



Morphometric and demographic differences between tropical and temperate Norway rats (*Rattus norvegicus*)

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Rattus norvegicus (Norway rat) is one of the most abundant and geographically widespread mammals. Ecological studies focusing on urban Norway rat populations are restricted to temperate regions, and data describing populations from tropical cities are lacking. We compared the morphometrics and demographic characteristics of rats captured in urban low-income settlements in Salvador, Brazil, to a season, environmental area of capture, and sex-matched sample from Baltimore, Maryland. Norway rats of both sexes were significantly smaller in Salvador, although the threshold mass marking sexual maturity was equivalent for both cities. Pregnancy rates were comparable (~50%); however, juveniles were commonly trapped in Salvador (20%) while they were rarely trapped in Baltimore during winter months (2%). These findings suggest that tropical and temperate rats differ with respect to body metrics, while size at sexual maturity is similar. Further studies conducted over different seasons are required before any firm conclusions are reached; however, this study provides preliminary support for Bergmann's rule that species at higher absolute latitude are larger than the same species sampled at lower latitudes.

Key words: Bergmann's rule, invasive species, Norway rat, rodent control, urban ecology

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Norway rats (*Rattus norvegicus*) possess the most extensive geographic range of any terrestrial mammal. In the Western Hemisphere, established populations extend from the Arctic Circle at Nome, Alaska (Schiller 1956) to sub-Antarctic, heavily glaciated South Georgia Island (Pye and Bonner 1980). Wherever they have been introduced, their extraordinary capacity for adaptation and procreation distinguish them as one of, if not the most, successful of vertebrate invasive species (Davis 1953).

Although Norway rats are well adapted to rural, semirural, and agricultural settings (Bishop and Hartley 1976; Taylor 1978; Glass et al. 1989), the realization of their maximum demographic potential is best exemplified in urban and periurban environments that provide high resource abundance (Glass et al. 1989). Understanding the ecology of this introduced species is critical, as rats cause significant agricultural losses and infrastructural damage (Pratt et al. 1991; Buckle and Smith

1994; Singleton et al. 1999), and serve as reservoir host to numerous viral and bacterial agents. Many of these agents are considered zoonotic pathogens (Gratz 1988; Meerburg et al. 2009), such as Seoul virus, *Yersinia pestis*, *Rickettsia typhi*, and *Leptospira* serogroups. Evidence suggests that many of these pathogens have been distributed concomitantly with the global spread of Norway rats (LeDuc et al. 1986; Ellis et al. 1999).

Despite the global impact of rats on health and food production, ecological studies focusing on urban Norway rat populations are scarce and restricted to cities in temperate regions (e.g., Davis 1953; Farhang-Azad and Southwick 1979; Glass et al. 1989; Himsworth et al. 2013). Moreover, only a limited number of studies have been performed outside of the Northern Hemisphere (Kataranovski et al. 1991; Gómez-Villafañe et al. 2013). Like other rodent taxa living in both tropical and temperate environments (e.g., Madsen and Shine 1999), it may be expected that demographic characteristics of tropical Norway

rat populations, such as age structure, size, growth rates, onset of sexual maturity, and survival, will differ from data reported in temperate regions.

In attempts to test Bergmann's rule (Bergmann 1847), a number of studies have demonstrated that differences in the body size of different mammalian taxa vary along a latitudinal gradient, with increasing size associated with increasing absolute latitude (reviewed in Ashton et al. 2000; Yom-Tov and Geffen 2011; Clauss et al. 2013). Although the size–latitude relationship is typically weaker for rodents (Ashton et al. 2000), evidence exists that *Rattus exulans*, introduced into islands in the Pacific Ocean approximately 1,000 years ago, has shown a size–latitude decrease in body size, while *Rattus rattus*, the black rat, and *R. norvegicus* introduced only in the last 200–250 years have not shown a similar diminishment in size (Yom-Tov et al. 1999). However, caution is warranted when evaluating these data in the context of Bergmann's rule, as mammals on islands trend toward larger body sizes compared to those on continents (Millien 2006), and the comparatively recent introduction of Norway and black rats may have provided insufficient time for morphological adaptation. Additionally, although temperature has been recognized to play an important role in these trends, biotic factors such as food resources and intra- and interspecific competition have also been hypothesized as important mediating factors (Yom-Tov et al. 1999; Yom-Tov and Geffen 2011).

In an effort to rule out any island effects, and to control for other factors that confound direct population comparisons for evidence of Bergmann's rule (Iskjaer et al. 1989), we hypothesized that individuals of *R. norvegicus* populations would trend toward smaller body sizes and reach sexual maturity earlier at lower latitudes. To test this hypothesis, we examined metrics of body size and mass at sexual maturity among rats trapped in Salvador, Brazil (12°58'6"S) and compared these parameters with the same metrics acquired from a seasonally, environmentally (low socioeconomic areas), and sex-matched cohort of rats trapped in the temperate city of Baltimore, Maryland (39°16'60"). During this investigation, we examined rats captured in winter months, June to August, in Salvador and January to March in Baltimore, as differences in demographic characteristics and reproduction would be maximized due to the harsh environmental conditions that rats are exposed to in temperate latitudes.

MATERIALS AND METHODS

Study area.—Rat trapping was performed in the city of Salvador, Brazil, which has a subtropical climate (mean temperature 25.3°C), with average winter temperatures (June to September) ranging between 23.8°C and 24.3°C and summer temperatures ranging between 26.7°C and 27.1°C. Seasons are marked by heavy rains during winter (203–324 mm per month) compared to the summer months (112–131 mm per month). Three low-income communities (*favelas*) were selected for study, Pau da Lima, Sete de Abril, and Valeria, based on the high annual incidence of human leptospirosis reported from the areas (Ko et al. 1999; Sarkar et al. 2002). Norway rats serve

as the principal reservoir host for leptospires infecting humans (Sarkar et al. 2002; de Faria et al. 2008; Reis et al. 2008; Ko et al. 2009), so these sites were expected to have substantial rat populations.

At each trap site, groups of 6–8 contiguous households, semi-isolated from adjacent residences by intervening physical barriers such as abandoned lots, stairways, or open sewers were chosen as the sampling unit. These groupings were selected to limit the amount of egress and ingress of rats during the sampling period, so that our cross-sectional study of morphometrics would target a somewhat closed population, which was also a robust assumption due to the short trapping period. In total, 10 study sites were selected: 6 in Pau da Lima (33 households), 3 in Sete de Abril (17 households), and 1 in Valeria (8 households). Each site was systematically sampled over 6–8 consecutive days, using ~5 Tomahawk-like live traps placed in peridomestic areas of the households in each defined trap site.

Trapping.—Rats were livetrapped after a prebaiting period of 2–3 days to mitigate the impact of trap-shyness (Chitty and Shorten 1946; Chitty and Kempson 1949). Traps were set at sundown each day and collected at sunrise the following morning. Traps containing a rat were removed and double-bagged for transport using heavy-duty garbage bags, and a replacement trap was set in the same location for each night of the trapping period. Study areas were trapped exhaustively, as indicated by 2–3 days of 0% trapping success.

Data collection.—Owing to the presence of transmissible biological agents among the rats captured (Costa et al. 2014), animals were processed using modified BSL-3/BSL-4 field precautions (Mills et al. 1995) at an outdoor mobile processing facility. External metrics including body, tail, right ear, and right hind foot lengths were recorded to the nearest millimeter, and body mass was recorded to the nearest gram. Mass has commonly been used as an index of rat age in Baltimore studies and has been shown to be an accurate surrogate (Calhoun 1962; Iskjaer et al. 1989). The sex of the animals and external indications of reproductive status were noted (vagina perforate or imperforate; testes scrotal or nonscrotal).

Animals were anesthetized with ether and euthanized with a lethal 1 cc dose of 1:10 thiopental solution injected into the abdominal cavity. Dissections were performed to assess the internal reproductive characteristics of each rat. Placental scars and number of embryos (if pregnant) were recorded (Davis 1948), as were the presence of epididymal convolutions, indicating spermatogenesis (Davis and Hall 1948).

Matched sample.—A random sample of 100 animals, 50 females and 50 males, was selected from animals captured in Baltimore (Gardner-Santana et al. 2009) to provide a cohort of rats matched by season, environment of capture, and sex to compare to the Salvador animals. All Baltimore rats were captured in winter, from January through March of 2007 (average winter temperature 3.9°C, average winter rainfall 237 mm), in low socioeconomic urban areas characterized by a marked lack of sanitation (poor housing conditions and significant garbage accumulation) and the presence of numerous vacant dwellings.

Analyses.—Statistical analysis was performed using SAS v.9.2 (SAS Institute Inc. 2008). Univariate analyses included 2-tailed Student's *t*-tests for comparing group means and chi-square tests for evaluating associations between categorical variables within rats sampled from Salvador and Baltimore. One-tailed *t*-tests were used to compare results between Salvador and Baltimore as our hypothesis predicted that rats from Salvador would have smaller body metrics in a tropical setting. When group sizes were 5 or less, Fischer's exact tests were used. Correlation analyses were performed to evaluate association between mass and body, right hind foot, and right ear lengths for Salvador and Baltimore rats. Multivariate analyses of variance (MANOVAs) were performed to compare multivariate measures of body size between sexes within and between rats sampled from Salvador and Baltimore, and principal components analysis (PCA) was used to validate our use of body mass as a measure of body size in both samples.

Salvador and Baltimore samples were divided into males, nonpregnant females, and pregnant females; further, subgroups of adult males and adult nonpregnant females were evaluated.

RESULTS

Trapping.—A total of 108 Norway rats were captured over 934.5 trap nights from June to September 2010, in Salvador, Brazil, yielding an overall trap success of 11.6%. One black rat (*R. rattus*) and 3 opossums (*Didelphis marsupialis*) were captured during the study period but excluded from analyses. Fifty-nine Norway rats were captured in Pau da Lima, 37 in Sete de Abril, and 7 in Valeria; no data were collected from 9 rats that either escaped or were killed by household members. The number of rats trapped per site ranged from 2 to 21.

Demographic and morphometric characteristics.—The overall sex ratio of males to females was 1.0 (50/49), and this finding was consistent across all study areas. Analysis of pooled metrics from all trapping sites in Salvador did not differentiate male and female rats based on comparisons of mean body length

($P = 0.20$) or mean body mass (Table 1; $P = 0.32$), calculated via 2-tailed Student's *t*-tests. Furthermore, multivariate comparisons of body size measures (body mass, and body, tail, foot, and ear lengths) indicated that males and females (including juveniles of both sexes [less than 200 g, as based on measures of sexual maturity described below] and pregnant females) did not differ with respect to their multivariate means. Of note, the largest rat captured in Salvador weighed 518 g and was a hermaphrodite, having an imperforate vagina externally, and nonscrotal testes internally. This animal was excluded from the analyses.

PCA of the pooled Salvador sample, including external metrics, revealed one significant component explaining 74% of the variation. Body mass explained the most variation in this component. We observed this pattern for each demographic group (males, adult males, females, and adult females) where the 1st principal component contained all of the body size measurements (69%, 58%, 84%, and 69%, respectively), and the contribution of mass was comparable in magnitude for all comparisons.

Although we expected pregnancy to influence size–mass relationships among female rats, univariate 2-sided Student's *t*-tests, MANOVA, and PCA revealed that pregnant and nonpregnant females did not differ with respect to body size or mass, even though the number and size of embryos varied among pregnant females. Based on this finding, all of the 22 pregnant females were included in additional morphometric analyses between females and males.

Reproduction.—In total, 101 of the rats trapped in Salvador were examined externally and 87 were necropsied. Of the 48 males examined externally, 91.7% had scrotal testes (mass range 47–503 g, $\bar{X} = 320.5$ g), and the other 4 nonscrotal rats (8.3%) weighed less than 200 g. Of the 42 males necropsied, 32 had epididymal convolutions (76.2%; mass range 211–503 g, $\bar{X} = 357.2$ g), and each of the 10 males (23.8%) without epididymal convolutions weighed less than 203 g. Based on this finding, we characterized Salvador males having mass < 200 g to be juveniles.

Table 1.—Mean body size measures for Salvador males/females and Baltimore males/females Norway rats (*Rattus norvegicus*; juveniles and pregnant females included).

Characteristics	Salvador males	Salvador females	$\bar{X} \pm SD$	
			Baltimore males	Baltimore females
Body mass (g)	304.9 ± 119.9	281.6 ± 110.7	411.4 ± 104.6	417.9 ± 101.3
Minimum	47.0	71.0	40.0	138.0
Maximum	503.0	490.0	570.0	611.0
Body length (mm)	233.4 ± 36.0	224.4 ± 33.0	249.2 ± 28.7	249.1 ± 21.9
Minimum	139.0	123.0	90.0	165.0
Maximum	280.0	275.0	280.0	285.0
Tail length (mm)	195.1 ± 25.8	188.1 ± 31.9	188.0 ± 27.9	203.2 ± 21.5
Minimum	124.0	82.0	95.0	130.0
Maximum	240.0	235.0	225.0	248.0
Foot length (mm)	41.5 ± 3.36	40.1 ± 3.43	45.1 ± 2.88	43.5 ± 2.06
Minimum	32	31.0	32.0	39.0
Maximum	50	48.0	49.0	49.0
Ear length (mm)	20.6 ± 2.65	19.5 ± 2.90	21.3 ± 2.81	21.9 ± 2.56
Minimum	15.0	11.0	15.0	15.0
Maximum	30.0	24.0	27.0	27.0

Of the 22 nonpregnant female rats from Salvador, 16 (72.7%) had perforate vaginas (mass range 88–468 g, \bar{X} = 296.9 g) and the remaining 6 (27.3%), all weighed less than 200 g. Placental scars, indicating past pregnancies, were present among 26 rats (59.1%); 7 pregnant animals did not have placental scars, indicating that they were primiparous (Davis and Emlen 1948). All pregnant females weighed more than 200 g, and 9 out of 10 nulliparous females (nonpregnant females lacking placental scars) weighed less than 200 g; 1 female was not evaluated for placental scars. The mean mass of primiparous pregnant females was 287.3 g \pm 85.8, while the mean mass of nulliparous females was 138.8 g \pm 70.5. Based on this finding, we also characterized females with mass < 200 g to be juveniles.

Matched comparison with Baltimore sample.—Two-sided Student's *t*-tests comparing mean body mass and mean body length of male and female rats from Baltimore indicated that the sexes did not differ significantly with respect to either of these characteristics (Table 1; P = 0.76 and P = 0.98, respectively). However, MANOVA results indicated that Baltimore adult males were larger than Baltimore adult females with respect to their multivariate means for mass and body length measures (P < 0.001). Pregnant and nonpregnant females from Baltimore did not differ with respect to their multivariate means for body size measures (P = 0.18).

Of the 50 males from Baltimore, 49 were scrotal (mass range 189–570 g, \bar{X} = 419.0 g) and the 1 nonscrotal animal had uncoiled epididymes, a body mass of 40 g and body length of 90 mm.

Overall, 23 (46.0%) of the 50 Baltimore females were pregnant, similar to the finding of 50% pregnancy rate in Salvador. Of the nonpregnant Baltimore females (n = 27), only 1 was imperforate (3.7%), with body mass 138 g and body length 168 mm. As data on the presence/absence of placental scars was not reported for the Baltimore sample, no further analyses were performed.

Previous studies from Baltimore have used the 200 g threshold to distinguish between adult and juvenile Norway rats (Davis and Hall 1948; Glass et al. 1989); this threshold also held for Salvador rats. Correlation analyses showed that mass and body length were highly correlated but revealed only moderate association between mass and right hind foot and moderate/poor association between mass and ear length (Fig. 1). These associations were stronger for Salvador rats. Figure 1 indicated that Salvador rats were smaller than Baltimore rats, which was confirmed using univariate analysis (1-sided Student's *t*-tests) and MANOVAs that demonstrated that both adult males and adult females from Salvador were significantly smaller with respect to their multivariate means for mass and body size than Baltimore rats (P < 0.001, all comparisons). PCA of the Baltimore sample showed similar patterns when compared to the Salvador sample. The 1st principal component was significant and explained 63% of the variation. This axis contained all of the body size measurements (with loadings of comparable magnitude) for each demographic group (males [67%], adult males [67%], females [77%], and adult females [60%]).

DISCUSSION

In this study, we compared morphometric and demographic characters of Norway rats trapped in tropical Salvador with those trapped in temperate Baltimore. We matched our 2 samples with regard to season of capture, sex, and urban environment. By doing so, we sought to minimize the bias that could affect comparisons of the same species from different latitudes, thus complicating the testing of Bergmann's rule. We note that overall trap success, used as an index of rat abundance when more exact estimates are not available, were comparable between Salvador (11.6%) and Baltimore (10.8%—Glass et al. 1989). The similar trap success observed in Salvador and Baltimore suggested there was no obvious bias in the trappability of rats sampled at the 2 locations. However, if trapping selectively captured rats of different age/mass at the 2 sites, this would influence our results and conclusions.

Correlation and MANOVA analyses, supported by PCA, indicated that there were several differences between temperate and tropical rats sampled during winter months. First, male and female rats captured from Salvador did not differ with respect to their overall size, while Baltimore males were larger than females. Second, support for our hypothesis that rats captured from an area of lower absolute latitude (i.e., tropical zones) would be smaller than those captured at higher absolute latitude (i.e., temperate zones) was supported by results showing that male and female rats from Salvador were significantly smaller than their counterparts from Baltimore. These findings are consistent with Bergmann's rule. Third, in contrast to our expectations, the sexual maturity of Norway rats, based on external and internal evidence of sexual status, did not show that Salvador rats were sexually mature at a smaller mass/age than Baltimore rats but rather that sexual maturity occurred at a similar threshold mass of ~200 g in both populations. All primiparous females in the Salvador population had masses greater than 200 g, and all but one of the nulliparous females had masses less than 200 g. For Salvador males, using either the scrotal status of the testes or the development of the epididymes, the results indicated that males also reach maturity at ~200 g. Studies from Baltimore have also specified 200 g as the mass/age threshold for reproduction in both males and females (Davis and Hall 1948; Glass et al. 1989).

A commonly cited driver of the association between smaller body size in conspecific mammals trapped in lower latitudes is that small body size promotes heat loss by increasing the surface-area-to-volume ratio (Bergmann 1847; Ashton et al. 2000; Freckleton et al. 2003). However, biotic factors such as food resources, intra- and interspecific competition, predators, and possibly infectious agents could influence body size measures obtained from areas with different ecological characteristics (Yom-Tov et al. 1999; Yom-Tov and Geffen 2011). As noted above, this study attempted to limit the confounding influence of many of these factors.

Rats from both Salvador and Baltimore were captured from low socioeconomic settings where sanitation and housing quality are suboptimal for human habitation. Most of the food resources for Norway rats are from human-generated refuse.

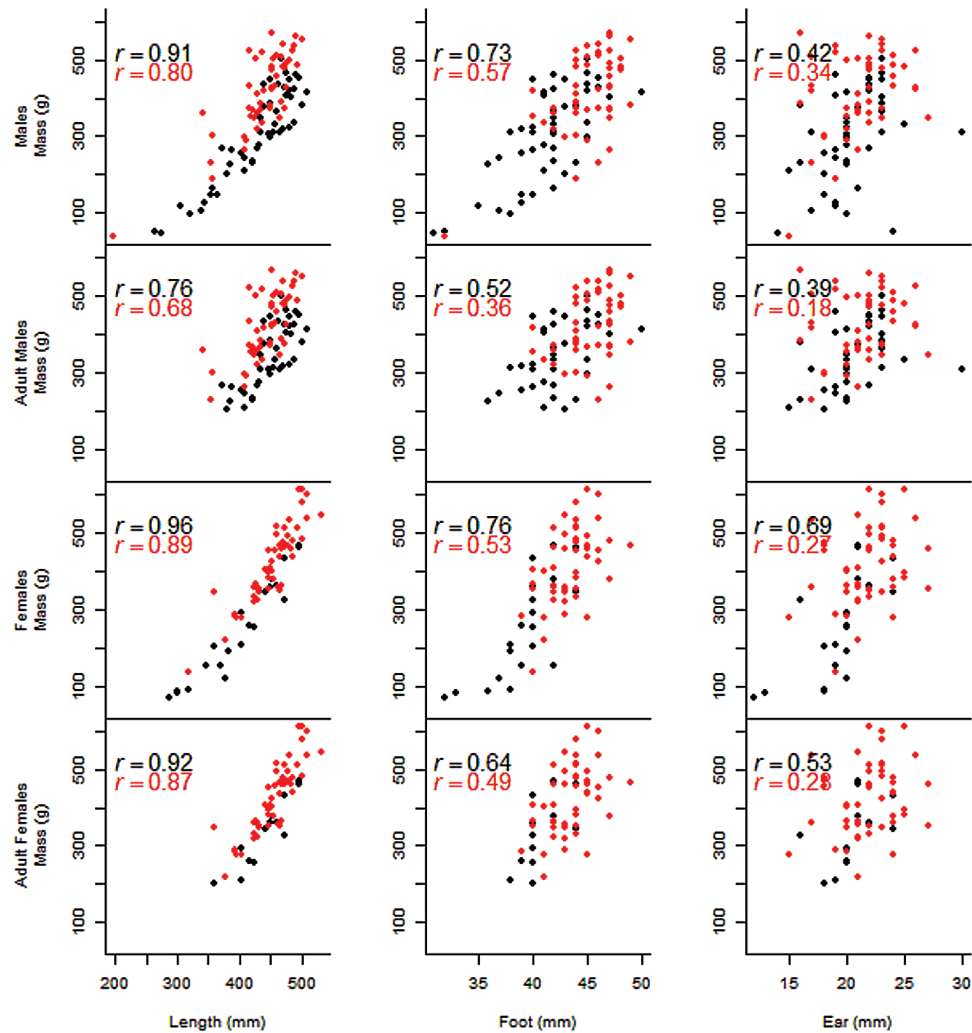


Fig. 1.—Correlation between weight and body size measures for Salvador and Baltimore male and female rats (*Rattus norvegicus*; red dots for Baltimore rats and back dots for Salvador rats).

However, virtually nothing is known about the quality or quantity of this resource, with the exception of preliminary findings from studies in Baltimore (Schein and Orgain 1953). Variation in quantity or caloric quality of available food resources by location is a complete unknown. Cats and dogs are the dominant species coexisting in locations in both Salvador and Baltimore, and these species share, and may compete, for food. The major predator of Norway rats, at least in Baltimore, are cats, which preferentially target juvenile animals under 100–200 g; cats have been shown to feed from the same refuse piles (Childs 1986; Glass et al. 2009). Stray cats are widespread in Salvador, but the predation pressure on rats and the corresponding impact on local rodent population dynamics are unstudied. Finally, although Norway rats in Salvador and Baltimore have been shown to be infected by several common microbes, as reviewed by Costa et al. (2014), the resulting impact on the body metrics and overall condition of rats is largely unknown. However, a recent study from Vancouver, Canada, found that rats infected with leptospires had greater amounts of body fat (Himsworth et al. 2013). It is possible that the prevalence of leptospiral or other infections could influence the size and mass of animals

sampled from different locations. However, the prevalence of leptospiral carriage is similar between rats sampled from Salvador (overall prevalence ranging from 63% to 83%) and those sampled from Baltimore (65%—Costa et al. 2014).

Our study was limited in duration and sample size, so additional data and analyses across seasons are warranted to support our findings and to further investigate the applicability of Bergmann's rule to this system. We matched our samples from Salvador and Baltimore to reduce obvious biases relating to time and location of rat trapping. Many of the existing meta-analyses of Bergmann's rule do not take these potential confounders into account, which present a significant complication when assessing different mammalian populations, especially small mammals (Yom-Tov and Geffen 2011). Results from Baltimore indicate how bias could be introduced by not matching on environment and season. Mass distributions of Norway rat populations vary depending on the environment sampled, with rats captured from semirural settings weighing less and growing at decreased rates than their urban counterparts. Additionally, mass distributions within urban rat populations vary with the season of capture and growth rates become slow

or become negative during winter months (Glass et al. 1988). Data from tropical areas are currently too sparse to draw similar conclusions.

These preliminary findings support our initial hypothesis that tropical Norway rats would be smaller than temperate Norway rats in keeping with Bergmann's rule. Of particular value would be future analyses across seasons, and those that explore differences among rat populations from low-income areas at different stages of succession (i.e., areas with intact patches of seminatural native habitat versus developed low-income areas with few species of trees and shrubs). Such studies could provide critical information pertaining to comparative life history characteristics such as absolute age at sexual maturity, the timing and duration of reproduction, fecundity, and survivorship of individuals within a given population. Such studies would offer insights into how such a successful invasive species has adapted to tropical climate and environmental conditions.

RESUMO

Rattus norvegicus (ratazana ou rato-marrom) é um dos mamíferos mais abundantes e de maior distribuição geográfica. Os estudos ecológicos focados nas populações de *R. norvegicus* tem sido restritos às regiões temperadas e existe falta de dados sobre esta espécie em áreas urbanas tropicais. No presente trabalho, comparamos as características morfométricas de ratos capturados em favelas de Salvador, Brasil, com uma amostra de Baltimore, Maryland, pareada por estação (inverno) e sexo. Embora em Salvador as ratazanas de ambos os sexos foram significativamente menores, o limiar indicador de maturidade sexual foi equivalente para ambas as cidades. As taxas de gravidez também foram comparáveis (~50%), porém, juvenis foram frequentemente capturados em Salvador (20%) mas raramente capturados em Baltimore (2%). Estes resultados sugerem que populações de ratos de regiões temperadas e tropicais diferem em relação às características morfométricas, mas o tamanho no qual alcançam maturidade sexual é similar. Estudos adicionais a serem realizados durante diferentes estações do ano são necessários antes de alcançar conclusões definitivas, porém, este estudo prove suporte à regra de Bergmann na qual indivíduos de latitudes mais elevadas são maiores que indivíduos da mesma espécie em latitudes mais baixas.

Palavras chaves: Regra de Bergmann, rato Norueguês, controle de roedores, espécies invasoras, ecologia urbana.

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