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# A case of reversed sexual size dimorphism in a polygynous small mammal, *Apodemus flavicollis* (Rodentia: Muridae)

Prípad obráteného veľkostného pohlavného dimorfizmu u ryšavky žltohrdlej *Apodemus flavicollis* (Rodentia: Muridae)

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**Abstract**. In the present study we analysed the occurrence and magnitude of sexual size dimorphism (SSD) in body weight and length of *Apodemus flavicollis*. We studied three different populations living at two localities in Slovakia: a lowland deciduous forest representing an optimal habitat (Sur Nature Reserve, Bratislava); and a mountain mixed forest representing a habitat close to margin of the distribution range of the studied species (Osobita Nature Reserve, West Tatra Mts.). The male-biased SSD in both body weight and length seems to be a general pattern in the studied species, which is in agreement with the expectation for a species with polygynous mating system. However, in the year 2004 we registered a case of a female- biased SSD at the mountain locality. In this year females were larger and males smaller than during all the other years of study at this locality. We expect that during this year of an exceptionally high population density on the locality, the reversed SSD could have been a result of two different, mutually acting selection pressures: selection favouring smaller males and selection favouring larger females. Our study provides evidence that both body weight and length in *A. flavicollis* show plasticity in terms of adapting to changes in the short term, which can consequently influence patterns of sexual size dimorphism.

**Key words**. *Apodemus flavicollis*, sexual size dimorphism, body weight, body length.

## INTRODUCTION

Sexual size dimorphism (SSD), the difference in body size between sexes, is a common feature in many mammal species. The hypotheses explaining the origin and maintenance of SSD include sexual selection; selection on reproductive life-history traits and intersexual ecological-niche divergence (Hood 2000). Most mammals exhibit male-biased SSD, which is usually attributed to the prevalent polygynous mating system, but some species exhibit female-biased SSD (Schulte-Hostedde & Millar 2000). Male-biased SSD may have evolved through sexual selection on male body size, as larger males can be more successful in acquiring mating opportunities. The degree of male-biased SSD is correlated with the intensity of intrasexual competition for mates, and as such is thought to be the greatest in polygynous mating systems with territorial males (Heske & Ostfeld 1990). Sexual size dimorphism can be also a result of dichotomous selection on male and female strategies of growth in relation to reproduction. In polygynous mammals, these strategies reflect sexual selection on males for access to females and competitive selection on females for access to food. Consequently, in such species, males display rapid early growth to large adult size, whereas females invest in physical condition and early sexual maturity at the expense of size (Post et al. 1999, Isaac 2005). The magnitude of SSD in adults can vary within species in response to environmental factors differentially influencing the growth of males and females (Post et al. 1999, Isaac 2005). While the occurrence of sexual size dimorphism among mammals is widely recognized, relatively little is known about how environmental variables affect its phenotypic expression in the short term (LeBlanc et al. 2001, Hood 2000). Several studies of small mammals documented non-uniform pattern of sexual size dimorphism, with the magnitude of SSD changing between habitats, seasons and/or different population densities (Hood 2000, Isaac 2005).

In the present study we analysed the SSD in body weight and body length of *Apodemus flavicollis* (Melchior, 1834), a polygynous small mammal species with male-biased sexual size dimorphism. We examined the occurrence and magnitude of SSD in three populations of *A. flavicollis* living at two localities during six consecutive years.

## METHODS

The study was carried out in a sixyear period (2000–2005) at two localities in Slovakia, differing in altitude, vegetation composition and climatic conditions. In the Sur Nature Reserve, Bratislava (48° 13.4' N, 17° 13.2' E; 128–132 m a. s. l.), two trapping grids were established: one in an alder forest (Sur 1) and another one in an oak forest (Sur 2). In the Osobita Nature Reserve, West Tatra Mts. (49° 16.4' N, 19° 44.7' E; 1018–1092 m a. s. l.), one trapping grid was placed in a beech-spruce forest.

Small mammals were live-trapped on the study plots of 3.24 ha in each habitat type, on average six times per year. The capture-mark-recapture (CMR) method was used. Traps were set during six consecutive nights and checked twice a day, mornings and evenings. All captured small mammals were individually marked and released at the trapping points immediately after data collection. Reproductive condition of the captured animals was assessed on the basis of external sexual characters (males: scrotal testes; females: perforated vagina, lactation, post-lactation, or pregnancy). Weight of the animals was measured using a Pesola spring scale (±0.5 g). The body length of the animals was measured using plastic rulers (±0.5 mm). Only adult individuals were included in the analysis of sexual size dimorphism. The age of each individual was determined based on external features (pelage colour and reproductive status), and all individuals were classified as adult (adult coloured pelage and reproductive activity achieved) or young (grey pelage, transitional pelage and sexual activity not achieved) age classes. Pregnant females and females after delivery were excluded from the analysis, to avoid bias caused by overestimation of female weight. The possible temporal variation in the course of the day was dealt with by averaging obtained body measures for an individual in one trapping session. The magnitude of SSD was evaluated on the basis of the sexual dimorphism index (SDI), which was calculated according to Badyaev (1997) as the ratio of male to female weight (length) using untransformed values. Both for body weight and length, the Levene's test for equality of variances was used to determine whether the data were homogeneous. Than factorial MANOVA (factors: sex, year, locality) was performed for both variables. Specific between-group differences were evaluated using the Tukey's test. Statistical analyses were performed using Statistica Version 7 (StatSoft 2004). The field study was performed in accordance with the permission of the Ministry of Environment of SR no. 6846/06/3.1/jam./5. and no. 2141/556/03-5.1 pil.

## RESULTS

Factorial MANOVA showed significant differences between localities, years and sexes in both body weight and length (Table 1). Animals of both sexes tended to be heavier on both lowland localities compared to the mountain locality (Fig.1). Although we registered annual fluctuations in both body weight and length on all studied localities (Figs. 1, 2), in most cases a significant

Table 1. Factorial MANOVA on body weight and size of the sampled indivuals of *Apodemus flavicollis*. WL = Wilk's Lambda
Tab. 1. Štatistické hodnoty (faktorová MANOVA) pre porovnanie hmotnosti a rozmerov jedincov *Apodemus flavicollis*. WL = Wilk's Lambda

| | multivariate | | | | univariate | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | weight | | length | |
| variation source | WL | F | p | df | F | p | F | p |
| locality*year | 0.898 | 14.046 | p < 0.001 | 14 | 6.915 | p < 0.001 | 14.831 | p < 0.001 |
| year*sex | 0.982 | 8.196 | p < 0.001 | 4 | 15.668 | p < 0.001 | 6.903 | p < 0.010 |
| locality*year*sex | 0.976 | 3.074 | p < 0.001 | 14 | 4.275 | p < 0.001 | 5.216 | p < 0.001 |

male-biased SSD was recorded (Tables 2, 3). The only exception from this general pattern of SSD was recorded during the year 2004 at the mountain locality Osobita, where females were found to be significantly heavier and larger than males (Tables 2, 3). In this year males were smaller and lighter and females larger and heavier than in any other year of study at this locality (Tables 2, 3). In 2004 both population density and the number of adult females were exceptionally high at this locality (Fig. 3).

The magnitude of SSD expressed as SDI was moderate (slightly above 1) at both lowland localities during all years of study. The highest SSD found during this study was registered

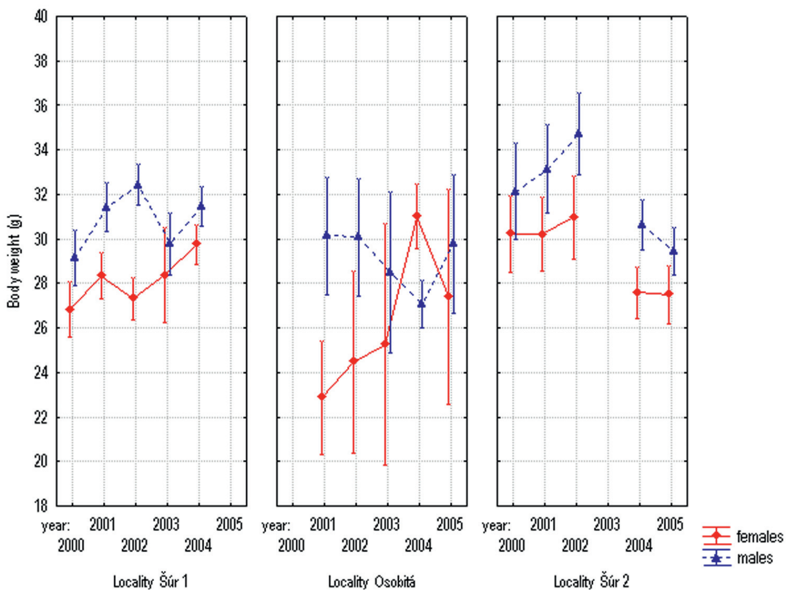


Fig. 1. Body weight in the sampled males and females of *Apodemus flavicollis*.
Obr. 1. Hmotnosť examinovaných samcov a samíc *Apodemus flavicollis*.

during the years 2001–2003 at the mountain locality, especially for body mass (Tables 2, 3). However, during 2004 the SDI for both body weight and length fell considerably below 1, indicating a pronounced female-biased SSD.

## DISCUSSION

The results of our study showing male-biased SSD as a predominant pattern for *A. flavicollis* are in agreement with other studies reporting male-biased SSD for most *Apodemus* species (Montgomery 1989, Ueda & Takatsuki 2005). *A. flavicollis* is considered to be primarily polygynous (de Mendonça 2003, Bryja et al. 2008) and according to the sexual selection hypothesis, male-biased SSD can be expected for this species.

Although the sexual selection hypothesis is the one most widely accepted as an explanation for male-biased SSD, recent studies have shown that sexual dimorphism in mammals can be associated with a number of other factors, e.g. population density (LeBlanc et al. 2001, Isaac & Johnson 2003), latitude and climatic variables (Levenson 1990).

The values of SDI detected in our study suggest a predominantly moderate degree of SSD, especially at lowland localities.

Usually higher average weights of both sexes at the lowland localities in comparison with the mountain locality are most probably connected with habitat productivity.

However, the above mentioned pattern of SSD was interrupted during the year 2004 at the mountain locality Osobita, where we detected a reversed SSD which was maintained throughout

Table 2. Body weight of males and females *Apodemus flavicollis*, sexual dimorphism index (SDI) and the significance of male-female differences (M-F)
Tab. 2. Hmotnosť jedincov *Apodemus flavicollis*, index pohlavného dimorfizmu (SDI) a preukaznosť rozdielov medzi pohlaviami

| | | females | | | males | | | | |
|---|---|---|---|---|---|---|---|---|---|
| locality | year | mean | SE | n | mean | SE | n | SDI | M-F, p |
| Šúr 1 | 2000 | 26.83 | 0.630 | 77 | 29.14 | 0.626 | 78 | 1.086 | p < 0.010 |
| Šúr 1 | 2001 | 28.34 | 0.537 | 106 | 31.43 | 0.570 | 94 | 1.109 | p < 0.001 |
| Šúr 1 | 2002 | 27.45 | 0.485 | 130 | 32.52 | 0.459 | 145 | 1.185 | p < 0.001 |
| Šúr 1 | 2003 | 28.37 | 1.084 | 26 | 29.85 | 0.707 | 61 | 1.052 | NS |
| Šúr 1 | 2004 | 29.75 | 0.454 | 148 | 31.51 | 0.459 | 145 | 1.059 | p < 0.010 |
| Šúr 2 | 2000 | 30.24 | 0.830 | 40 | 32.12 | 1.050 | 25 | 1.062 | NS |
| Šúr 2 | 2001 | 30.20 | 0.801 | 43 | 32.97 | 0.943 | 31 | 1.092 | p < 0.050 |
| Šúr 2 | 2002 | 31.05 | 0.901 | 34 | 34.72 | 0.888 | 35 | 1.118 | p < 0.010 |
| Šúr 2 | 2004 | 27.82 | 0.554 | 90 | 30.74 | 0.528 | 99 | 1.105 | p < 0.001 |
| Šúr 2 | 2005 | 27.46 | 0.619 | 72 | 29.59 | 0.510 | 106 | 1.077 | p < 0.050 |
| Osobitá | 2001 | 22.87 | 1.454 | 18 | 30.14 | 1.496 | 17 | 1.318 | p < 0.001 |
| Osobitá | 2002 | 24.79 | 2.180 | 8 | 30.26 | 1.454 | 18 | 1.221 | p < 0.05 |
| Osobitá | 2003 | 25.25 | 3.084 | 4 | 28.48 | 2.056 | 9 | 1.128 | NS |
| Osobitá | 2004 | 30.82 | 0.810 | 58 | 26.89 | 0.583 | 112 | 0.873 | p < 0.001 |
| Osobitá | 2005 | 27.41 | 2.758 | 5 | 29.78 | 1.780 | 12 | 1.086 | NS |

Table 3. Body length of males and females *Apodemus flavicollis*, sexual dimorphism index (SDI) and the significance of male-female differences (M-F)
Tab. 3. Dĺžka jedincov *Apodemus flavicollis*, index pohlavného dimorfizmu (SDI) a preukaznosť rozdielov medzi pohlaviami

| | | females | | | males | | | | |
|---|---|---|---|---|---|---|---|---|---|
| locality | year | mean | SE | n | mean | SE | n | SDI | M-F, p |
| Šúr 1 | 2000 | 98.96 | 0.782 | 78 | 102.58 | 0.782 | 78 | 1.037 | p < 0.001 |
| Šúr 1 | 2001 | 100.03 | 0.671 | 106 | 103.48 | 0.713 | 94 | 1.034 | p < 0.001 |
| Šúr 1 | 2002 | 100.02 | 0.611 | 128 | 106.91 | 0.576 | 144 | 1.069 | p < 0.001 |
| Šúr 1 | 2003 | 100.12 | 1.355 | 26 | 103.54 | 0.892 | 60 | 1.034 | p < 0.050 |
| Šúr 1 | 2004 | 107.59 | 0.566 | 149 | 110.91 | 0.580 | 142 | 1.031 | p < 0.001 |
| Šúr 2 | 2000 | 105.11 | 0.926 | 40 | 107.54 | 1.172 | 25 | 1.023 | NS |
| Šúr 2 | 2001 | 103.15 | 0.904 | 42 | 106.20 | 1.070 | 30 | 1.030 | NS |
| Šúr 2 | 2002 | 100.67 | 1.020 | 33 | 103.29 | 0.990 | 35 | 1.026 | NS |
| Šúr 2 | 2004 | 101.96 | 0.632 | 86 | 106.76 | 0.595 | 97 | 1.047 | p < 0.001 |
| Šúr 2 | 2005 | 103.41 | 0.700 | 70 | 106.49 | 0.566 | 107 | 1.030 | p < 0.010 |
| Osobitá | 2001 | 99.29 | 1.740 | 18 | 108.17 | 1.790 | 17 | 1.089 | p < 0.001 |
| Osobitá | 2002 | 99.62 | 2.790 | 7 | 103.50 | 1.790 | 17 | 1.039 | NS |
| Osobitá | 2003 | 103.80 | 2.460 | 9 | 105.97 | 2.225 | 11 | 1.021 | NS |
| Osobitá | 2004 | 107.35 | 0.986 | 56 | 103.35 | 0.717 | 106 | 0.963 | p < 0.001 |
| Osobitá | 2005 | 105.57 | 3.301 | 5 | 106.25 | 2.131 | 12 | 1.006 | NS |

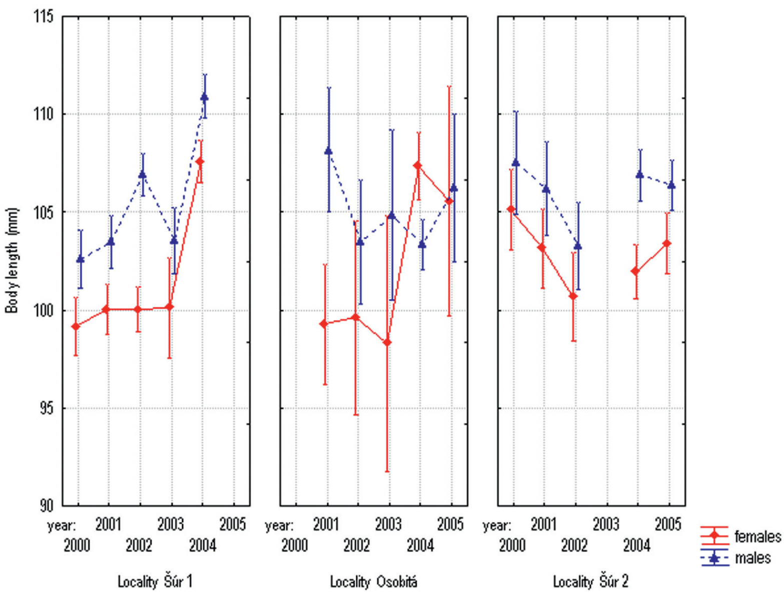


Fig. 2. Body length in the sampled males and females of *Apodemus flavicollis*.
Obr. 2. Dĺžka tela examinovaných samcov a samíc *Apodemus flavicollis*.

the year. During this year males were smaller and females larger than during the other years of study at this locality, with female weights reaching values typical for the lowland populations.

During the year 2004 a population outbreak in the population of *A. flavicollis* was recorded at the locality Osobita, following a heavy seed crop of the previous year (Michalec ad verb.). In this year an exceptionally high number (proportion) of adult females was also recorded. We suppose that during this year of exceptionally good food conditions and demographic characteristics of the local population, the reversed SSD could have been a result of two different, mutually acting selection pressures: selection favouring larger females and selection favouring smaller males.

Males and females have different reproductive strategies in response to changing environmental conditions. Males can maximize their reproductive success by seeking, defending, and mating with many females, whereas females typically invest a larger amount of energy in reproduction (e.g. Schulte-Hostedde et al. 2001). Hence, the magnitude of adult SSD can be susceptible to divergence of the sexes in response to environmental and demographic factors differentially influencing their growth.

Larger females are able to invest more energy into their offspring, either by producing larger litters or by having litter more times a year (Schulte-Hostedde & Millar 2000, Reiss 1987, Ribble 1992, Jančová & Baláž 2007). Fitness of the offspring is positively related to the body mass of females (Jacquot & Vessey 1998), so under favourable conditions it can be advantageous for females to invest primarily into their somatic growth and then to the offspring, thus ensuring better fitness and higher probability of the offspring survival. Low mortality of adult females enables them to postpone their investment to the reproduction (Jacquot & Vessey 1998). Exceptionally good food conditions at the locality Osobita before and during winter could have enabled females to invest primarily into their somatic growth and then to reproduction. The fact that the average weight of females at the locality Osobita in 2004 was similar to the

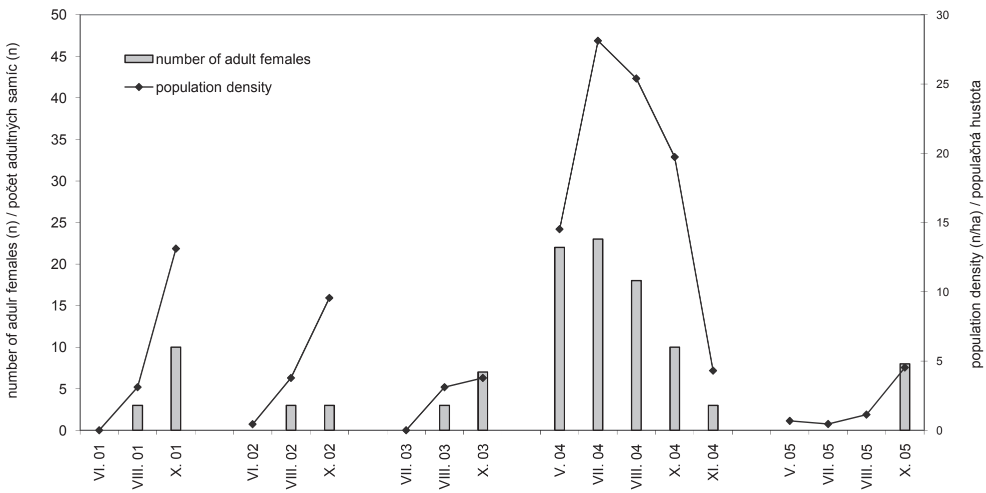


Fig. 3. Population density and number of adult females of *Apodemus flavicollis* in the locality Osobitá.
Obr. 3. Populačná hustota a počet adultných samíc *Apodemus flavicollis* na lokalite Osobitá.

average weight of females at the lowland localities, while during the other years of study it was considerably lower, also supports this assumption.

On the other hand, having a smaller size can be beneficial for males under certain circumstances (Levenson 1990, Ralls 1976). Small males may be favoured when food is limited, which is likely to happen during a population density outbreak, because they require lower absolute amounts of food. Thus, given a trade-off between foraging and mate acquisition, small males may be able to devote more time to the latter (Blackenhorn et al. 1995). The decrease in male size can be also associated with reduced male-male competition for access to breeding females (Sachser et al. 1999). Shifts in reproductive strategy from polygyny to promiscuity, connected with population density have been previously reported for *A. flavicollis*. Gryczyňska-Siemiątkowska et al. (2008) consider promiscuous mating system as an alternative breeding strategy for this species. These authors believe that seasonal variability in the living conditions, density of the population and the availability of various resources is the most likely explanation for the shifts in a breeding strategy. According to Weckerly (1998) if the large dominant males are unable to control access to large numbers of females, there will be less benefit to allocating energy into additional growth. We can therefore suppose that exceptionally high population density together with a high number of adult females led to decreased male-male competition and a shift in reproductive strategy towards promiscuity, which subsequently resulted in smaller-sized males.

Our study provides evidence that both body weight and length in *A. flavicollis* show plasticity in terms of adapting to short-term changes in environmental and demographic conditions which can consequently influence patterns of sexual size dimorphism.

## SÚHRN

V práci je analyzovaný veľkostný pohlavný dimorfizmus ryšavky žltohrdlej v troch dlhodobo sledovaných populáciách na Slovensku. Terénny výskum prebiehal počas rokov 2000 až 2005 na dvoch lokalitách: nížinnej (NPR Šur pri Bratislave), ktorá bola na základe predchádzajúcich štúdií považovaná za optimálne prostredie pre sledovaný druh a horskej (NPR Osobitá, Západné Tatry), blízko hypsometrickej hranici rozšírenia druhu. Vo všeobecnosti je možné povedať že pre *A. flavicollis* je charakteristický veľkostný pohlavný dimorfizmus v prospech samcov, čo je v súlade s očakávaním pre polygýnny druh. Počas obdobia výskumu sme však zaznamenali prípad prevráteného veľkostného pohlavného dimorfizmu na jednej lokalite v priebehu jedného roka. Uvedená situácia bola zaznamenaná na horskej lokalite v roku netypickej vysokej populačnej denzity nasledujúcej po bohatej úrode semien. Keďže v tomto roku boli súčasne zaznamenané väčšie veľkosti samíc a menšie veľkosti samcov v porovnaní s ostatnými rokmi výskumu na lokalite, predpokladáme, že pozorovaná situácia bola dôsledkom súčasného pôsobenia selekcie v prospech väčších samíc a menších samcov.

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## REFERENCES

Badyaev A. V., 1997: Altitudinal variation in sexual dimorphism: a new pattern and alternative hypotheses. *Behavioral Ecology*, **8**: 675–690.

Blackenhorn W. U., Prezoisi R. F. & Farbain D. J., 1995: Time and energy constraints and the evolution of sexual size dimorphism – to eat or to mate: *Evolutionary Ecology*, **9**: 369–381.

Bryja J., Patzenhauerová H., Albrecht T., Mošanský L., Stanko M. & Stopka P., 2008: Varying levels of female promiscuity in four *Apodemus* mice species. *Behavioral Ecology and Sociobiology*, **63**: 251–260.

de Mendonça P. G., 2003: *Aspects of the social ecology of the yellow-necked mouse Apodemus flavicollis*. Unpubl. PhD. Thesis. University of Cambridge, Cambridge, 134 pp.

Gryczyñska-Siemiątkowska A., Gortat T., Kozakiewicz A., Rutkowski R., Pomorski J. & Kozakiewicz M., 2008: Multiple paternity in a wild population of the yellow-necked mouse *Apodemus flavicollis*. *Acta Theriologica*, **53**: 251–258.

Heske E. J. & Ostfeld R. S., 1990: Sexual dimorphism in size, relative size of testes, and mating systems in North American voles. *Journal of Mammalogy*, **71**: 510–519.

Hood C. S., 2000: Geometric morphometric approaches to the study of sexual size dimorphism in mammals. *Hystrix*, *n. s*., **11**: 77–90.

Isaac J. L., 2005: Potential causes and life-history consequences of sexual size dimorphism in mammals. *Mammal Review*, **35**: 101–115.

Isaac J. L. & Johnson C. N., 2003: Sexual dimorphism and synchrony of breeding: variation in polygyny potential among populations in the common brushtail possum, *Trichosurus vulpecula*. *Behavioral Ecology*, **14**: 818–822.

Jacquot J. J. & Vessey S., 1998: Recruitment in white-footed mice (*Peromyscus leucpus*) as a function of litter size, parity, and season. *Journal of Mammalogy*, **79**: 312–319.

Jančová A. & Baláž I., 2007: Reproductive potential of *Apodemus flavicollis* in hillock landscape level (Hronská, Nitrianska, Žitavská pahorkatina). Pp.: 53–59. In: Baláž I., Cápay M., Jakab I. & Palmárová V. (eds.): *8. Scientific conference of PhD Students and Young Scientists*. Constantine the Philosopher University, Nitra, 916 pp (in Slovak, with a summary in English).

LeBlanc M., Festa-Bianchet M. & Jorgenson J. T., 2001: Sexual size dimorphism in bighorn sheep (*Ovis canadensis*): effects of population density. *Canadian Journal of Zoology*, **79**: 1661–1670.

Levenson H. 1990: Sexual size dimorphism in chipmunks. *Journal of Mammalogy,* **71**: 161–170.

Montgomery W. I., 1980: Population structure and dynamics of sympatric *Apodemus species* (Rodentia: Muridae). *Journal of Zoology*, *London*, **192**: 351–377.

Montgomery W. I., 1989: *Peromyscus* and *Apodemus*: patterns of similarity in ecological equivalents. Pp.: 293–366. In: Kirkland G. L. Jr. & Layne J. N. (eds.): *Advances in the Study of Peromyscus* (*Rodentia*). Texas Tech University Press, Texas, 236 pp.

Post E., Langvatn R., Forchhammer M. C. & Stenseth N. Ch., 1999: Environmental variation shapes sexual dimorphism in red deer. *Ecology*, **96**: 4467– 4471.

Ralls K., 1976: Mammals in which females are larger than males. *Quarterly Review of Biology*, **51**: 245–276.

Reiss M. I., 1987: The intraspecific relationship of parental investment to female body weight. *Functional Ecology*, **1**: 105–107.

Ribble D. O., 1992: Lifetime reproductive success and its correlates in the monogamous rodent, *Peromyscus californicus*. *Journal of Animal Ecology*, **61**: 457–468.

Sachser N., Schwarz-Weig E., Keil A. & Epplen J. T., 1999: Behavioural strategies, testis size, and reproductive success in two caviomorph rodents with different mating systems. *Behaviour*, **136**: 1203–1217.

Schulte-Hostedde A. I., Millar J. S. & Hickling G. J., 2001: Sexual dimorphism in body composition of small mammals. *Canadian Journal of Zoology*, **79**: 1016–1020.

Schulte-Hostedde A.I. & Millar J. S., 2000: Measuring sexual size dimorphism in the yellow-pine chipmunk (*Tamias amoenus*). *Canadian Journal of Zoology*, **78**: 728–733.

StatSoft, 2004: *STATISTICA® (data analysis software system)*. *Version 7*. StatSoft Inc., Tulsa.

Ueda H. & Takatsuki S., 2005: Sexual dimorphism of *Apodemus speciosus* in wild populations. *Mammal Study*, **30**: 65–68.

Weckerly F. W., 1998: Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy*, **77**: 33–42.