.3591–0.0461 |

**Table 3** Results of RMA regression of log (testes volume) on log (male size) for population means of three morphometric traits from *Ctenomys* populations.
For abbreviations of traits, see Materials and methods. r=Pearson's correlation coefficient; t=Student's t statistic; β=slope of the RMA regression line; T=Clarke's T statistic; df=degrees of freedom; [1]df=Clarke's adjusted degrees of freedom for T; a=intercept of the RMA regression line; 95% CI=95% confidence interval; SE=standard error; p=probability.

| | Correlation coefficient | | | | RMA slope | | | | | RMA intercept | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Trait | r | t | df | p-Value | β (SE) | T | df[1] | p-Value | 95% CI | a (SE) | 95% CI |
| TBL | 0.793 | 5.21 | 16 | $8.6\times10^{-5}$ | 1.867 (0.284) | 5.87 | 14.93 | $3.1\times10^{-5}$ | 1.264–2.470 | -3.917 (0.691) | -5.381–-2.453 |
| HBL | 0.837 | 6.11 | 16 | $1.5\times10^{-5}$ | 1.527 (0.209) | 4.29 | 14.59 | $6.8\times10^{-4}$ | 1.084–1.971 | -2.853 (0.475) | -3.861–-1.845 |
| BM | 0.440 | 3.36 | 16 | 0.0040 | 0.535 (0.073) | 2.86 | 14.57 | 0.0122 | 0.381–0.688 | -0.632 (0.170) | -0.9915–-0.2717 |

**Table 4** Results of RMA regression of log (testes volume) on log (male size) for population means of three morphometric traits from *Ctenomys perrensi* populations.
For abbreviations of traits, see Materials and methods. r=Pearson's correlation coefficient; t=Student's t statistic; β=slope of the RMA regression line; T=Clarke's T statistic; df=degrees of freedom; [1]df=Clarke's adjusted degrees of freedom for T; a=intercept of the RMA regression line; 95% CI=95% confidence interval; SE=standard error; p=probability.

## Individual analyses of testicular allometry

To test the allometry of testes with respect to body size measurements using individual males and not population means, we performed two kinds of analyses. First, OLS regressions of log testes mass on logBM and logTL were calculated for all males for which testes data were available, independently of species and population. Results shown in Table 5 indicate negative allometry of testes size with respect to body size in both cases. Thus, at the individual level, larger males showed relatively smaller testes than smaller ones.

The second analysis involved males of *Ctenomys perrensi*. In this case, testes size showed negative allometry with respect to BM but positive allometry when TL was the independent variable (Table 5). Thus, heavier males had relatively smaller testes than lighter ones.

## Geographic variation of testicular volume

As the $\log_{10}$ of total testicular volume departed from normality (Kolmogorov-Smirnov's D=0.114, df=141, p<0.001), testing of absolute testicular volume trends against geographic independent variables was performed through non-parametric correlation (Spearman's ρ). Significant trends were observed for longitude (ρ=0.188, p=0.025) and altitude (ρ=0.187, p=0.026) but not for latitude (ρ=-0.066, p=0.435). However, the log-transformed proportion of total testicular volume/mass in relation to body mass did show significant positive correlations with latitude (Spearman's ρ=0.296, p=0.003), longitude (Spearman's ρ=0.373, p<0.001), and altitude (Spearman's ρ=0.200, p<0.046). The proportion of testes volume to head and body length also increased significantly with longitude (Spearman's ρ=0.267, p=0.001) and altitude (Spearman's ρ=0.187, p=0.027), but not with latitude (Spearman's ρ=0.046, p=0.589) (Figure 1).

## Expected percentage of testes mass relative to body mass

On the basis of the results of OLS and RMA regressions performed for *Ctenomys*, we estimated the expected testes mass for the range of tuco-tucos body masses found and the percentage of the body mass represented by the testes. It is clear that the larger the body size is, the smaller the proportion of testes (Table 6). A comparison with results from other large mammalian and rodent databases showing body and testes masses (Kenagy and Trombulak 1986, Breed and Taylor 2000) is also shown in Table 6. In the case of Kenagy and Trombulak's (1986) data, the published equations were used for the estimations; negative allometry, although much less pronounced than in *Ctenomys*, was observed. Breed and Taylor (2000) used independent contrasts for their regression analysis; however, for the present study, we performed OLS regression of the whole dataset to allow the comparisons. We obtained an isometric relation between testes masses and body masses (Table 6). In their original publication, Breed and Taylor (2000) also found a nearly isometric trend using the phylogenetic method.

# Discussion

It is accepted that sexual selection is a major determinant of size differences between males and females (Darwin 1871, Andersson 1994), although SSD may also result from ecological selective pressures relating to differences of niche utilization in males and females (Selander 1966, Mysterud 2000, Pérez-Barbería et al. 2002).

Contest competition for the mate that represents the scarcer reproductive resource is the usual explanation of SSD. For example, if males compete for territories and/or females' preference, increased male body size may be selected for, resulting in MSSD. Thus, MSSD is certainly

| | | Correlation coefficient | | | | Linear regression and ANOVA | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Trait | r | t | df | p-Value | a | b | F | df | p-Value |
| Whole sample | BM | 0.508 | 5.83 | 98 | $10^{-6}$ | 0.167 | 0.203 | 34.03 | 1.98 | $<10^{-6}$ |
| | TBL | 0.457 | 6.04 | 140 | $<10^{-6}$ | -0.845 | 0.611 | 36.44 | 1.138 | $<10^{-6}$ |
| *C. perrensi* | BM | 0.928 | 13.45 | 31 | $<10^{-6}$ | -0.666 | 0.550 | 181.20 | 1.29 | $<10^{-6}$ |
| | TBL | 0.774 | 7.92 | 42 | $<10^{-6}$ | -0.293 | 1.459 | 62.74 | 1.42 | $<10^{-6}$ |

**Table 5** Analyses of testes allometry at the individual level in the whole *Ctenomys* sample and in *Ctenomys perrensi* males.
OLS regressions of log (testis volume) against log (morphometric trait) were performed. For abbreviations of traits, see Materials and methods. r=Pearson's correlation coefficient; t=Student's t statistic; a=OLS intercept; b=OLS slope; F=F statistic; df=degrees of freedom; p=probability.

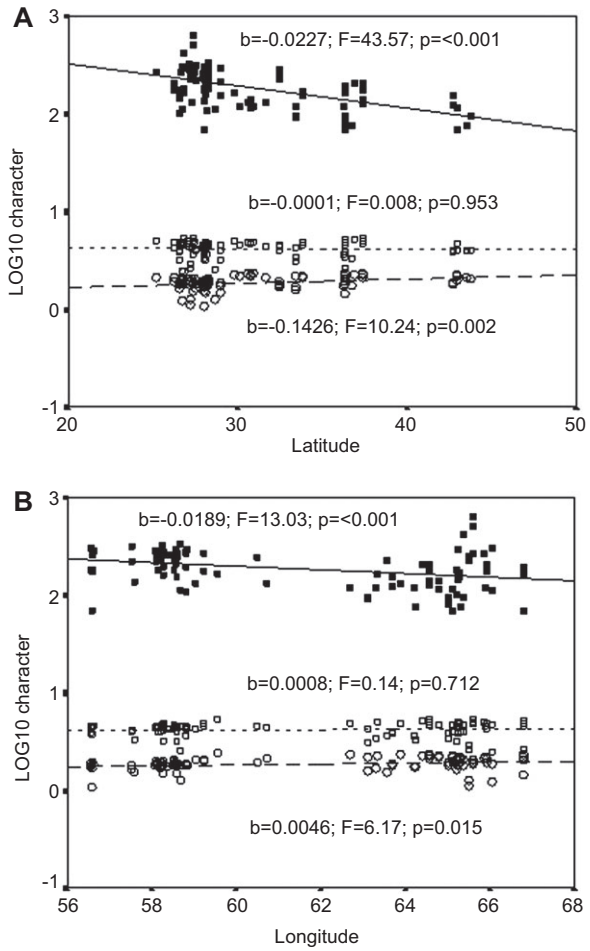


**Figure 1** Linear regressions between body mass (black squares), total testicular volume (open squares), and the proportion of total testicular volume to body mass (open circles), and (A) latitude and (B) longitude. All measurements were $\log_{10}$ transformed. In each case, the slope of the regression line (b), the F-statistic from the ANOVA analysis (F), and the statistical significance of F (p) are indicated.

correlated with mating system: more pronounced MSSD should be associated more to polygynic systems than to monogamy or overtly promiscuous systems (Alexander et al. 1979, Heske and Ostfeld 1990). Alternatively, if there is a positive correlation between female size and fecundity, FSSD is expected (Darwin 1871). Although it is sometimes not easy to distinguish between the different hypotheses, there exist a number of indirect evidences that could help decide between alternative possibilities. There is no evidence in tuco-tucos that niche utilization is different in males and females. Both sexes inhabit the same type of subterranean environment with very narrow margins of microenvironmental variation (although female burrows tend to be smaller) and consume the same food items (Busch et al. 2000, Medina et al. 2007). As in other subterranean rodents, most tuco-tuco species are solitary, territorial, and aggressive, and males normally engage in contests for the access to females (Busch et al. 1989, Bennett et al. 2000, Zenuto et al. 2002). Thus, sexual selection is a plausible cause for the increase in size of males with respect to females. However, as demonstrated in this article, because of Rensch's rule, smaller species of tuco-tucos show less MSSD than larger ones.

A further indication of sexual selection would be the existence of SC among males. SC is said to occur when the ejaculates of two or more males compete for fertilization of the same set of ova (Parker 1970, 1984, 1998) and is characteristic of polygynic mating systems. Very few studies on SC have been performed in the ca. 63 species of tuco-tucos, with the exception of *Ctenomys talarum* Thomas, 1898 and *Ctenomys haigi* Thomas, 1919 (Zenuto et al. 1999a,b, Graziani and Lacey 2004). In both species, the use of microsatellite markers to determine paternity

| | | | *Ctenomys*[1] | | Mammals[2] | | Rodents[2] | | Murine rodents[3] | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | OLS | | RMA | | OLS | | OLS | | OLS |
| BM (g) | TM (g) | %TM/BM | TM (g) | %TM/BM | TM (g) | %TM/BM | TM (g) | %TM/BM | TM (g) | %TM/BM |
| 50 | 3.25 | 6.50 | 2.73 | 5.46 | 0.63 | 1.26 | 0.59 | 1.17 | 0.71 | 1.42 |
| 100 | 3.74 | 3.74 | 3.48 | 3.48 | 1.07 | 1.07 | 0.96 | 0.96 | 1.42 | 1.42 |
| 200 | 4.31 | 2.16 | 4.43 | 2.21 | 1.83 | 0.92 | 1.59 | 0.70 | 2.84 | 1.42 |
| 300 | 4.68 | 1.56 | 5.10 | 1.70 | 2.50 | 0.84 | 2.12 | 0.71 | 4.26 | 1.42 |
| 500 | 5.19 | 1.54 | 6.09 | 1.22 | 3.71 | 0.74 | 3.07 | 0.61 | 7.10 | 1.42 |
| 100 | 5.97 | 0.58 | 7.76 | 0.78 | 6.33 | 0.63 | 5.06 | 0.51 | 14.19 | 1.42 |
| 1500 | 6.48 | 0.43 | 8.94 | 0.60 | 8.65 | 0.58 | 6.77 | 0.45 | 21.28 | 1.42 |

**Table 6** A comparison of expected testes masses (TM), and testes/body percentage (%TM/BM) for a range of body masses (BM) found in *Ctenomys*, with other published databases.
For *Ctenomys*, the results of OLS and RMA regressions were used for the calculations. All other data represent results of OLS regressions.
[1]This paper. [2]Kenagy and Trombulak (1986). [3]Breed and Taylor (2000).

strongly suggested that both species are polygynous, and this is probably true of most tuco-tuco species.

An indirect clue to the existence of SC is the relation between testes mass and body mass (Harvey and Harcourt 1984, Kenagy and Trombulak 1986, Møller 1989, Heske and Ostfeld 1990, Breed and Taylor 2000). In species with polygynous mating systems, intrasexual selection among males is expected to be stronger than in monogamous or promiscuous systems; thus, SSD should be also greater. Regarding testes size, in cases of promiscuous or polygynous (multi-male) breeding systems, which exhibit great copulatory frequency and a number of males copulate with every female at estrous, SC is intense; thus, relatively larger testes than in single-male systems have evolved (Harvey and Harcourt 1984, Kenagy and Trombulak 1986, Møller 1989).

We have shown that in *Ctenomys*, the relation between testes mass and body mass is negatively allometric: relative testes size decreases as male body size increases at the interspecific, intrapopulational, and individual levels (Tables 3–5). The interspecific and interpopulational negative allometry is very pronounced, and relative testes mass is much higher than that observed in other mammal or rodent species (Table 6). This large relative testes size strongly suggests that tuco-tucos are polygynous and SC is an important component of their mating systems as suggested by paternity studies (Zenuto et al. 1999a,b, Graziani and Lacey 2004).

It is worth noting that in the case of male tuco-tucos, although body mass of individuals for which testes measurements were available (n=100) ranged between 69.5 and 642.0 g (mean=204.4 g) with a coefficient of variation of CV=44.91, total testes mass as estimated from testes volume (mean=4.32 g) showed CV=15.74. Testes size shows a very restricted range of variation as compared with body size, and it is clear that this variation reflects an allometric pattern where larger tuco-tucos have proportionally smaller testes than smaller individuals. The allometric pattern of testes size is also reflected in their geographic variation: as the body size of *Ctenomys* decreases toward higher latitudes (the converse to Bergmann's rule; Medina et al. 2007) and longitudes, testes mass increases proportionally although maintaining a relatively constant size.

A further suggestion that SC is operating in tuco-tucos came from the result of relative testes size within the *Ctenomys perrensi* superspecies, a group of chromosomally differentiated populations with low genetic divergence and more or less continuous gene flow (Giménez et al. 2002, Bidau 2006, Mirol et al. 2010). Within this monophyletic group, the relation between testes mass and body mass showed the same trend as in the general analyses: smaller males have relatively larger testes than larger ones. This "intraspecific" trend is also not unusual in polygynic species (Stockley and Purvis 1993, Pochron and Wright 2002, Schulte-Hostedde et al. 2003, Schulte-Hostedde and Millar 2004) and is an empirical indication that testis size is associated with the strength of SC. Thus, within a *Ctenomys* population, small males would invest more than larger males in testes growth and thus in ejaculate quality, which would counterbalance their presumably lower chances of accessing females due to their smaller body size.

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# Appendix

| Species | Locality | LAT (S) | LON (W) | ALT (m) | MHBL | FHBL | M/F | MBM | FBM | M/F | n | Ref. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. goodfellowi** | Esperanza | 16°15′ | 62°04′ | 515 | 240 | 203 | 1.18 | – | – | – | 1/3 | Anderson 1997[2] |
| *C. boliviensis boliviensis** | Est. Cachuela Esperanza | 16°47′ | 63°14′ | 300 | 276 | 221 | 1.25 | 650 | 420 | 1.55 | 2/1 | Anderson 1997[2] |
| *C. leucodon** | SW S. Andrés de Machaca | 16°48′ | 68°53′ | 3850 | 122 | 172 | 0.71 | – | – | – | 1/1 | Anderson 1997[2] |
| *C. opimus opimus** | 3.5 km E Huancaroma | 17°40′ | 67°27′ | 3710 | 251 | 202 | 1.24 | 457 | 284 | 1.61 | 3/2 | Anderson 1997[2] |
| *C. minutus** | 7 km N, 38 km W Roboré | 18°16′ | 60°07′ | 303 | 141 | 157 | 0.90 | 79 | 105 | 0.75 | 1/1 | Anderson 1997[2] |
| *C. frater mordosus** | Tambo | 21°27′ | 64°19′ | 2461 | 196 | 184 | 1.07 | 290 | 215 | 1.35 | 3/2 | Anderson 1997[2] |
| *C. lewisi** | Sama | 21°29′ | 65°02′ | 4184 | 219 | 204 | 1.07 | – | – | – | 7/6 | Anderson 1997[2] |
| *C. conoveri** | Colonia Fernheim | 22°15′ | 60°10′ | 175 | 293 | 293 | 1.00 | 900 | 520 | 1.73 | 4/5 | Osgood 1946[2] |
| *C. fulvus** | Pingo Pingo | 24°00′ | 69°00′ | 3300 | 223 | 220 | 1.01 | 360 | 330 | 1.09 | 7/5 | Pine et al. 1979[2] |
| *C. juris* | Finca El Chaguaral | 24°16′ | 64°48′ | 553 | 105 | 145 | 0.72 | 58 | 126 | 0.46 | 1/1 | Medina et al. 2007[1] |
| *C. opimus luteolus* | Piedra del Molino | 25°11′ | 65°51′ | 3500 | 193 | 166 | 1.16 | 270 | 138 | 1.96 | 2/3 | Medina et al. 2007[1] |
| *C. saltarius* | Tolombón | 26°15′ | 65°55′ | 1590 | 181 | 186 | 0.97 | 190 | 191 | 0.99 | 2/1 | Medina et al. 2007[1] |
| *C. latro* | Tapia | 26°35′ | 65°16′ | 711 | 172 | 164 | 1.05 | – | – | – | 2/2 | Medina et al. 2007[1] |
| *C. latro* | Ticucho | 26°36′ | 65°14′ | 615 | 161 | 153 | 1.05 | – | – | – | 1/1 | Medina et al. 2007[1] |
| *C. argentinus* | Campo Winter | 26°36′ | 59°15′ | 68 | 180 | 166 | 1.08 | 223 | 166 | 1.34 | 2/1 | Medina et al. 2007[1] |
| *C. argentinus* | Campo Bermejo | 26°36′ | 59°09′ | 70 | – | – | – | 223 | 159 | 1.40 | 1/1 | Medina et al. 2007[1] |
| *C. knighti* | INTA Santa María | 26°43′ | 66°03′ | 1885 | 168 | 162 | 1.04 | 207 | 169 | 1.22 | 3/3 | Medina et al. 2007[1] |
| *C. viperinus* | Villa San Javier | 26°46′ | 65°23′ | 1041 | 223 | 189 | 1.18 | 420 | 258 | 1.63 | 2/2 | Medina et al. 2007[1] |
| *C. bonettoi* | Colonia Elisa | 26°48′ | 59°33′ | 59 | 172 | 155 | 1.11 | 164 | 121 | 1.36 | 3/2 | Medina et al. 2007[1] |
| *C. tucumanus* | San Miguel de Tucumán | 26°49′ | 65°13′ | 430 | 182 | 173 | 1.05 | 182 | 162 | 1.12 | 1/2 | Medina et al. 2007[1] |
| *C. pilarensis* | Yatayty | 26°52′ | 58°18′ | 45 | 189 | 169 | 1.12 | 205 | 144 | 1.42 | 3/3 | Medina et al. 2007[1] |
| *C. tucumanus* | Quilmes, km 30, NR 306 | 27°04′ | 65°15′ | 290 | 184 | 172 | 1.07 | 298 | 175 | 1.70 | 2/1 | Medina et al. 2007[1] |
| *C. pilarensis* | Desmochado | 27°06′ | 58°04′ | 63 | 202 | 177 | 1.14 | 287 | 170 | 1.69 | 1/1 | Medina et al. 2007[1] |
| *C. pilarensis* | Mayor Martínez | 27°08′ | 58°13′ | 57 | 205 | 175 | 1.17 | 301 | 172 | 1.75 | 2/1 | Medina et al. 2007[1] |
| *C. pilarensis* | Paso Pucú | 27°08′ | 58°13′ | 57 | 209 | 177 | 1.18 | 272 | 191 | 1.42 | 1/1 | Medina et al. 2007[1] |
| *C. viperinus* | Yonopongo | 27°13′ | 65°30′ | 324 | 200 | 208 | 0.96 | 240 | 306 | 0.78 | 3/1 | Medina et al. 2007[1] |
| *C. argentinus* | Colonia Benítez | 27°19′ | 59°02′ | 54 | 168 | 165 | 1.02 | 132 | 139 | 0.95 | 1/1 | Medina et al. 2007[1] |
| *C. tuconax* | La Calera | 27°20′ | 63°35′ | 469 | 176 | 199 | 0.88 | 225 | 410 | 0.55 | 1/1 | Medina et al. 2007[1] |
| *C. tuconax* | Alto Verde | 27°22′ | 65°37′ | 342 | 252 | 212 | 1.19 | 576 | 360 | 1.60 | 1/2 | Medina et al. 2007[1] |
| *C. tuconax* | Aguilares | 27°24′ | 65°37′ | 333 | 206 | 225 | 0.92 | 270 | 410 | 0.66 | 1/1 | Medina et al. 2007[1] |
| *C. dorbignyi* | Mbarigüí | 27°33′ | 57°31′ | 55 | 207 | 183 | 1.13 | 263 | 193 | 1.36 | 2/2 | Medina et al. 2007[1] |
| *C. dorbignyi* | Paraje Angostura | 27°36′ | 57°58′ | 59 | 163 | 179 | 0.91 | – | – | – | 5/3 | Medina et al. 2007[1] |
| *C. perrensi* complex sp. 2 | Estancia Curuzú Laurel | 27°55′ | 58°30′ | 61 | 205 | 183 | 1.12 | 249 | 181 | 1.38 | 4/4 | Medina et al. 2007[1] |
| *C. perrensi* complex sp. 4 | Manantiales | 27°58′ | 58°08′ | 60 | 184 | 183 | 1.01 | 207 | 182 | 1.14 | 6/3 | Medina et al. 2007[1] |
| *C. perrensi* complex sp. 6 | Estancia Tacuarita 2 | 28°01′ | 56°36′ | 53 | 195 | 178 | 1.10 | 287 | 175 | 1.64 | 2/2 | Medina et al. 2007[1] |
| *C. perrensi* complex sp. 8 | San Miguel | 28°01′ | 57°36′ | 61 | 167 | 180 | 0.93 | 137 | 166 | 0.83 | 4/3 | Medina et al. 2007[1] |
| *C. perrensi* complex sp. 9 | Mburucuyá | 28°02′ | 58°14′ | 70 | 201 | 191 | 1.05 | 284 | 268 | 1.06 | 2/1 | Medina et al. 2007[1] |
| *C. perrensi* complex sp. 11 | Estancia Rosarito | 28°05′ | 58°16′ | 70 | 187 | 170 | 1.10 | 190 | 179 | 1.06 | 12/8 | Medina et al. 2007[1] |
| *C. roigi* | Estancia Yacyretá | 28°05′ | 58°50′ | 56 | 185 | 181 | 1.02 | 290 | 162 | 1.79 | 5/3 | Medina et al. 2007[1] |

(Appendix Table continued)

| Species | Locality | LAT (S) | LON (W) | ALT (m) | MHBL | FHBL | M/F | MBM | FBM | M/F | n | Ref. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. roigi* | Costa Mansión | 28°08′ | 58°49′ | 60 | 193 | 193 | 1.00 | 212 | 221 | 0.96 | 2/3 | Medina et al. 2007[1] |
| *C. perrensi* complex sp. 12 | Pago Alegre | 28°08′ | 58°22′ | 77 | 180 | 150 | 1.20 | 206 | 165 | 1.25 | 3/3 | Medina et al. 2007[1] |
| *C. perrensi* complex sp. 13 | 8 km N Santa Rosa | 28°11′ | 58°07′ | 76 | 187 | 174 | 1.07 | 226 | 209 | 1.08 | 5/3 | Medina et al. 2007[1] |
| *C. perrensi* complex sp. 14 | Estancia La Clarita | 28°15′ | 58°29′ | 70 | 184 | 176 | 1.05 | – | – | – | 3/2 | Medina et al. 2007[1] |
| *C. perrensi* complex sp. 18 | Saladas | 28°15′ | 58°37′ | 77 | 198 | 165 | 1.20 | 258 | 159 | 1.62 | | Medina et al. 2007[1] |
| *C. perrensi* | Rincón de Ambrosio | 28°16′ | 58°53′ | 65 | 166 | 174 | 0.95 | – | 160 | – | 8/7 | Medina et al. 2007[1] |
| *C. perrensi* complex sp. 19 | 6 km S Cuatro Bocas | 28°17′ | 58°41′ | 67 | 205 | 196 | 1.05 | 335 | 230 | 1.46 | 4/4 | Medina et al. 2007[1] |
| *C. perrensi* | Arroyo Saty | 28°22′ | 58°56′ | 60 | 178 | 181 | 0.98 | – | – | – | 5/5 | Medina et al. 2007[1] |
| *C. perrensi* complex sp. 20 | 12 km S San Roque | 28°41′ | 58°42′ | 70 | 143 | 157 | 0.91 | 112 | 176 | 0.64 | 2/2 | Medina et al. 2007[1] |
| *C. perrensi* complex sp. 21 | Chavarría | 28°58′ | 58°35′ | 60 | 185 | 186 | 0.99 | 222 | 90 | 2.47 | 7/5 | Medina et al. 2007[1] |
| *C. perrensi* | Goya | 29°11′ | 59°13′ | 24 | 191 | 171 | 1.12 | – | – | – | 4/3 | Medina et al. 2007[1] |
| *C. rosendopascuali* | Candelaria | 29°49′ | 63°21′ | 304 | 177 | 159 | 1.11 | 165 | 113 | 1.46 | 1/1 | Medina et al. 2007[1] |
| *C. dorbignyi* | Paraje Sarandicito | 30°10′ | 59°30′ | 35 | 160 | 168 | 0.95 | – | – | – | 5/4 | Medina et al. 2007[1] |
| *C. rosendopascuali* | Los Mistoles | 30°38′ | 63°54′ | 434 | 167 | 166 | 1.01 | – | – | – | 1/1 | Medina et al. 2007[1] |
| *C. bergi* | Cruz del Eje | 30°44′ | 65°05′ | 390 | 160 | 138 | 1.16 | 125 | 76 | 1.64 | 1/2 | Medina et al. 2007[1] |
| *C. rosendopascuali* | Mar Chiquita | 30°55′ | 62°41′ | 65 | 160 | 165 | 0.97 | 118 | 94 | 1.26 | 1/1 | Medina et al. 2007[1] |
| *C. yolandae* | Loteo Santa Ana | 31°38′ | 60°43′ | 18 | 173 | 155 | 1.12 | 133 | 96 | 1.39 | 1/1 | Medina et al. 2007[1] |
| *C. dorbignyi* | Concepción del Uruguay | 32°26′ | 58°12′ | 2 | 196 | 175 | 1.12 | 284 | 190 | 1.49 | 2/1 | Medina et al. 2007[1] |
| *C. dorbignyi* | Paso Vera | 32°27′ | 58°12′ | 10 | 185 | 184 | 1.01 | 249 | 211 | 1.18 | 4/4 | Medina et al. 2007[1] |
| *C. pundti* | La Carlota | 33°27′ | 63°18′ | 130 | 157 | 138 | 1.14 | 85 | 83 | 1.02 | 5/4 | Medina et al. 2007[1] |
| *C. pundti* | Puente Olmos | 33°27′ | 63°07′ | 117 | 144 | 133 | 1.08 | 111 | 71 | 1.56 | 6/4 | Medina et al. 2007[1] |
| *C. torquatus** | Colonia | 33°30′ | 57°30′ | 119 | 190 | 185 | 1.03 | 229 | 190 | 1.21 | 29/28 | Barlow 1965[2] |
| *C.* sp. 22 | Río Quinto | 33°51′ | 65°16′ | 486 | 174 | 159 | 1.09 | 164 | 101 | 1.62 | 2/1 | Medina et al. 2007[1] |
| *C. pearsoni** | Arroyo Limetas | 34°00′ | 58°00′ | 27 | 182 | 180 | 1.01 | 220 | 212 | 1.04 | 6/5 | Lessa and Langguth 1983[2] |
| *C. talarum talarum* | Cerro de la Gloria | 35°57′ | 57°27′ | 10 | 190 | 178 | 1.07 | – | – | – | 2/1 | Medina et al. 2007[1] |
| *C. talarum occidentalis* | El Guanaco | 36°13′ | 64°12′ | 201 | 146 | 135 | 1.08 | – | – | – | 1/2 | Medina et al. 2007[1] |
| *C. mendocinus* | Río Salado | 36°18′ | 66°48′ | 645 | 163 | 151 | 1.08 | 149 | 98 | 1.52 | 4/3 | Medina et al. 2007[1] |
| *C. talarum occidentalis* | La Florida | 36°22′ | 65°02′ | 174 | 144 | 150 | 0.96 | 89 | 107 | 0.83 | 2/1 | Medina et al. 2007[1] |
| *C. talarum talarum* | San Clemente del Tuyú | 36°22′ | 56°43′ | 0 | 171 | 168 | 1.02 | – | – | – | 3/3 | Medina et al. 2007[1] |
| *C. talarum talarum* | Mar del Tuyú | 36°32′ | 56°40′ | 0 | 181 | 154 | 1.18 | – | – | – | 2/2 | Medina et al. 2007[1] |
| *C. talarum talarum* | Santa Teresita | 36°33′ | 56°41′ | 0 | 168 | 151 | 1.11 | – | – | – | 3/2 | Medina et al. 2007[1] |
| *C. talarum talarum* | Costa del Este | 36°35′ | 56°42′ | 0 | 162 | 153 | 1.06 | – | – | – | 2/1 | Medina et al. 2007[1] |
| *C. mendocinus* | Santa Rosa | 36°37′ | 64°17′ | 175 | 144 | 148 | 0.97 | 95 | 105 | 0.90 | 3/4 | Medina et al. 2007[1] |
| *C. talarum talarum* | Aguas Verdes | 36°38′ | 56°42′ | 0 | 173 | 164 | 1.05 | – | – | – | 2/3 | Medina et al. 2007[1] |
| *C. talarum talarum* | La Lucila del Mar | 36°39′ | 56°42′ | 0 | 180 | 156 | 1.15 | – | – | – | 3/3 | Medina et al. 2007[1] |
| *C. talarum talarum* | San Bernardo | 36°41′ | 56°41′ | 62 | 182 | 158 | 1.15 | – | – | – | 3/2 | Medina et al. 2007[1] |
| *C. mendocinus* | Estancia El Indio Blanco | 36°42′ | 64°15′ | 175 | 126 | 144 | 0.88 | 77 | 98 | 0.79 | 1/1 | Medina et al. 2007[1] |
| *C. talarum talarum* | Mar de Ajó | 36°42′ | 56°44′ | 0 | 166 | 160 | 1.04 | – | – | – | 4/3 | Medina et al. 2007[1] |
| *C. talarum talarum* | Punta Médanos | 36°56′ | 56°50′ | 0 | 191 | 168 | 1.14 | – | – | – | 2/2 | Medina et al. 2007[1] |
| *C. talarum talarum* | Pinamar | 37°01′ | 57°05′ | 0 | 178 | 169 | 1.05 | – | – | – | 2/3 | Medina et al. 2007[1] |

(Appendix Table continued)

| Species | Locality | LAT (S) | LON (W) | ALT (m) | MHBL | FHBL | M/F | MBM | FBM | M/F | n | Ref. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. talarum talarum* | Villa Gesell | 37°13′ | 57°06′ | 0 | 183 | 173 | 1.06 | – | – | – | 2/2 | Medina et al. 2007[1] |
| *C. azarae* | General Acha | 37°22′ | 64°35′ | 252 | 163 | 145 | 1.12 | 154 | 102 | 1.51 | 4/3 | Medina et al. 2007[1] |
| *C. emilianus** | Chos Malal | 37°23′ | 70°16′ | 806 | 201 | 174 | 1.16 | – | – | – | 1/2 | Thomas and St. Leger 1926[2] |
| *C. chasiquensis* | Chasicó | 38°19′ | 62°39′ | 157 | 182 | 166 | 1.10 | – | – | – | 3/3 | Medina et al. 2007 |
| *C. maulinus brunneus** | Río Colorado | 38°27′ | 71°22′ | 900 | 197 | 200 | 0.99 | – | – | – | 4/6 | Osgood 1943[2] |
| *C.* sp. 23 | Médanos | 38°49′ | 62°41′ | 33 | 172 | 150 | 1.15 | – | – | – | 3/5 | Medina et al. 2007[1] |
| *C.* sp. 24 | Algarrobo | 38°53′ | 63°09′ | 47 | 162 | 173 | 0.94 | – | – | – | 1/2 | Medina et al. 2007[1] |
| *C. australis* | Monte Hermoso | 38°54′ | 61°32′ | 24 | 186 | 141 | 1.32 | – | – | – | 2/4 | Medina et al. 2007[1] |
| *C. talarum recessus* | Monte Hermoso | 38°54′ | 61°32′ | 24 | 176 | 154 | 1.14 | – | – | – | 2/3 | Medina et al. 2007[1] |
| *C. sociabilis** | Ea. Fortín Chacabuco | 40°58′ | 71°11′ | 1075 | 170 | 180 | 0.94 | 213 | 207 | 1.03 | 3/4 | Pearson and Christie 1985[2] |
| *C. haigi** | El Maitén | 42°03′ | 71°10′ | 700 | 163 | 155 | 1.05 | – | – | – | 3/6 | Pearson 1984[2] |
| *C.* sp. 29 | Puerto Madryn | 43°00′ | 65°08′ | 17 | 145 | 132 | 1.10 | – | – | – | 5/9 | Medina et al. 2007[1] |
| *C.* sp. 30 | Estancia Medina | 43°30′ | 65°18′ | 200 | 147 | 138 | 1.07 | 76 | 64 | 1.19 | 2/3 | Medina et al. 2007[1] |
| *C.* sp. 31 | Estancia La Clara | 43°45′ | 65°22′ | 250 | 149 | 144 | 1.03 | 96 | 73 | 1.32 | 1/2 | Medina et al. 2007[1] |
| *C. fodax* | Lago Blanco | 45°55′ | 71°12′ | 598 | 161 | 137 | 1.18 | – | – | – | 2/3 | Medina et al. 2007[1] |
| *C. coyhaiquensis** | Chile Chico | 46°33′ | 71°46′ | 330 | 154 | 157 | 0.98 | 140 | 116 | 1.21 | 17/22 | Kelt and Gallardo 1994[2] |
| *C. colburni* | Casa de Piedra-Río Ecker | 47°07′ | 70°51′ | 517 | 166 | 146 | 1.14 | – | – | – | 2/3 | Medina et al. 2007[1] |
| *C. sericeus* | Río Chico-Río Belgrano | 48°15′ | 71°13′ | 70 | 111 | 133 | 0.83 | – | – | – | 1/2 | Medina et al. 2007[1] |

**Appendix Table** Species, populations, and localities of tuco-tucos (*Ctenomys*) studied with relation to geographic body size variation.
MHBL, FHBL, mean head and body length (mm) of males and females, respectively; MBM, FBM, mean body mass (g) of males and females respectively. n, sample size (males/females). Ref., references of the source of body size data. Asterisks indicate those specimens not measured by the authors. [1]Deposited at the "Félix de Azara" collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina. [2]Specimens not measured by the authors are deposited in the institutions referred to in the relevant papers.

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