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Sex-specific patterns in body mass and mating system in the Siberian flying squirrel

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Abstract

Background: Reproductive strategies and evolutionary pressures differ between males and females. This often results in size differences between the sexes, and also in sex-specific seasonal variation in body mass. Seasonal variation in body mass is also affected by other factors, such as weather. Studies on sex-specific body mass patterns may contribute to better understand the mating system of a species. Here we quantify patterns underlying sex-specific body mass variation using a long-term dataset on body mass in the Siberian flying squirrel, *Pteromys volans*.

Results: We show that female flying squirrels were larger than males based on body mass and other body measures. Males had lowest body mass after the breeding season, whereas female body mass was more constant between seasons, when the pregnancy period was excluded. Male body mass did not increase before the mating season, despite the general pattern that males with higher body mass are usually dominant in squirrel species. Seasonal body mass variation was linked to weather factors, but this relationship was not straightforward to interpret, and did not clearly affect the trend in body mass observed over the 22 years of study.

Conclusions: Our study supports the view that arboreal squirrels often deviate from the general pattern found in mammals for larger males than females. The mating system seems to be the main driver of sex-specific seasonal body mass variation in flying squirrels, and conflicting selective pressure may occur for males to have low body mass to facilitate gliding versus high body mass to facilitate dominance.

Keywords: Sexual size dimorphism, Climate change, Scramble competition mating system, Female defence

Background

Reproductive strategies and evolutionary pressures differ between sexes and often lead to sex differences in body size, in body mass as well as in bone measurements [1–3]. The same factors may also lead to sex-specific seasonal variation in body mass, depending on energy expenditure and condition of individuals [4, 5]. Studies on sex-specific seasonal patterns of body mass are relatively scarce [6–9], but may contribute to understand the mating system of a species.

In mammals, lactation is one of the main factors contributing to the seasonal difference in energy expenditure between sexes. In addition, the levels of intra-sexual competition during the breeding season typically differ between sexes, depending on the mating system of a species [3, 10–13]. An interesting mating system to study intra-sexual patterns in body mass is the so called scramble competition mating system [14]. This mating system has been frequently reported for insects [15], but is poorly studied in mammals, although it may occur, for example, in arboreal squirrels (subfamily Sciurinae; [16, 17]). In a scramble competition mating system, females are solitary and males move to visit different females which may be in oestrus during different days. Within this context, selection may favour males that are effective in locating female territories scattered across the landscape [16, 18].

Mating system and sexual selection are, however, not the only factors shaping differences in body mass between sexes [19]. For example, the seasonality of resource availability (such as food) and weather conditions (e.g. harsh winter periods) may also affect body mass difference between sexes beyond the more commonly recognised

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effect of reproductive strategies [20, 21]. Consequently, climate change can have sex-specific effects on body mass [22], potentially creating temporal changes also in sexual body mass dimorphism of the species.

In this study, we broadly aim to quantify patterns underlying sex-specific body mass variation between and within years in the Siberian flying squirrel, *Pteromys volans* (Linnaeus, 1758) in Central-Western Finland. We used long-term datasets on body mass of individuals spanning 22 years and also a short-term dataset on body measurements. In flying squirrels, the locomotor system of gliding likely places a unique set of selective forces related to body mass in this group [23, 24]. Female flying squirrels live in isolation and males need to rapidly move between females during the mating season [17]. In addition, Siberian flying squirrels, like tree squirrels [25], perform mating chases, whereby a few males glide and run one after another from tree to tree following a female [26]. These behaviours may promote high movement abilities of males in competition with each other, and may favour fast gliders with low body mass. However, within the mating system of tree and flying squirrels, the defence of females by large dominant males may promote high body mass necessary for dominating mating opportunities and prevent smaller subdominant males from reproducing [17, 25, 27]. Earlier studies indicate that flying squirrels may have female-biased sexual dimorphism, with females being larger than males based on body mass [17] and body measurements of few museum specimens [28]. However, these studies are based on a limited number of individuals. In addition, the links between the mating system and the seasonal variation in body mass are still poorly understood in squirrels. For example, conflicting pressures between a defence mating system and a scramble competition mating system [16, 18] may affect seasonal variation in body mass in male flying squirrels. In addition, seasonal sexual dimorphism in body mass may be related to different seasonal patterns in energy expenditure between the sexes.

We predict (i) that seasonal patterns in body mass underlie the specific mating system: if males have highest body mass before the breeding season and lowest body mass after the breeding season, then the female defense mating systems is dominant in this species [2, 9]. Instead, if the scramble competition mating system is operative, then we predict that males should not have the highest body mass before the mating season in order to be fast in mating chases and in locating females. We also predict (ii), against the general pattern in mammal species, that in flying squirrels the females will have a larger body mass (measured outside of the breeding season) and other body measurements than males. Finally, we predict (iii) that weather conditions affect seasonal variation in body mass. Spring weather, which corresponds to the start of the breeding season of flying squirrels and, thus, may have sex-specific effects on body mass, has significantly warmed in Finland during our study period [29, 30]. Thus, climate change has the potential to affect the 22 year trend in body mass of the two sexes in flying squirrels.

Methods

Study species

The Siberian flying squirrel is a nocturnal arboreal rodent which nests in tree cavities, nest-boxes and dreys (twig nests) in spruce-dominated boreal forests. Flying squirrels feed on deciduous trees within spruce-dominated forests. The mating season starts in mid-March and the first litter is born in late April [26]. Females can sometimes have a second litter which is born in late June. Females are territorial and live in non-overlapping home ranges (on average 4 ha in size), whereas males have much larger home ranges (average size of 60 ha) that can overlap with several other male and female home ranges [17]. The movement activity of males increases during the mating season when males actively move between territories of different females. Females come into oestrus, albeit not synchronously, within a short period starting from mid-March [17, 26].

Study areas and data collection

The study was carried out in two areas: Luoto (63°49′N, 22°49′E) and Vaasa (63°3′N, 22°41′E). In Luoto, flying squirrels were studied between 1993 and 2014 within an area of 44 km^2. The main land-uses in Luoto are shoreline spruce-dominated mixed forests, clear-cuts, and cultivated Scots pine plantations. The Vaasa study area is located about 90 km southwest of Luoto. The marking of flying squirrels started in 1992 in Vaasa within an area of 4 km^2, after the year 2000, the area was expanded to cover 25 km^2. Vaasa is covered by spruce-dominated forest patches, clear-cuts, and agricultural fields (for more information see [31, 32]).

The studied populations bred in nest-boxes. Nest-boxes were placed in forest patches of various sizes in groups of 2 to 4 nest-boxes per site, on average 2 nest-boxes per mature spruce forest hectare. The nest-boxes were made from a piece of aspen or spruce trunk, so that they resembled natural cavities. No known differences are apparent in behaviour or reproductive output, e.g. in number of offspring produced or communal nesting patterns, between individuals living in nest-boxes and those living in dreys or natural cavities (unpublished data; [32]), nor are we aware of significant differences in predator communities between sites. The nest-boxes have an entrance-hole diameter of 4.5 cm. This diameter is the same of that of the entrance of cavities made by the Great spotted woodpecker, *Dendrocopus major*, which represent the most common natural nesting site for flying squirrels in our study area. This size of the entrance-hole prevents main predators (e.g. the pine marten, *Martes martes*, and also large owls) from entering the nest-box. The same size of the entrance-hole, as well as the cavity size, between nest boxes and natural cavities makes the former readily accepted by flying squirrels for breeding and resting.

In total 489 male and 562 female flying squirrels were captured by hand from nest-boxes, sexed, weighed, and marked with ear-tags (Hauptner 73850, Hauptner, Germany). The main nest-box checking session was in June, and sites found occupied were checked again in August. In addition, in the years 1992–2003 part of the nest boxes were checked also between September and March, but for the following years there were only sporadic observations during these months. In total there were 1812 observations in June and August and 284 observations for October-March (for the 1051 studied individuals). The same observer (R. Wistbacka) was responsible for measurements taken in Luoto study area and also in Vaasa after 2001. Before 2001, weighing in Vaasa was made by R. Wistbacka and A. Mäkelä. The same weighing scale type was used (Pesola) and the scale was calibrated with a similar scale used in another flying squirrel population [33]. Thus, biases due to observer error between study areas were reduced.

We knew the age of 182 out of 489 males and 239 out of 562 females, because those individuals had been previously captured and marked as juveniles. Recapturing probability of individuals was high, above 0.8 for females and 0.7 for males [31], and we can conclude that new unmarked adult individuals located within our study area were very likely new recruits to our study system. Recruits arrive during the natal dispersal period, typically concentrated in September, whereas breeding dispersal is rare in flying squirrels [34, 35]. In other words, within our study areas the likelihood of an unmarked adult individual of being 1 year old is very high ([31], unpublished data). We used age based on this assumption in our models, because it was better aiming to control for the possible effect of age than leaving age out of the analyses (the same approach was used by [16]). The results for age were similar when only individuals captured as juveniles were used (Additional file 1: Figure S1).

Female body mass is affected by pregnancy between the start of mating season in mid-March and the birth of summer litters. Based on our data, second litters are born by mid-July at the latest. Thus, for the analysis of the effect of age and year on body mass, we excluded female observations recorded between 15 March and end of July. Nevertheless, the energy expenditure during the breeding season may have carry over impacts on body mass of females still in August.

For analysing sexual dimorphism in size, in addition to body mass, we measured skull length of 72 individuals, femur length of 60 individuals, and tail length of 56 individuals, all adults, during June 2014 and 2015 (the same individuals were used for measurements of skull, femur and tail, but femur and tail length were missing for some individuals). All these measurements were taken by the same observer (A. Santangeli) to avoid observer-induced measurement bias.

Weather variables

We used weather information from the weather station (maintained by the Finnish Meteorological Institute) nearest to each study area. For Vaasa, the closest weather station was located within our study area, and for Luoto it was 10 km southeast of the study area. Weather recording stations were at the same altitude as the study areas. We used monthly average temperature and precipitation indices between December and June. Early winter weather was averaged for December and January, late winter was February and March. Spring season was represented by April and May, and June described the summer weather. For the spring weather, we also used the starting date of the tree growing season. Temperatures consistently above +5 °C indicate the beginning of tree growing season (Finnish Meteorological Institute; http://en.ilmatieteenlaitos.fi/seasons-in-finland), and have also been shown to correlate with birch bud burst in Finland [36].

Statistical analyses

Models on sexual differences in body measurements

We first built three generalized linear mixed models (GLMM) using as a response the skull, femur and tail length ($n = 56–72$). Because the main rationale for these models was to quantify sex differences in the abovementioned three measurements, we used sex as a categorical predictor, and territory identity nested within year in the random part to account for multiple observations from different individuals in the same territory (e.g. measurements of male and female from the same territory). We then used all observations where body mass was measured ($n = 695$) during the months from January to March, and from August to November to explore sex differences in body mass. Thus we excluded the months when females were pregnant in order to make the comparison in body mass between the two sexes. Additionally, we fit a GLMM with similar structure as those explained above, but now also with age and month controlled for in the model.

Models on seasonal and weather effects on body mass

We used GLMMs to investigate the relationship between body mass of flying squirrels (separately for sex and for two seasons, see below) in relation to environmental, life-history and temporal predictors. Specifically, we ran four GLMMs using in turn the body mass of adult females or males separately within two different seasons (winter and summer) as the response variable. Here we considered as winter all measurements of body weight collected between

January and March from males and females ($n = 120$ and 99, respectively), and as summer the measurements collected between June and November for males ($n = 804$), and between August and November for females ($n = 284$). We excluded female measurements collected in June from all analyses as these are affected by the breeding state (pregnancy). We run separate sex-specific models for the winter and summer season because data for the winter season were only collected up to the year 2003, whereas those from the summer period spanned until the year 2014 (see above).

In each of the four models, we included the individual identity nested within the study area (Luoto or Vaasa) in the random part of the model to account for pseudoreplication (i.e. multiple measurements collected on the same individual in the same study area over the years). We then included, in each of the four models, the month when body mass was measured (as a categorical variable), the age of the individual and the year (both as continuous variables). Finally, for the winter models we also included as predictors the average temperature and average precipitation during December and January, and for the summer models, the average temperature and precipitation in December and January combined, February and March combined, as well as average temperature and precipitation in May, April and June separately. In the summer models we also included the starting date of the tree growth season, with the rationale that an early start of the growth season would result in higher body mass later in the summer. We also tested the effect of age squared (to fit non-linear trends) by including this variable in each full model, and removing it if non-significant. We assessed the significance of each level combination within the categorical variables (e.g. between body mass in January and February within the month variable) by means of post-hoc comparisons adjusted for multiple testing using the Tukey method.

Before fitting the models we checked for collinearity using variance inflation factor (VIF) analyses. All variables had a VIF value lower than 2.5, indicating low collinearity levels and no need for excluding any of them from the models. We then built the four full models (i.e. the ones with all candidate predictor variables), one for each sex-class and season combination (see above). Next we applied model selection based on the Akaike's information criterion (AIC), followed by multi-model inference and averaging [37] using the MuMin package in R [38]. We derived averaged model coefficients and p-values for each variable from across the set of best ranked models (i.e. with $\Delta AIC < 4$; listed in Additional file 1: Table S1).

Finally, we tested whether there was any temporal trend in body mass during winter (from early January to 15th of March), i.e. before the start of the mating season. This model was similar to the above models for body mass of males and females, but month was replaced with the day of the year so that 1st January got a value of 0 and 15th of March a value of 105. For this latter analysis we did not have repeated measurements from the same individual, therefore there was no need to include the individual identity as a random effect, whereas study area was included as a class variable.

All analyses were performed in R software v. 3.0.3 [39].

Results

Sexual differences in body measurements

Females body mass was on average 12 g higher than that of males (using data from the 22 years study period: $t = -14.61$, $p < 0.001$). Moreover, based on data from the years 2014 and 2015 only, females appear to have longer femur than males ($t = -3.10$, $p = 0.01$), whereas skull ($t = 0.30$, $p = 0.77$) and tail length ($t = -1.32$, $p = 0.22$) were similar between the two sexes (Fig. 1).

Seasonal and weather effects on body mass

We found considerable model uncertainty when running all possible combinations of body mass sub-models for the four separate analyses (see Additional file 1 for the list of 10 best supported models for males and females). This underscores the need for multi-model averaging, from which results are shown below.

Body mass of adult flying squirrels did not vary significantly between the different winter months (Fig. 2) and there was no change in body mass over the period preceding the start of the mating season for male or female flying squirrels. This was tested with the correlation between date, from January to mid-March, and body mass: males: $n = 104$, $F_{1,\ 95.6} = 0.35$, $p = 0.55$; females: $n = 93$, $F_{1,\ 21.5} = 0.81$, $p = 0.38$. However, we show that male body mass declined after the breeding season, amounting to about 10 % loss of weight from the winter body mass (Fig. 2). This decline was observable right after the start of the mating season as the pattern seems clear already in April (i.e. the decline from March to April was on average 5 g from the raw data, $n = 32$ measurements in April). Conversely, the body mass of females did not vary between seasons and summer months (Fig. 2).

For both sexes, low temperatures in late winter, as well as the early start of the tree growth season, resulted in increased body mass during the following summer season (Fig. 3, Table 1). Moreover, for male flying squirrels higher temperature in spring was associated to lower body mass in summer, whereas increased rain in June was related to lower body mass of females. Winter body mass was not related to any weather variable (Tables 1 and 2). The only significant temporal trend observed over the years of study was an increasing trend in female weight measured in

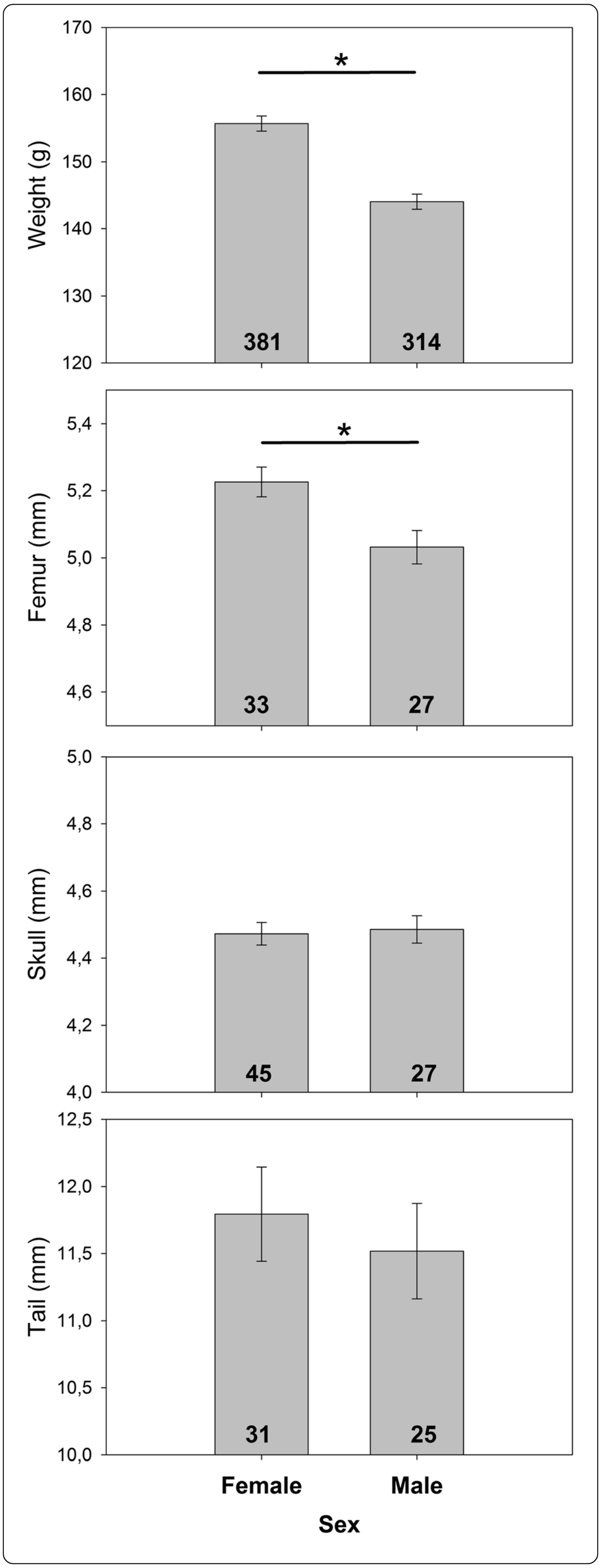

Fig. 1 Predicted mean values (and standard errors) for weight, femur, skull and tail length of male and female adult flying squirrels. Sample sizes are given with values within the column bars, whereas the * depicts significant differences between sexes

winter. Moreover, body mass increased with age in both sexes (Tables 1 and 2).

Discussion

We did not observe changes in male body mass before the breeding season. This was against our prediction for the female defence mating system. The only observable seasonal pattern we found was a decrease in male body mass after the breeding season. As we predicted, female flying squirrels were larger than males, but there were no detectable seasonal variation in female body mass outside of the pregnancy period. Unexpectedly, cold winter and cold spring conditions were linked to an increase in body mass of males and females in the following summer. The only temporal trend observed over the 22 year study period was a slight increase in winter body mass of females. Thus, no measurable temporal trends that might be related to sexual-size dimorphism were detected.

The observed female-biased sexual size dimorphism in the Siberian flying squirrels of this study is consistent with patterns observed for the southern flying squirrel *Glaucomys volans* [24]. In our study, the female-biased body mass was largest after the breeding season, because female body mass did not vary much within the year (outside of the pregnancy period). Similar observations of a stable female body mass between seasons have been noted for North American red squirrels [40]. We observed no difference in skull size between sexes. Conversely, femur length was longer in females than in males. The explanation for this may be the need for females to secure gliding potential when pregnant, and, thus, increase the aerofoil area compared to males [23]. For example, it is known that for flying mammals (i.e. bats) pregnancy restricts the ability to move [41]. Larger female body mass, as compared to that of males in flying squirrels may be related to reproductive benefits from large size due to the territoriality of females ([17, 24], see also [42]). Alternatively, it may also be due to the benefits for males to be smaller and thus more vagile within a scramble competition mating system.

We predicted changes in male body mass before the start of the mating season, but did not find any indication for these changes, within winter or between autumn and winter. Thus, there was no clear pattern in male body mass that would support the female defence mating system. For example in North American red squirrels [40] and grey-headed flying-foxes, *Pteropus poliocephalus* [9], body mass of males increased before the start of the

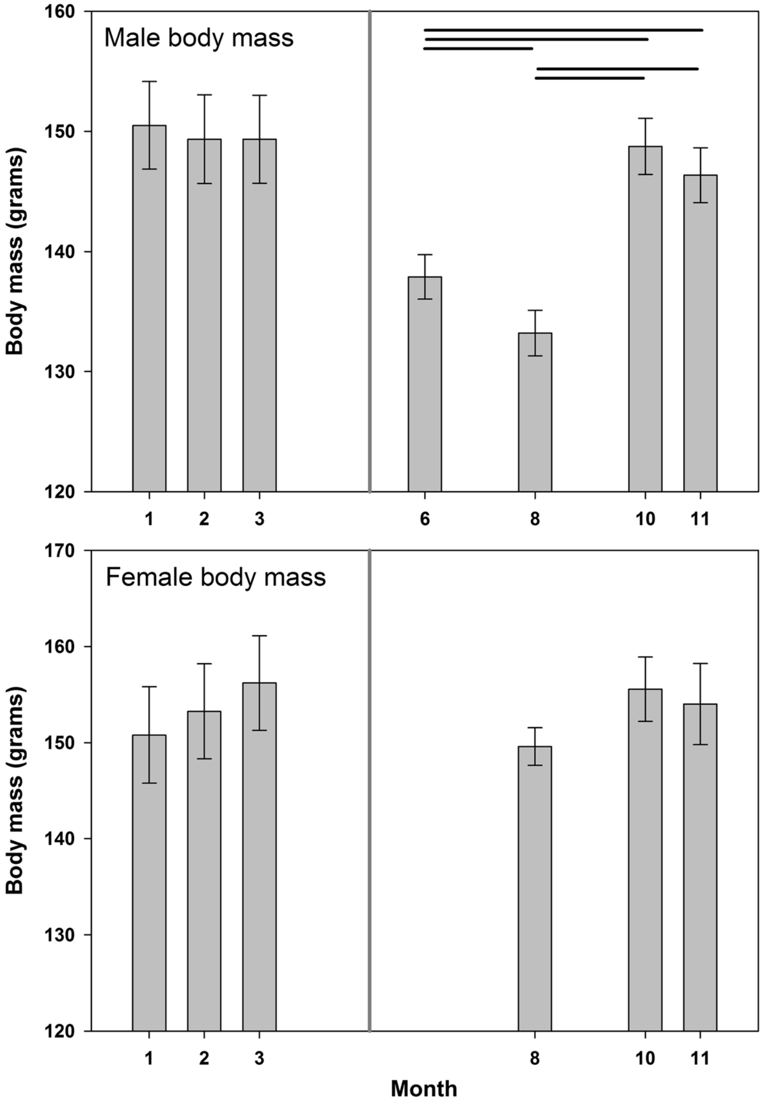

Fig. 2 Male and female body mass (least square means and standard errors) for each month from the winter model (1 January to 3 March) and for the summer model (6 June to 11 November). For females, June was omitted because they may still be pregnant in June. Lines above the bars join months for which body mass was significantly different after post-hoc testing (adjusted for multiple testing using the Tukey method). For females, there were no significant differences in body mass between the months of the winter season and between the months of the summer season

mating season and declined rapidly then after. However, it is known that in the Siberian flying squirrel the male body mass is positively related to reproductive success [17]. Thus, some aspects of the female defence mating system may be operative in flying squirrels, as is the case for tree squirrels [25, 27]. However, the stable body mass of males during winter seems to fit the hypothesis that extra weight just before breeding may not enhance fast movement to locate females. This fits the scramble competition mating system. Perhaps in the case of the Siberian flying squirrel, the selective forces for increased gliding potential versus dominance (i.e. low versus high body mass, respectively) at some level cancel each other out.

Body mass before the mating season is likely affected by environmental factors during the preceding winter. However, food availability for flying squirrels during the winter months is relatively stable, since the main winter food, catkins of deciduous trees, develop already during the autumn and persist on the trees during winter. In other words, food availability does not vary within the winter season [30]. Only after bud burst in spring do flying squirrels start consuming leaf material, but this is after the start of the mating season (from mid-May onwards in our study area). In addition, we did not find any weather variable to have an effect on body mass in winter, which is in line with a previous study

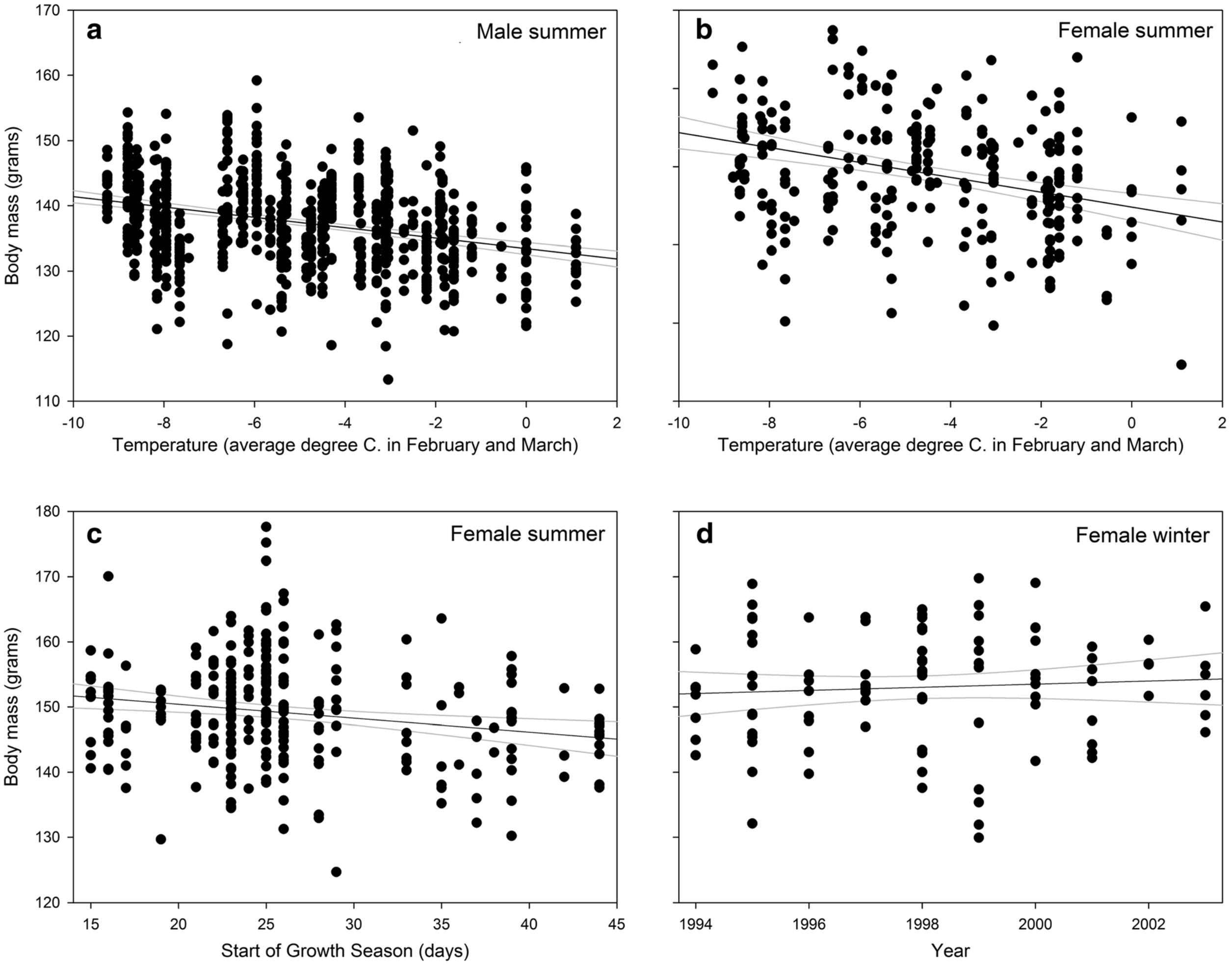

Fig. 3 Decrease in summer body mass of **a**) male and **b**) female flying squirrels with the increase in average temperature during the preceding winter (February and March). **c** Change in summer body mass of female flying squirrels in relation to the onset of tree growth season. **d** Trend in winter body mass of female flying squirrels over the years of study. Dots depict predicted values from the full model, with fitted lines and confidence intervals

where no effect of winter temperature on communal nesting behaviour of flying squirrels was found [32].

Surprisingly, male body mass did not increase during summer, from June to August, although the breeding season for male flying squirrels ends already in the spring after they have fertilised the females. Males had even lower body mass in August than in June. Instead, for some other species male mass is observed to decline rapidly during the mating season, but also increased rapidly during the summer [8, 43, 44]. In August, male flying squirrels frequently move between forest patches occupied by different females [45], perhaps to increase social links with new females which might affect future reproductive success. This may increase the energy expenditure of male flying squirrels and explain the decline in body mass observed during the late summer months. Moreover, another possible explanation for the observed monthly variation in body mass might also relate to the food available to flying squirrels in the different periods, because in early summer flying squirrels eat mainly leaves [46]. However, food would affect body mass in both sexes. In addition, whether the nutritional value of leaves differs from that of catkins for flying squirrels is still unknown. In any case, food obviously is related to observed increase in male body mass from August to October, as squirrels likely prepare for winter by increasing body mass in late autumn.

Body mass increased with the age of Siberian flying squirrels in both sexes, which is in line with earlier studies reporting body mass increases with age in adult squirrels [25, 27, 47]. It should be noted that our analysis did not separate mortality and individual growth curves and is not suitable for determining growth patterns related to senescence [48, 49]. Nevertheless, age, body mass, dominance

Table 1 Generalized Linear Mixed Model results for adult male body mass measurements

	Variable	Estimate	SE	Z value	*p*-value
a)	(Intercept)	11,29	414,58	0,03	0,978
	Age	**3,01**	**0,59**	**4,89**	**<0,001**
	T_DecJan	0,27	0,32	0,81	0,419
	Year	0,24	0,34	0,66	0,507
	R_DecJan	−0,04	0,07	0,54	0,592
b)	(Intercept)	137,35	54,18	2,53	0,011
	Age	**0,80**	**0,22**	**3,70**	**<0,001**
	R_June	−0,02	0,01	1,72	0,086
	SGS	**−0,12**	**0,05**	**2,43**	**0,015**
	T_April	**−0,76**	**0,27**	**2,81**	**0,005**
	T_DecJan	−0,16	0,09	1,77	0,076
	T_FebMar	**−0,38**	**0,11**	**3,54**	**<0,001**
	T_May	**−0,58**	**0,20**	**2,90**	**0,004**
	R_DecJan	0,02	0,02	1,11	0,267
	R_May	−0,01	0,01	1,00	0,318
	R_FebMar	−0,02	0,02	0,89	0,376
	R_April	0,01	0,02	0,68	0,498
	T_June	−0,10	0,19	0,52	0,605
	Year	0,02	0,07	0,33	0,745

a) Winter (years 1992–2003) and b) summer (years 1992–2014). Statistics show the model averaged results from across the best supported models (listed in Additional file 1: Table S1). T depicts Temperature, R precipitation, DecJan the months of December and January combined, FebMar is February and March combined. SGS indicates the start of the growth season of trees. Significant variables are highlighted in bold font. Results for the month variable (which was set as categorical) are omitted here and are shown in Fig. 2

Table 2 Generalized Linear Mixed Model results for adult female body mass measurements

	Variable	Estimate	SE	Z value	*p*-value
a)	(Intercept)	−1448,00	1212,00	1,19	0,235
	Age	**14,30**	**3,49**	**3,90**	**<0,001**
	age*age	**−1,48**	**0,47**	**3,03**	**0,002**
	Year	**1,03**	**0,48**	**2,06**	**0,039**
	T_DecJan	−1,02	0,55	1,79	0,074
	R_DecJan	0,01	0,10	0,12	0,902
b)	(Intercept)	83,69	173,40	0,48	0,631
	Age	**3,97**	**0,65**	**6,04**	**<0,001**
	R_June	**−0,07**	**0,03**	**2,22**	**0,027**
	SGS	**−0,23**	**0,10**	**2,23**	**0,026**
	T_FebMar	**−0,69**	**0,26**	**2,56**	**0,010**
	R_DecJan	0,05	0,05	1,01	0,311
	R_April	0,05	0,05	0,98	0,329
	T_May	−0,43	0,50	0,85	0,398
	Year	0,14	0,14	0,96	0,335
	T_April	0,87	0,76	1,13	0,260
	R_FebMar	−0,03	0,06	0,43	0,671
	T_June	0,18	0,47	0,38	0,703
	T_DecJan	−0,14	0,28	0,50	0,620
	R_May	0,00	0,03	0,00	0,998

a) Winter (years 1992–2003) and b) summer (years 1992–2014). Statistics show the model averaged results from across the best supported models (listed in Additional file 1: Table S2). T depicts Temperature, R precipitation, DecJan the months of December and January combined, FebMar is February and March combined. SGS indicates the start of the growth season of trees. Significant variables are highlighted in bold font

hierarchies and reproductive success are linked in squirrels, as older individuals are usually heavier, higher in dominance hierarchy, and consequently have increased reproductive success [17, 25, 47].

Our results do not suggest any impact of climatic trends on body mass dimorphism in flying squirrels. The only temporal pattern observed during our study period was a slight increase in female body mass during winter. Our temporal data for winter months was limited (winter body mass data ended in year 2003) and it remains unclear what process is behind the observed temporal trend, because winter body mass was not linked to winter temperatures. In addition, the observed trend was against the expectation that climate warming would result in smaller body size ([50, 51]; but see [52]). The increasing trend in early spring temperatures over our study period ([29], for more detailed analysis on weather changes in our study area, see [30]) indicates potential for temporal changes in sexual dimorphism in body mass. However this was not the case, as we did not observe any trends in summer body mass of males or females.

Weather in winter had unexpected effects on summer body mass of flying squirrels. The summer body mass of both sexes increased when the preceding winter and spring seasons were colder. The reasons for this pattern remain unknown, but a possible explanation could be that warm weather at the beginning and during the breeding season may increase the intensity of mating season and result in high energy expenditure and low body mass after a successful reproduction. Lower body mass in summer was also associated with delayed tree growth in spring. This correlation might indicate a poor food situation in the late spring, because after the flowering of catkins in early spring leaves represent the main food for flying squirrels. Late start of the tree growing season indicates delay in leave growth. We also found a negative correlation between increased rain in June and female body mass in August, which may indicate that rainy conditions in summer have negative impacts on female body mass. In earlier studies, weather has been observed to affect timing of reproduction and reproductive success in Siberian flying squirrels [30] and red squirrels [53, 54]. In addition, for example in ungulates, body mass interacts strongly with weather and food availability in spring and summer [55, 56].

Conclusions

Our study supports the general view that tree and flying squirrels often deviate from the general pattern in mammals for males being larger than females [24, 57, 58]. Seasonal body mass patterns of male flying squirrels support the hypothesis that competition during the breeding season is the main driver of seasonal body mass variation in males. Instead, female body mass was more constant between seasons, when the effects of pregnancy are not considered. However, we also suggest that, in the case of Siberian flying squirrels, competing forces may play a role in selecting for male size that would represent an optimal balance between fast gliding (i.e. low body mass) and dominant (i.e. high body mass), with these competing pressures potentially masking some of the seasonal variation (before breeding season) in male body mass. However, verifying this hypothesis would require further studies. Our results also support the view that the effects of temperature on body mass may be complex and in correlative studies not necessarily straightforward to interpret [52]. Nevertheless, no indication that climate change had affected sexual body mass dimorphism was detected.

Additional file

Additional file 1: Table S1. The best ranked models explaining body mass of male Siberian flying squirrels measured in summer and winter (upper and lower panel respectively). Columns show the variables included in each model (see main text for an explanation of the variable names), the degrees of freedom of each model, the Akaike value corrected for small sample size (AICc) and the difference in AIC between best ranked and the target model (ΔAICc) as well as the AIC weight of each model. List is restricted to 10 best ranked models. **Table S2.** The best ranked models explaining body mass of female Siberian flying squirrels measured in summer and winter (upper and lower panel respectively). Columns show the variables included in each model (see main text for an explanation of the variable names), the degrees of freedom of each model, the Akaike value corrected for small sample size (AICc) and the difference in AIC between best ranked and the target model (ΔAICc) as well as the AIC weight of each model. List is restricted to 10 best ranked models. **Figure S1.** Male and female body mass (least square means and standard errors) for each month from the winter model (1 January to 3 March) and for the summer model (6 June to 11 November). Only observations where the exact age was known have been used for this supporting analysis (see methods). For females, June was omitted because they may still be pregnant in June. Lines above the bars join months for which body mass was significantly different after post-hoc testing (adjusted for multiple testing using the Tukey method). For females, there were no significant differences in body mass between the months of the winter season and between the months of the summer season. (DOCX 127 kb)

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Availability of data and material

The data set supporting the results of this article is available in the European Boreal Forest Biodiversity (EBFB) database repository, https://www.earthcape.com/.

Authors' contributions

RW collected data, VS and AS analysed data and wrote the manuscript. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

Consent for publication

Not applicable.

Ethics approval and consent to participate

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. No ethical approval was required from an institutional or national ethics review board.

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