

Is it sexual mass dimorphism season?

Denis Réale based on peer reviews by **Philip McLoughlin**, **Patrick Bergeron** and **Achaz von Hardenberg**

A. J. Mark Hewison, Nadège Bonnot, Jean-Michel Gaillard, Petter Kjellander, Jean-François Lemaitre, Nicolas Morellet & Maryline Pellerin (2024) Body mass change over winter is consistently sex-specific across roe deer (*Capreolus capreolus*) populations. bioRxiv, ver. 4, peer-reviewed and recommended by Peer Community in Ecology.

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Polygyny is assumed to have led to the evolution of strong sexual size dimorphism (SSD) in mammals, males often being heavier or showing more developed armaments than females (Weckerly 1998; Loison et al. 1999; Pérez-Barbería et al. 2002). SSD generally increases with the degree of polygyny of the species. However, the degree of SSD, and particularly of sexual mass dimorphism, is not fixed for each species, and differences exist between populations (Blanckenhorn et al. 2006; Cox & Calsbeek 2010) or even between seasons within populations (Rughetti & Festa-Bianchet 2011).

In this study, Hewison et al. propose that studying seasonal variation in sexual mass dimorphism and how this can be affected by winter harshness and latitude allows us to better assess the energetic costs associated with the eco-evolutionary constraints acting on each sex. To achieve their goal, Hewison et al. use a formidable, long-term dataset of over 7,000 individuals, in five roe deer populations (Capreolus capreolus), from south-west France and Sweden.

According to the authors, sexual mass dimorphism should be at its lowest in early spring in this species due to a stronger trade-off between antler growth and body weight maintenance in males over winter than in females. Furthermore, harsher conditions, varying both in time and space (i.e., Sweden vs. France), should increase winter weight loss, and thus, mass change differences between the sexes should be stronger and show more variation in Sweden than in France.

Their results support their hypotheses. In the two Swedish populations, males lost more mass than females. In the three French populations, males maintain their body mass while females gain some over the winter. Because of these sex-dependent loss/gain in body mass, sexual dimorphism was stronger early in the winter and null at the onset of spring. Furthermore, sexual dimorphism was stronger in southern than in northern populations. In France, males weighed about 10% more than females, while they weighed about 5% more in

Sweden. Roe deer, however, do not show any dimorphism early in the spring, when males start defending their territory.

The authors also found more variation in mass change among years in Swedish than in French roe deer, suggesting a stronger effect of winter severity on the dynamics of mass change in northern than in southern populations. The authors interpret the decrease in sexual dimorphism throughout the winter by the fact that, during this period, the energetic cost paid by males associated with the growth of their antlers and the effort of establishing their mating territory. They thus attribute the greater mass change in males to the competitive allocation of resources to antler growth or body mass. They also discuss the low probability that such sex differences in mass change could be caused by females' gestation in this species.

Interestingly, Hewison et al. found that individual differences represented more than 70% of the total variation in body mass, and the low estimated among-individual variance in slopes with time might indicate that, despite a lower SSD, selection pressures on body mass can still be maintained at times when body mass may play an important role, such as in spring with territorial defense or later during mating (Vanpé et al. 2010).

I recommend this article because it produces strong results, which show, without a shadow of a doubt, sex differences in their seasonal mass changes, resulting in a marked seasonal variation in SSD. The differences observed between southern and northern populations confirm the idea that the severity of the winters endured by these populations acts as a constraint on the deer's patterns of mass change. I hope this study will encourage more examinations of how eco-evolutionary constraints affect the sexual size dimorphism.

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Reviews

Evaluation round #2

DOI or URL of the preprint: https://doi.org/10.1101/2022.09.09.507329 Version of the preprint: 3

Authors' reply, 19 August 2024

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Decision by Denis Réale, posted 19 July 2024, validated 22 July 2024

Minor modifications

Dear Mark and coauthors,

I have read the new draft of the manuscript and your responses to the two reviewers (and my) comments. I greatly appreciate that you proivided thorough explanations and justifications of your choices. However, I still think it would be very important to provide information on the random effects in the manuscript for two main reasons:

1) a complete description (i.e. both coefficients and 95%CI of fixed effects and variance estimates of random effects e.g. shown as a proportion of the total variance) of the selected model (Table S1-5) for each population is essential for the readers to make their opinion about the results.

2) variance among years will provide important biological information on how body mass in the middle of the winter (intercept) vary among years in each population. This type of results totally fits with your objectives: based on your second hypothesis we should expect higher among-year variance in body mass at the intercept in Swedend than in France. You may also quickly discuss the variance in slopes among years, and the among-individual variance.

I would suggest you to add one table in the core document showing these effects. I'm convinced that once this table is added to the paper I will very quickly (this time!) write my recommandation for your publication.

Best

Denis Réale

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2022.09.09.507329 Version of the preprint: 1

Authors' reply, 22 April 2024

Please find attached the revised version of our manuscript and the point by point response to the reviewers' comments. The modifications are highlighted in yellow in this tacked changes version.

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Decision by Denis Réale, posted 06 March 2023, validated 06 March 2023

Some important revisions are needed before I could recommend this paper.

Dear Mark and coauthors, First, I'd like to apologize for the delays in the review process. It was tough to find reviewers and we only got the three reviews completed by the end of February. Based on the comments by the three reviewers and my reading of the paper, I am willing to recommend your paper. However, I think you need to address the reviewers' comments and mine, before I can do it.

I appreciate the great work and the amazing dataset used in this study to tackle an important ecological question about body mass plasticity and the constrains on each sex in a poloygynous speices showing a low sexual mass dimorphism. I only have a couple of comments, including this important one:

1) You run mixed models with individual ID and year as random effects. However, you only show the fixed effects part of the results. I understand the goal of the study is not to look at individual variation in body mass, but I think we still need to see these results, because you models may suffer type 1 errors. Type 1 error rate for the slope x treatment interaction (in your case the sex by date interaction) increases with between-individual variation in slopes if that effect is omitted in the model (Schielzeth and Forstmeier 2012). This is because omitting random slopes in a model when you have a lot of replicates per unit of your random effect generates pseudoreplication. I assume in your case you may also have the same issue with the between-year variation in slopes.

I would, thus, strongly recommend you run the models by including random slopes for both individual ID and years to make sure that you still find significant interactions between date and sex once controlling for pseudoreplication. Additionally, including random slopes could give you interesting biological information. You'll obtain estimates for the correlation between intercept and slope (I assume that you're scaling dates so that the intercept is estimated at the average Julian date), which will tell you whether bigger individuals at the intercept show weaker or stronger slopes (i.e., they lost/gained more/less weight with time whatever their sex). It will also tell you whether weight loss or gain varies according to the year, which you may link to climatic severity if you have weather data. Schielzeth, H. & Forstmeier, W. (2008). Conclusions beyond support: overconfident estimates in mixed models. Behav Ecol, Behav Ecol, 20, 416–420.

2) You are not testing your second hypothesis: it's only a qualitative examination. You justify the reasons why you do not pool all the populations into one single model. But you'll have to discuss that point.

Denis Réale

Reviewed by Patrick Bergeron, 21 November 2022

The authors are presenting a study about indirect sex-specific costs of reproduction in the moderately dimorphic roe deer. Males tend to lose more, or gain less, body mass than females during the winter months. This analysis is based on a robust long-term dataset conducted on five populations distributed along a north south gradient. I find that this manuscript is well written, the analyses sounded, and the topic is also relevant to non dimorphic species where body mass is associated with fitness.

Comments.

The populations cannot be statistically compared because the analyses were conducted on each population separately. I believe this somewhat reduces the quantitative comparison of the populations along a latitudinal gradient (and the scope of the second objective), but still allows to qualitatively evaluate over-winter body mass variations between populations. This aspect could be mentioned in the discussion.

I think it could be important to mention how many times an individual was measured per year. Given that the variance in body mass is extremely high, it could be an aspect you comment on with respect to the expected within-individual seasonal change in body mass (i.e. mass specific change in body mass during winter).

I think it could be relevant to also provide the AIC and weights for the main effects of Sex and Julian date alone in your models?

Download the review

Reviewed by Achaz von Hardenberg, 26 February 2023

I read this manuscript with great interest. It is well written, and analyses an impressive dataset (more than 7000 individuals) to explore overwinter variation in body mass of male and female roe deer in 5 European populations on a latitudinal gradient.

My comments are mostly minor as can be seen in the attached pdf, and therefore I would recommend publication after minor revisions.

I hope my comments are useful to the authors to improve this interesting paper.

Download the review