Are there sex differences in the body size of the Eurasian red squirrel in Slovakia?

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ABSTRACT

Sexual dimorphism of the Eurasian red squirrel on five somatic variables (head-and-body length, tail length, hind foot length, ear length and body weight) was evaluated on 55 squirrels. The overlap of values of the measured traits among sexes was high, but in all traits (with exception of the tail length) males seem to exhibit slightly higher mean values than females. However, these differences were non-significant, with the exception of a small significant difference in the tail length and tail-to-head-and-body ratio. Similarly, the results of discriminant function analysis show no differences between the sexes. Positive correlation analyses, together with PCA values, confirmed that tail length and hind foot length are traits that play a significant role in overall variability. We suggest that this relationship could explain their mutual importance in locomotion, where the feet are essential for movement in the trees. By contrast, the tail maintains balance on thin branches, or during jumps from one crown to another. Longer tails also demonstrate differential selection on males and females for a locomotor trait. Similarly, we discuss whether variations in tail length were connected to female reproductive success. Our results suggest that the non-significant results regarding SSD provide the benefit of the same size for both sexes in the protection of territory as well as inter- and intra-sexual interaction.

INTRODUCTION

In Eurasian red squirrels, both males and females are the same in both size and colouration and this species is treated as mono-morphic (Thorington et al. 2012). Nevertheless, for several species of squirrels significant differences in the tail length between sexes were confirmed (Hayssen 2008). Several authors (Schulte-Hostedde et al. 2002; Schulte-Hostedde 2007; Koprowski 2007; Lindenfors et al. 2007; Nandini 2011; McPehrson & Chenoweth 2012; Matějů & Kratochvíl 2013; Mori & Lovari 2014) showed that differences in body size between the sexes is a widespread phenomenon in animals, and this is called sexual size dimorphism (SSD). According to cited authors, the evolution of SSD is usually ascribed to different selection pressures (natural or sexual selection) operating on both sexes. Male size is largely explained by male–male competition for resources and mates, both for large males in male-biased SSD species and small males in female-biased SSD species, while large female size in female-biased SSD species is explained by hypoth-

eses pertaining to fecundity selection, functional morphology and behavioural advantages (Nandini 2011). Nandini (2011) confirmed that some genera of tree and ground squirrels and all flying squirrels exhibited female-biased SSD. By contrast, Matějů and Kratochvíl (2013) showed that several marmot and ground squirrel genera displaced male-biased SSD. Hayssen (2008) divided the sciurids into three groups according to size components, especially in tail length as ground, tree or flying squirrels. She showed that with respect to body mass, flying squirrels are lighter for their size than other squirrels, reflecting the influence of gliding locomotion. Mainly, the tail length has a clear relationship with the ecological profile in squirrels. Tails are shorter in ground squirrels, longer in tree squirrels and longest in flying squirrels. In addition, in arboreal squirrels, females have longer tails relative to body length than males. Hayssen and Kunz (1996) reported that reproduction could also influence body size in bats, because the additional mass that a female may carry during gestation and when transporting

young has clear aerodynamic and energetic consequences for females but not for males. Therefore, Hayssen (2008) tested this hypothesis by sex differences in tail length relative to body length and made comparisons across ground, tree and flying squirrels. She assumed that if tails have a function in locomotion (as rudders or for balance), females and males should differ in tail length. Moreover, the tail is important in the three-dimensional locomotion of tree and flying squirrels and contributes to maneuverability while helping to stabilise yaw, pitch and roll. A longer tail increases drag but improves gliding performance and balance. Thus, tails will enhance predator escape in arboreal squirrels, and the longer tails of females will enable better maneuverability when carrying young either in utero or during lactation. Gestation has an influence on gliding and climbing in females. Thus, females have greater need for increased maneuverability, better balance and, hence, longer tails. The longer tails of female tree and flying squirrels may assist with steering and stabilisation.

It should also be noted that tail length may also differ due to sexual selection or allometry. Allometry describes the relationship of the components of an organism with a change in the overall body size (Hayssen & Kunz 1996). Moreover, it has been reported that sexually selected traits often show positive allometry and exhibit high degrees of phenotypic variation as a result of directional sexual selection (Green 1992; Petrie 1992; Bonduriansky & Day 2003; Bonduriansky 2007). The above-mentioned authors showed that sexual selection is generally thought to favour the evolution of positive-trait allometries and, conversely, positive allometries have been interpreted as being evidence of sexual selection. Green (1992) and Petrie (1992) suggested that positive allometry may evolve when a larger trait size confers a direct advantage in sexual competition, resulting in stronger directional selection on trait size than on body size, or when the relative costs of trait expression are lower for larger individuals.

In this study, we provide complete morphological analyses of squirrels from Slovakia. Accordingly, the main aims of our research were (i) to contribute to the knowledge of quantitative characteristics of somatic measures and describe their variability; (ii) to identify factors influencing size variations in Slovakian squirrels; (iii) to test the sexual dimorphism and (iv) to assess the influence of allometry on sex differences.

1. METHODS AND MATERIALS

The squirrels analysed in this study came from several localities in Eastern Slovakia and were taken from the collections of the Department of Natural History of the Saris Museum Bardejov (SMB) and the East Slovakian Museum Kosice (ESM) (Čanády et al. 2015).

The material was collected at the following sites: Saris Museum Bardejov (37): Bardejov (20), Šiba (4), Kurov (3), Jedlovec (1), Nižná Voľa (1), Cígeľka (1), Plavnica (1), Hertník (1), Prešov (1), Kružlov (1), Slovenska Kajna (1), Lenartov (1), Ostrovany (1); East Slovakian Museum in Kosice (18): Košice

(9), Muráň (2), Jasov (1), Malá Ida (1), Ruskov (1), Nižná Myšľa (1), Moldava nad Bodvou (1), Štós (1), Tatranská Javorina (1)

Shortly after being hunted, the individuals were measured and prepared. The skulls and skins were removed from the body and after preparation were kept in museum boxes. The important feature of these datasets is that all specimens were collected and measured by the same method and by same persons, i.e. by T. Weisz (main collector from SMB) and A. Mošanský (main collector from ESM). Moreover, the data associated with most specimens include information on basic somatic measurements, locality, date, colouration and age estimated from gonads.

In all evaluated individuals (30 males, 25 females), five somatic parameters were measured on fresh material shortly after their collection by means of a metallic pushing-measure (ruler) Vernier caliper with accuracy of 0.02 mm: HBL – the head-and-body length, TL – the tail lenth, HFL – the hind foot length, EL – ear length. The weight (W) was measured in 0.01 grams (g).

The obtained data-set (untransformed data) was evaluated using the following statistical parameters: medians and quartiles (1st Q–3rd Q), instead of means and standard deviation (SD) have been used, as no measurement was normally distributed. The D'Agostino-Pearson omnibus K^2 test and the Shapiro-Wilk W-test were used to determine whether the values come from Gaussian distribution. Before other analysis, measurements were $\log_{10}$ transformed to reduce intra-sample variation and to improve normality. The body measurements were tested by the non-parametric Mann–Whitney test, which does not require normality of data.

Morphometric variation was examined using principal component analysis (PCA) and the differentiation was estimated using discriminant function analysis (DFA). Discriminant analyses (DFA) were used to determine whether a set of variables is able to differentiate the sexes. DFA were performed using Wilk's lambda statistics, entering all the variables at once, not stepwise, with equal prior probabilities for the groups and covariance within the groups. Mahalanobis generalised distances (D^2) was calculated from DFA.

Hotelling T^2 and Mann-Whitney tests were performed to test the sexual size dimorphism. Using to Hayssen (2008) the proportion of tail length relative to head-and-body length was calculated as the average tail length (TL) divided by the average head-and-body length (HBL). This was done separately for females and males. To assess how much larger the tails of females were relative to body length compared with those of males, the proportionality index for females was divided by that for males (female (TL/HBL)/male (TL/HBL)). If males and females do not differ, then this index will be 1; thus, a one-sample t-test will test the hypothesis.

Allometric slopes were determined for the measured traits of the squirrel population for both sexes separately. We investigated allometric (log-log) relationships in two steps. First, ordinary least squares regression (OLS) was used to determine whether the slopes differed from zero. If the slopes were

significant, we then proceeded by using reduced major axis regression (RMA) to test for deviations from isometry. RMA regression is generally preferable to simple linear regression in allometric studies, because there is no distinction between explanatory and response variables and because all variables are measured with an error. Moreover, both types of regression are identical when $r = 1$, because in reduced major axis regression, the slope = b/r, where b is the slope in simple linear regression. For comparison, we also report the OLS regression slope estimates.

All analyses were performed using MS Excel 2003 for Windows XP and the statistical analysis system GraphPad Prism version 5.01 (GraphPad Software, Inc., San Diego, California, USA). Principal component analysis and Fisher's linear discriminant functions were done using the Statistical Software OriginPro8.6. (Microcal Software Inc., Northamptom, USA). The discriminant function analyses, ordinary least square (OLS) regression and reduced axis major (RMA) regressions were evaluated using the program PAST, version 2.17b (Hammer et al. 2001).

2. RESULTS

The descriptive statistics of the studied variables for adult squirrels of both sexes from Slovakia are reported in Table 1. The most variable measures for males and females both were body weight (W) and head-and-body length (HBL). The overlap of values of the measured traits in the sexes was high, but in all traits (with exception of the tail length), males seems to

exhibit slightly higher mean values. In contrast, females have slightly longer tails relative to body length (80% versus 77%; one-sample t-test of female tail-to-head-and-body ratio over male tail-to-head-and-body ratio = 1.05, n = 25, t = 3.03, df = 24, p = 0.006).

The results of principal component analysis (PCA), as an exploratory technique for discovering structure in data, are given in Table 2 and Figure 1. The PCA values showed that the first two principal components (PC1–PC2) explain 56.2% of the variation. The first principal component (PC1) explained 30.4% of the total variance and was associated mainly with hind foot length and tail length. A second factor (PC2) accounted for 25.8% and was correlated with body weight (0.60). Finally, a third principal component (PC3) accounted for only 21.3% of overall variation and was highly associated with the ear length.

Discriminant function analysis ($\lambda_{\text{Wilks' lambda}}$ = 0.87, $F_{5, 48}$ = 1.45, p = 0.22) and Hotelling T^2-test (T^2 = 7.88, F = 1.45, p = 0.22, Fig. 2) showed that there was no significant sexual size dimorphism in the museum specimens of Eurasian red squirrels collected in Slovakia. The Mahalanobis distance was relatively smaller between the sexes (D = 0.59, p = 0.07).

Summary results for our OLS and RMA analyses for both sexes, respectively, are shown in Table 3. Results for females confirmed the existence of a positive, linear and relatively weak relationship between body weight and head-and-body length in *S. vulgaris* (F = 9.226, N = 24, p<0.01, R^2 = 0.296). Similarly, results of RMA regression (RMA slope = 3.803) showed positive allometry among these traits (Fig. 3a). On the other hand, tail length, in relation to head-and-body length, showed

Table 1. Basic statistics for measurements of adult males and females of Eurasian red squirrel (Sciurus vulgaris). Statistics given are (median and quartiles, mean ± SD). Q= quartile. Abbreviations: body weight (W), head-and-body length (HBL), tail length (TL), hind foot length (HFL) and ear length (EL). Gender with higher mean values is shown with the significant levels: * p<0.05.

|	Sample size		Median	1st Q	3rd Q	Median	1st Q	3rd Q	Mean ± SD		Mann–Whitney U-test	
	Male	Female	Male			Female			Male	Female	U	p
W [g]	30	25	327.00	310.10	340.00	333.00	301.50	350.00	325.00±32.75	198.00–420.50	359.50	1.00
HBL [mm]	30	25	228.25	220.00	234.00	223.00	220.00	231.00	232.90±31.15	197.00–242.00	301.00	0.31
TL [mm]	29	25	172.00	171.00	178.00	180.00	173.00	185.00	173.70±10.08	164.00–195.00	215.00	0.02*
HFL [mm]	29	25	60.30	58.00	61.50	60.10	58.40	61.00	59.88±2.34	54.60–64.00	335.50	0.83
EL [mm]	29	25	32.40	31.00	33.60	31.75	30.70	33.30	32.27±2.13	28.00–35.20	337.00	0.85
TL/HBL [%]	28	25	76.46	72.71	79.86	79.34	76.82	81.53	76.50±4.90	74.00–88.00	185.00	0.01*
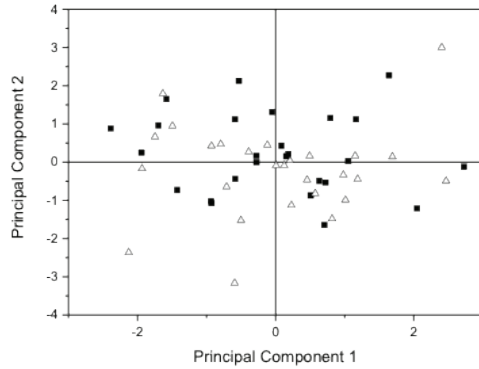
Figure 1. Bivariate plot of individual scores on PC1 and PC2 for adult individuals of Sciurus vulgaris (males – solid squares, females – open triangles).

Table 2. Loading values of principal component analysis (PCA) for the three main components (PC1–PC3) in adult Sciurus vulgaris; their eigenvalues, percentage (variability %) and cumulative percentage (cumulative %) expressions. Abbreviations: body weight (W), head-and-body length (HBL), tail length (TL), hind foot length (HFL) and ear height (EL).

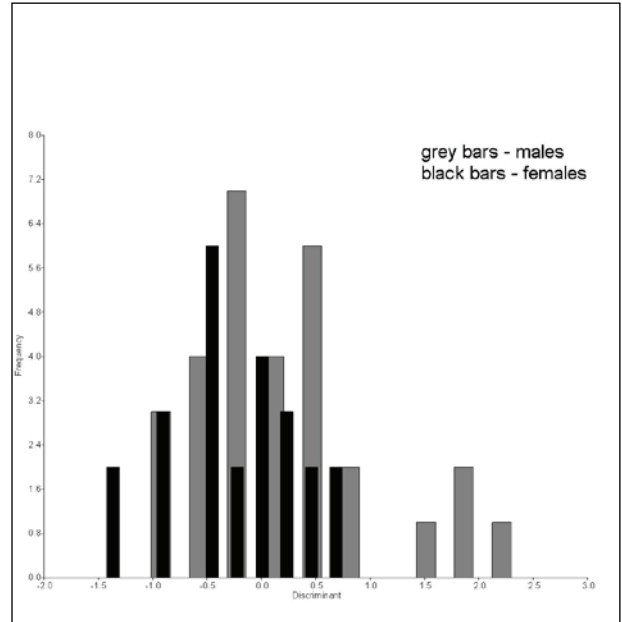|	PC1	PC2	PC3
W	0.40	0.60	-0.04
LC	0.33	0.39	-0.65
LCd	0.52	-0.48	-0.12
LTp	0.60	-0.38	0.10
LA	0.31	0.34	0.75
Eigenvalue	1.52	1.29	1.07
Percentage (%)	30.4	25.8	21.3
Cumulative (%)	30.4	56.2	77.5

Figure 2. Frequency histogram of the canonical scores for the standard DFA between sexes of Sciurus vulgaris fuscoater (males – grey bars, females – black bars)

contrasting results, depending on the regression model used. OLS regression indicated negative allometry (OLS slope = 0.420), but this was isometric based on RMA regression (RMA slope = 1.021, Table 3, Fig. 3b). Similar results were obtained for the relationship between tail length and hind foot length (Table 3, Fig. 3c).

In contrast, results for males exhibited negative allometry based on OLS regression, and the slopes differed from zero only between tail length and hind foot length (F = 5.447, N = 29, p<0.05, R^2 = 0.168). Moreover, the results had contrasting

values, depending on the regression model used. OLS regression indicated negative allometry (OLS slope = 0.595), while RMA regression (RMA slope = 1.453) exhibited positive allometry (Table 3, Fig. 3d).

3. DISCUSSION

Several authors (Degn 1973; Wiltafsky 1978; Bauer 2001; Wauters et al. 2004) have shown that Eurasian red squirrels from various parts of their range have different values in somatic traits. Moreover, the numerical values of most of these measurements overlap between age classes, sexes and different subspecies and populations as well. The aim of our study was to test the impact of sexual dimorphism on the body traits of squirrels from Slovakia. Both the univariate and multivariate evaluations proved that there were no differences in body variables between the sexes, with the exception of small difference in the tail length, but even this difference was not very pronounced. Our data support previous findings stated by Nandini (2011) that solitary species tend to show less sexual size dimorphism. Comparing our data with literature data from Austria and northern Italy (Wiltafsky 1978; Bauer 2001; Wauters et al. 2004, 2007) showed that the mean values in all commonly compared variables, despite small differences, were very similar and that all exist within the limits of variability for the subspecies fuscoater.

In light of these findings and their clarification, we discussed how the lack of a sexual size dimorphism (SSD) is related to the squirrel biology and ecology. Eurasian red squirrels belong to the tree squirrels which mainly use arboreal environments (Lurz et al. 2005; Nandini 2011). Our results are in
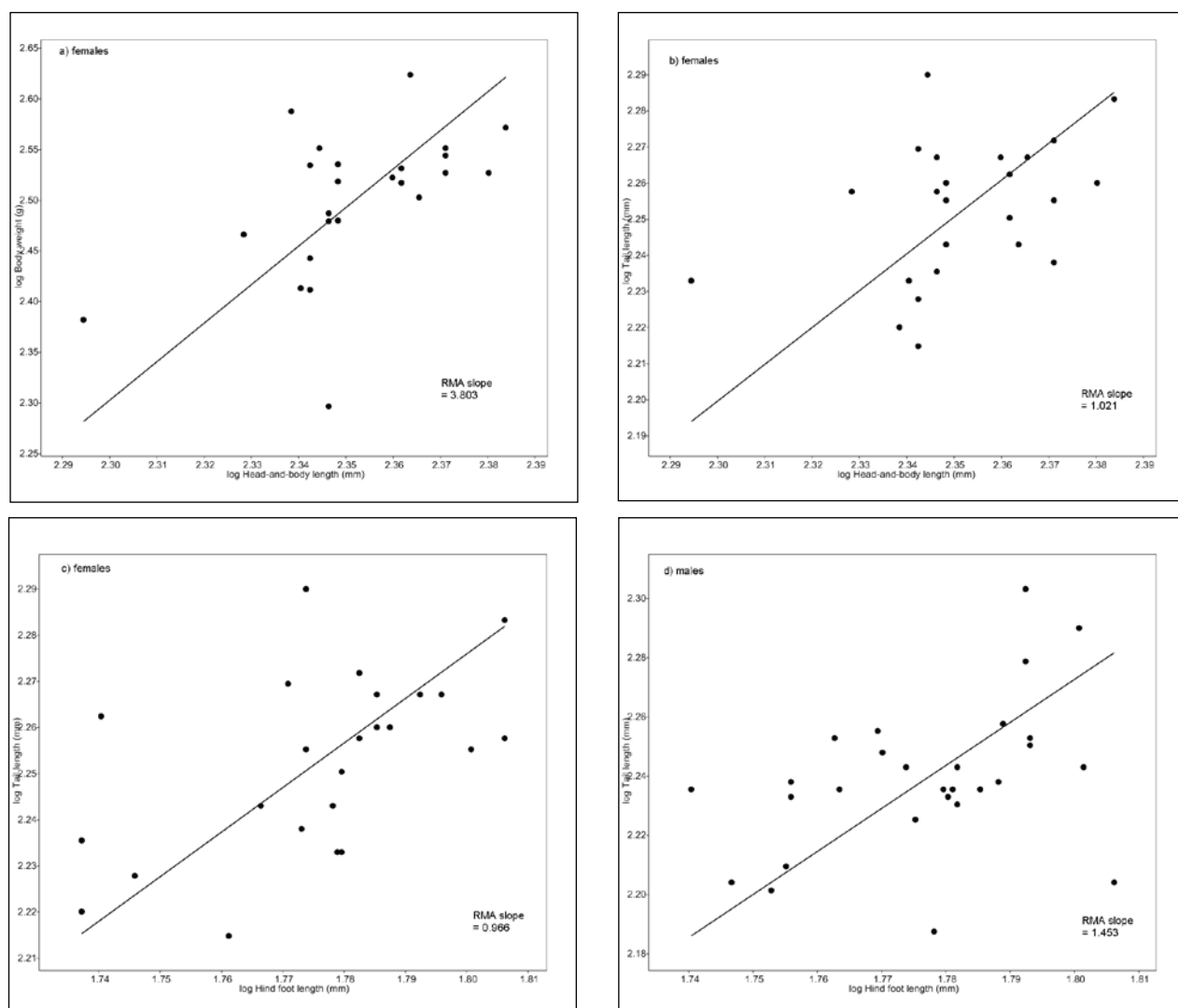
Figure 3. Relationship between: (a) body weight vs the head-and-body length; (b) tail length vs the head-and-body length, (c) tail length vs hind foot length for mature females. Relationship between (d) tail length in relation to hind foot length for mature males of Eurasian red squirrels (Sciurus vulgaris) from Slovakia. All variables are log10 transformed. The lines represent the slopes calculated from a reduced major axis regression (RMA).

agreement with previous findings obtained by Hayssen (2008) that females, in fact, have longer tails than males. These findings are very interesting in relation to locomotion and reproduction. According to Hayssen (2008), large female size in the tail length and body mass might have evolved to confer advantages of functional significance, since climbing and leaping might impose constraints on females while they are pregnant. At the same time, this hypothesis was also supported by our data on the positive allometry found in body weight in relation to head-and-body length. The results support the fact that body weight can play a significant role in the reproductive success of females. Nevertheless, it should be noted that our weight data were obtained from the protocol cards attached to the museum collections. Data on the pregnancy of females were not listed, but data on the swollen nipples, which suggests lactation, were noted. This could have also influenced the fact that females had higher values of body mass. This is in line with data obtained by

Wauters et al. (2007) that lactating females were heavier than oestrus females, and both were heavier than those that did not reproduce.

Schulte-Hostedde et al. (2001) showed that in many vertebrates a relatively high body mass in relation to body size is an indication of good health: such individuals are more likely to survive critical periods of food shortage or extreme weather conditions. Wauters and Dhondt (1989a, b) showed for squirrels from Belgium that the sexes did not differ in some body size measurements (body mass, head-and-body length) and had similar body mass in late autumn and winter, when females did not invest extra energy in lactation. In contrast, when females were pregnant or in early lactation they weighed more than males. Moreover, according to (Wauters & Dhondt 1989a, b; 1995), heavier animals are often more likely to reproduce successfully, particularly in female mammals, and tend to be better competitors (social dominance) than conspecifics of

Table 3. Results of the OLS and RMA regression slopes, intercepts and 95% confidence intervals (CI), F and p-values for relationships between traits are shown. Legend: number (N); coefficient of determination (R²), body weight (P), head-and-body length (HBL), tail length (TL), hind foot length (HFL). Significant relationships are shown with the significant levels: NS – statistically non-significant (p>0.05), * p<0.05, ** p<0.01.

	Log Y versus log X variable	N	R^2	OLS slope (95% CI)	Intercept (95% CI)	F	p-values	RMA slope (95% CI)	Intercept (95% CI)	Allometry
males	W vs HBL	30	0.051	0.219 (-0.148, 0.586)	1.992 (1.125, 2.860)	1.493	0.232[NS]	-	-	-
	TL vs HBL	29	0.001	-0.012 (-0.221, 0.196)	2.268 (1.775, 2.762)	0.015	0.904[NS]	-	-	-
	HFL vs HBL	29	0.006	0.029 (-0.115, 0.172)	1.709 (1.370, 2.048)	0.170	0.684[NS]	-	-	-
	W vs TL	29	0.007	0.146 (-0.535, 0.827)	2.185 (0.660, 3.711)	0.194	0.664[NS]	-	-	-
	W vs HFL	29	0.346	0.468 (-0.508, 1.444)	1.681 (-0.053, 3.415)	0.968	0.334[NS]	-	-	-
	TL vs HFL	29	0.168	0.595 (0.072, 1.119)	1.182 (0.252, 2.111)	5.447	0.025[*]	1.453 (0.876, 2.015)	-0.342 (-1.335, 0.685)	positive
females	W vs HBL	24	0.296	2.067 (0.656, 3.478)	-2.361 (-5.681, 0.958)	9.226	0.006[**]	3.803 (0.862, 5.147)	-6.444 (-9.614, 0.487)	positive
	TL vs HBL	24	0.169	0.420 (0.009, 0.832)	1.265 (0.297, 2.232)	4.485	0.046[*]	1.021 (0.378, 1.420)	-0.148 (-1.087, 1.368)	isometry
	HFL vs HBL	24	0.053	0.243 (-0.211, 0.698)	1.203 (0.134, 2.273)	1.233	0.279[NS]	-	-	-
	W vs TL	24	0.017	0.485 (-1.148, 2.118)	1.408 (-2.271, 5.087)	0.379	0.545[NS]	-	-	-
	W vs HFL	24	0.019	-0.497 (-2.073, 1.078)	3.383 (0.585, 6.182)	0.429	0.520[NS]	-	-	-
	TL vs HFL	24	0.301	0.530 (0.172, 0.887)	1.312 (0.678, 1.947)	9.455	0.006[**]	0.966 (0.536, 1.303)	0.537 (0.056, 1.303)	isometry

smaller size or lesser body mass. Similarly, Wauters et al. (2007) examined alpine populations of squirrels to explore differences in body size and body mass among neighbouring populations in relation to habitat type and variation in food supply. They also investigated sexual dimorphism in these traits and whether phenotypic variation affects local survival and female reproductive success. Their results confirmed that the mean hind foot length (a measure of body size) did not differ between the sexes but did differ between the studied areas. Seasonal variation in body mass was small, with no evidence of fattening in autumn. Females were slightly heavier than males, but this difference was largely explained by mass gain of females during reproduction. The authors assumed that the differences in size and mass between the populations were partially explained by habitat-related differences in body size and the

variability of seed crops, suggesting differential selection for smaller squirrels in spruce-larch forests against selection for larger and heavier animals in mixed broadleaf and conifer forests and in Scots pine forests with more stable seed production. The probability of reproduction by females increased with body mass but varied strongly between habitats and years, with more females reproducing in years with rich seed-crops. Moreover, their results suggest that in temporally variable environments differing in the overall amount of food resources, individual variation in body mass is related to habitat type, and that having a relatively high body mass positively affects male and female settlement success and local survival, and female reproductive success within each population.

A study of Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) showed that female body mass did

not increase during the winter in advance of spring and summer pregnancy and lactation, nor did body mass decrease significantly after the reproductive season (Koprowski 2005). In contrast, seasonality in male body mass was similar to that reported for other populations of red squirrels, with peak periods in winter. In conclusion, the author showed that annual fluctuations in male body mass suggest a peak during the winter after testicular recrudescence. Males, but not females, may increase fat stores in anticipation of breeding, which involves considerable range expansion and exploitative and interference competition.

Several authors (Fokidis et al. 2007; Fokidis & Risch 2008) made similar findings for gliding mammals. They proved that body mass is usually positively associated with reproductive output in females, with larger females having more offspring. Larger females produce more pups and have access to more food resources.

On the other hand, the ratios between tail length and hind foot length were different for both sexes. Our results on the allometric relationship between tail length and body length showed isometric growth for females. Moreover, results of tail length indices versus head-and-body length confirmed that the females have longer tails than males. These small sex differences in tail length associated with locomotion are demonstrable and were consistent with data obtained by Hayssen (2008). Similarly, positive correlation analyses, together with the PCA values, confirmed that the tail length, together with hind foot length, were traits that play a significant role in total variability. We suggest that this relationship could explain their mutual importance in locomotion. The feet are essential for movement in the trees, while the tail maintains balance on thin branches or during jumps from one crown to another. This is also consistent with the fact that a longer tail is a morphological adaptation of female tree squirrels, which may assist with steering and stabilisation (Hayssen 2008; Scheibe & Robins 1998).

The reproductive strategies and alternative behaviours of tree squirrels are diverse (Wauters et al. 1990; Lurz et al. 2005; Koprowski 2007), with the mating system of Eurasian red squirrels being polygynous–promiscuous. Red squirrels are typically solitary and territorial; therefore, males are able to assess the status of reproductive females from a distance. Moreover, females are in oestrus for only a few hours of a single day during the breeding season. As a result, females are a fitness-limiting resource for males, with an availability that varies in time and space. In male red squirrels, dominance during the mating chase was strongly related to dominant rank and body weight. The leading male in the following group tends to be the heaviest and dominant and accounts for most mating.

Wauters and Dhondt (1989a) proved that social organisation is based on dominance hierarchies among and between the sexes. Moreover, authors showed that males are not necessarily dominant to females. This fact was confirmed by the mutual interaction of both sexes. It should be stressed that in most cases females had a higher rank than the males or in one case, when a dominant female was in the immediate vicinity her litter-drey. Similarly, they confirmed that dominant animals tend to be larger and older than subordinate animals, and dominant males tend to have larger home ranges than subordinate males or females. Nevertheless, much variation in range size is related to habitat quality, season and sexual activity as well as changes in food availability (Lurz et al. 2000, 2005; Wauters & Dhondt 1989a, b; 1992). Several authors (Lurz et al. 2000; Wauters & Dhondt 1992, 1995) showed that both males and females are territorial, but the average home-range area for both sexes varies with location and habitat. In general, males tend to have larger home ranges than females. Moreover, home ranges overlap, particularly in areas of abundant food, but the extent of the overlap can be small, notably in breeding females, which reduce their range when suckling young. Later, Wauters and Dhondt (1995) reported that larger females of *S. vulgaris* had larger home ranges with greater resource availability and were typically more fecund. They found that body size (or body mass) correlated strongly with the number of litters a female produces. This suggests that this is an important phenotypic parameter for red squirrels, and selection should favour large and heavy females. Similarly, it was shown that female body size was not associated with either multiple male mating or home range size, but females with larger home ranges had higher indexes of body condition.

In conclusion, female and male squirrels from Slovakia do not differ in head-body length, hind-foot length, ear length and body mass. Females have tails which are on average 5 mm longer than those of males (close to 3%) but the range of female tail length lies completely within the range of male tail length. In relation to body size and the overall biology of the Eurasian red squirrel monomorphism is a good evolutionary advantage that allows both sexes to have an effective defense against the other, especially for females protecting their nests and offspring from cannibalising conspecifics and infanticide (Wauters et al. 1990; Wauters & Dhondt 1989a, b; 1992; 1995; Lurz et al. 2000, 2005; Koprowski 2007). We believe that the non-significant results of the SSD can be explained through the benefits of the same size for both sexes in the protection of territory as well as inter- and intra-sexual interaction. On the other hand, the slightly larger proportions in the tail length of females may have an advantage during locomotion when they are in pregnancy.

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