The coefficient of variation of body mass (and other traits)

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Abstract

Variation is a fundamental property of populations and provides the raw material upon which evolutionary processes can act. The coefficient of variation, defined as the standard deviation divided by the arithmetic mean, is widely used in evolutionary biology to quantify relative variation, for example to draw conclusions about the strength of selection. However, comparing coefficients of variation among traits can be problematic, because traits of higher dimensionality (e.g. volume) may exhibit greater variation as a mathematical consequence of their dependence on the variation in multiple underlying traits (e.g. length, width, height), independent of any biologically relevant difference in variation between higher- and lower-dimensional traits. Some interpreted this as the need for a correction factor before an honest comparison can be made and e.g. divide coefficients of variation of body mass by three to make it comparable with length measures. Here, we provide three arguments, why this procedure might be misleading. 1). Body mass is not a proxy of volume, as it is also caused by density in living organisms, and therefore should be treated as at least four dimensional. 2). As previously argued, correction factors are extremely difficult to use correctly, as their value depends on the coefficients of variation of, and the correlations between, all underlying traits, which often are difficult or even impossible to measure. 3). Dimensionality in this context refers not exclusively to physical dimensions but instead represents the number of underlying sources of variation contributing to the variation in higher-order traits. This broader interpretation is relevant to traits such as behaviour, for which the underlying causes of variation may be numerous and difficult to identify, or for traits like condition, that have abstract meaning. We therefore recommend caution when comparing coefficients of variation among traits, particularly when their underlying causes of variation differ, or are unknown.

Key words: evolvability, morphology, evolutionary ecology, behavioural ecology, life-history theory.

Introduction

Variation among individuals is a fundamental property of populations. It is essential for evolutionary processes because it provides the variation upon which selection and drift can act. The most commonly used statistical tools to describe variation in populations are standard deviations, variances and ranges (e.g. the interquartile range). Although these measures are informative in many contexts, their interpretation can become problematic when comparing traits or populations that differ substantially in their means (e.g. comparisons between species, populations, or between the sexes when there is sexual size dimorphism). For example, a standard deviation of 10 cm may represent relatively little variation in a population of giraffes but extremely large variation in insect populations. To deal with this issue, Pearson (1896) proposed the coefficient of variation, calculated as the standard deviation divided by the arithmetic mean of the population, and sometimes expressed as a percentage by multiplying the resulting value with 100. The coefficient of variation therefore provides a dimensionless measure of relative variation and facilitates comparisons of the same trait among groups that differ in their mean values.

Coefficients of variation are widely used in evolutionary biology. In quantitative genetics, the additive genetic coefficient of variation is commonly used as the definition of evolvability (Houle, 1992; Hansen *et al.*, 2011; Garcia-Gonzalez *et al.*, 2012; Hansen & Pélabon, 2021). Within the wider field of evolvability, the coefficient of variation of phenotypic traits is also frequently studied (e.g. Garcia-Gonzalez *et al.*, 2012; Pélabon *et al.*, 2020; Leventhal, 2023). In morphological research the coefficient of variation has been used for many years (e.g. Gingerich & Winkler, 1979; Michaels *et al.*, 1988; Demes *et al.*, 1991; Currey *et al.*, 2007; McKellar & Hendry, 2009; Martínez-Abadías *et al.*, 2012). Coefficients of variation are also commonly studied in a life-history context to estimate the strength of natural or sexual selection (e.g. Fitzpatrick, 1997; Simmons & Kotiaho, 2002; Komdeur *et al.*, 2005; Albert *et al.*, 2010; Jacobs & Podolsky, 2010; Chebib *et al.*, 2024; Hosken *et al.*, 2025; Zulian & Youngflesh, 2025).

While comparing coefficients of variation is more appropriate for comparisons between the same trait of different groups than variances or standard deviations, additional problems arise when comparing between traits. Lande (1977) demonstrated that traits of higher dimension, such as volume or area, often have higher coefficients of variation than linear traits (length, height, width), as the variation in these higher-dimensional traits is caused by the combined variation in the lower-dimensional traits, and by the correlation between these lower-dimensional traits:

$$V_a = \sqrt{\sum_{i=1}^{2}\sum_{j=1}^{2}\rho_{ij}V_iV_j}, \quad (1)$$

$$V_v = \sqrt{\sum_{i=1}^{3}\sum_{j=1}^{3}\rho_{ij}V_iV_j}. \quad (2)$$

Here, V_a and V_v are the coefficients of variation of area and volume, respectively, whereas V_i and V_j are the coefficients of variation of the underlying traits x_i and x_j. ρ_{ij} is the correlation between traits x_i and x_j. The sums are taken over all relevant underlying traits (e.g. length and width for area; and length, width and height for volume).

Consequently, when traits of different dimensionality have different coefficients of variation, this can be caused by mathematical reasons, instead of biological ones. Thus, one cannot conclude that selection on a lower-dimensional trait is stronger just because it has a lower coefficient of variation compared to a higher-dimensional trait. If the linear traits would be perfectly correlated ($\rho_{ij} = 1$) and all linear traits would have the same coefficient of variation, the relationship between the coefficients of variation of length, area, and volume would be 1:2:3.

Lande (1977) further showed that comparing coefficients of variation of two traits with that of the ratio of those two traits will lead to an unfair comparison, as well as when there is a negative correlation between the trait mean and the coefficient of variation.

The coefficient of variation of body mass: what is the problem?

The concerns raised by (Lande, 1977) have since then been widely recognised and in many papers a warning message is given to either not compare coefficients of variation between traits, or to be careful with its interpretation. However, others have misinterpreted the paper and divide the coefficient of variation of two-dimensional traits by two or that of three-dimensional traits by three, as a correction factor to make the coefficients of variation comparable with those of one-dimensional traits. Yet, as said above, this requires the strong assumption that there is a perfect correlation between all underlying traits (e.g. length, height, width) and that all underlaying traits have the same coefficient of variation, which is never explicitly tested. For many traits it can be challenging to test these assumptions, as organisms often have complex shapes and it can be difficult to measure all necessary traits, let alone find the correlations between them, and their coefficients of variation.

A related issue concerns body mass. Many studies using the coefficient of variation of body mass treat body mass as a proxy for volume and consequently classify it as a three-dimensional trait. However, this interpretation overlooks the role of density, which we argue is an important and variable trait. Most organisms consist of parts and are therefore not completely homogeneous in content. In other words, the relative amounts of for example water, air, bone, muscle or fat can heavily influence body mass, even when volume stays constant. Therefore, studying the coefficient of variation of body mass should be done with the understanding that it is a four-dimensional trait (namely based on length, height, width and density).

The coefficient of variation of body mass (V_m) is then:

$$V_m = \sqrt{\sum_{i=1}^{4}\sum_{j=1}^{4}\rho_{ij}V_iV_j}. \quad (3)$$

In this case, when all four traits would be perfectly correlated ($\rho_{ij} = 1$) and have the same coefficient of variation, body mass would have a coefficient of variation 4 times as large as that of the linear traits.

However, there are reasons to expect that the underlying components of body mass do not have identical coefficients of variation nor are perfectly correlated. Length, width and height may be constrained by developmental processes and morphology (e.g. skeletal growth), while density may be more flexible (and e.g. depends on food consumption). Consequently, density may exhibit a different coefficient of variation than length, width, and height. This in turn affects how much larger the coefficient of variation of body mass is expected to be, compared to that of for example length, see Figure 1.

Moreover, as density is likely partially dependent on other biological factors (again, e.g. resource consumption), it seems unlikely that density has a perfect correlation with length, width and height. This also affects how much larger the coefficient of variation of body mass will be compared to that of length, see Figure 2.

Accordingly, it is not clear how much larger the coefficient of variation of body mass is, compared to that of underlying traits such as length, height and width, purely for mathematical reasons. Hence, comparing coefficients of variation between traits to obtain biological conclusions should be done with care.

Condition

Condition is an important concept in evolutionary and behavioural ecology (and potentially more branches of evolutionary research), that is frequently linked to fitness. Condition is a somewhat abstract concept that sometimes is estimated through proxies linked to density and other times to body mass. For example, in some bird studies fat score is used a condition proxy, which reflects the amount of subcutaneous fat near the furcula. This amount of fat could to some extent change the volume of the bird, and it also changes their density. However, other times body mass itself or residual body mass from a correlation between body mass and a size measure is used as a proxy for condition. Hence, when studying condition, the dimensionality of the proxies is important to consider. Fair comparisons can only be made between coefficients of variation of condition that are defined and calculated

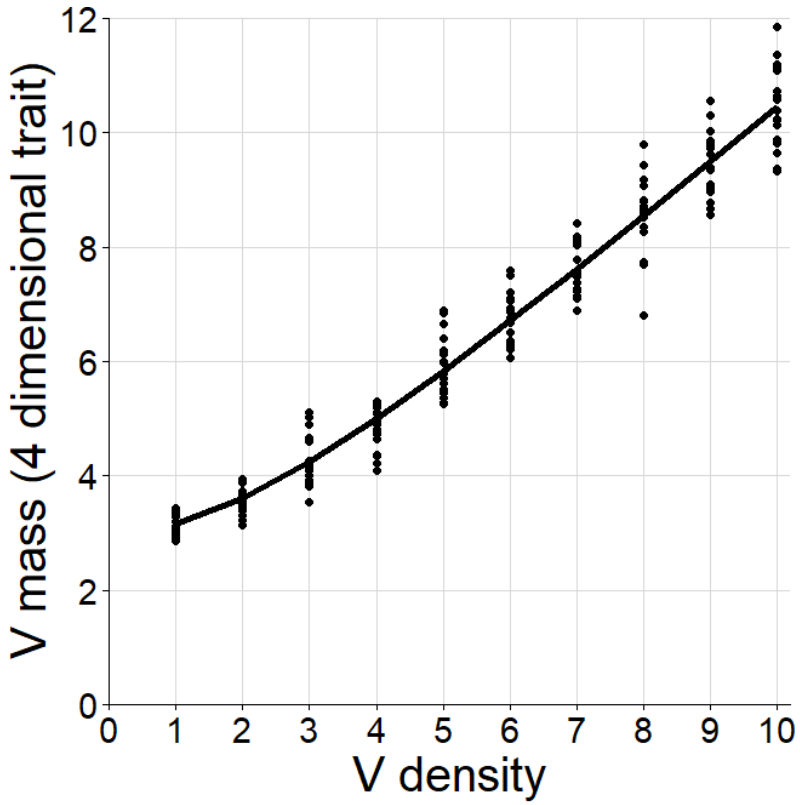

Figure 1: The coefficient of variation in mass relative to the coefficient of variation in density. Here, the variation in mass is caused by the variation in length, height, width and density. The correlation between length, height and width are each 1, while the correlation between one of those and density is 0 for this figure. Variation in density could be larger than variation in length, height and width, and could therefore affect the coefficient of variation of mass differently. On the x-axis is shown how much larger the coefficient of variation of density is compared to that of length, height and width, and on the y-axis the resulting coefficient of variation in mass is shown. The line shows the mathematical prediction as found by equation 3, and the dots show the outcome for simulated data.

in the same manner, e.g. coefficients of variation of condition defined as body mass, coefficients of variation of condition defined as residual body mass, and coefficients of variation of condition defined as fat score should not be compared.

Coefficients of variation of other traits

The issues described above are not restricted to body mass or to morphological traits. The concept of dimensionality as used above and in the formulas of Lande, (1977) is not necessarily limited to physical dimensions. Rather, dimensionality can be interpreted more

Figure 2: The coefficient of variation in mass relative to the correlation between density and the other lower order traits. Here, the variation in mass is caused by the variation in length, height, width and density, and in this figure, it was assumed that density has a coefficient of variation that is five times larger than that of the other lower dimensional traits. The x-axis shows the correlation between density on the one hand, and length, height and width on the other hand. The y-axis shows the resulting coefficient of variation in mass. The line shows the mathematical prediction as found by equation 3, and the dots show the outcome for simulated data.

broadly as the number of underlying traits or sources that contribute to variation in a higher-order trait. This broader interpretation is important because it extends the problem beyond morphology. For many biological traits, the underlying sources of variation may be numerous and difficult to identify. Behavioural traits provide a clear example of this. Variation in behavioural traits likely reflect variation in multiple underlying traits, including morphological, physiological and cognitive traits. However, the number and relative contribution of these traits are often difficult to quantify. Moreover, this could be different for different behavioural traits, and potentially even for the same behavioural trait in different species. Consequently, the dimensionality of behavioural traits may be difficult to interpret, making comparisons of their coefficients of variation potentially problematic, which thus should be done with care.

Conclusion

The coefficient of variation is a useful measure of relative variation, but comparisons of coefficients of variation among traits require careful consideration of the properties of those traits. In particular, we argue that the coefficient of variation of body mass or weight is not a three-dimensional trait, but at least a four-dimensional trait, as density is also important for body mass. Hence, dividing by three to compare the variation in body mass with the variation in one-dimensional traits is not sufficient. More generally, obtaining a good correction factor for a fair comparison is difficult to obtain, and in many cases not attainable. A correction factor would depend on the correlations between all underlying traits and the variation within those traits, which are often hard or even impossible to measure. As has been concluded before by others (e.g. Lande, 1977; Houle, 1992), we reiterate that it is better to not compare coefficients of variation between traits. Moreover, we emphasise that dimensionality in this context does not only refer to physical dimensions. Instead, it can be understood as the number of underlying sources contributing to variation in a higher-order trait. Our considerations are therefore not only relevant for morphological traits, but also for behavioural, physiological, life-history and many more traits. Therefore, we encourage researchers comparing coefficients of variation to consider whether the underlying sources of variation are sufficiently understood to know if their traits have the same dimensionality, and to always interpret differences in coefficients of variation with care.

Data availability

The data to produce our figures will be made available once the manuscript is published.

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References

Albert, C.H., Thuiller, W., Yoccoz, N.G., Soudant, A., Boucher, F., Saccone, P., *et al.* (2010) Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology*, **98**, 604–613.
Chebib, J., Jonas, A., López-Cortegano, E., Künzel, S., Tautz, D. & Keightley, P.D. (2024) An estimate of fitness reduction from mutation accumulation in a mammal allows assessment of the consequences of relaxed selection. *PLOS Biology*, **22**, e3002795.
Currey, J.D., Pitchford, J.W. & Baxter, P.D. (2007) Variability of the mechanical properties of bone, and its evolutionary consequences. *Journal of The Royal Society Interface*, **4**, 127–135.
Demes, B., Jungers, W.L. & Selpien, K. (1991) Body size, locomotion, and long bone cross-sectional geometry in indriid primates. *American Journal of Physical Anthropology*, **86**, 537–547.
Fitzpatrick, S. (1997) Patterns of morphometric variation in birds' tails: length, shape and variability. *Biological Journal of the Linnean Society*, **62**, 145–162.
Garcia-Gonzalez, F., Simmons, L.W., Tomkins, J.L., Kotiaho, J.S. & Evans, J.P. (2012) Comparing evolvabilities: common errors surrounding the calculation and use of coefficients of additive genetic variation. *Evolution*, **66**, 2341–2349.
Gingerich, P.D. & Winkler, D.A. (1979) Patterns of variation and correlation in the dentition of the red fox, *Vulpes vulpes*. *Journal of Mammalogy*, **60**, 691–704.
Hansen, T.F. & Pélabon, C. (2021) Evolvability: a quantitative-genetics perspective. *Annual Review of Ecology, Evolution, and Systematics*, **52**, 153–175.
Hansen, T.F., Pélabon, C. & Houle, D. (2011) Heritability is not evolvability. *Evolutionary Biology*, **38**, 258–277.
Hosken, D.J., Fitzpatrick, J.L., Pizzari, T. & Hodgson, D.J. (2025) On sperm length mean–variance relationships. *Journal of Evolutionary Biology*, **38**, 1548–1555.
Houle, D. (1992) Comparing evolvability and variability of quantitative traits. *Genetics*, **130**, 195–204.
Jacobs, M.W. & Podolsky, R.D. (2010) Variety is the spice of life histories: comparison of intraspecific variability in marine invertebrates. *Integrative and Comparative Biology*, **50**, 630–642.
Komdeur, J., Oorebeek, M., Van Overveld, T. & Cuthill, I.C. (2005) Mutual ornamentation, age, and reproductive performance in the European starling. *Behavioral Ecology*, **16**, 805–817.
Lande, R. (1977) On comparing coefficients of variation, **26**.
Leventhal, S. (2023) Aggregate trait evolvability and macroevolution in two sister species of the bryozoan Stylopoma, **50**, 78–89.
Martínez-Abadías, N., Mitteroecker, P., Parsons, T.E., Esparza, M., Sjøvold, T., Rolian, C., *et al.* (2012) The developmental basis of quantitative craniofacial variation in humans and mice. *Evolutionary Biology*, **39**, 554–567.
McKellar, A.E. & Hendry, A.P. (2009) How humans differ from other animals in their levels of morphological variation. *PLoS ONE*, **4**, e6876.
Michaels, H.J., Benner, B., Hartgerink, A.P., Lee, T.D., Rice, S., Willson, M.F., *et al.* (1988) Seed size variation: magnitude, distribution, and ecological correlates. *Evolutionary Ecology*, **2**, 157–166.

Pearson, K. (1896) VII. Mathematical contributions to the theory of evolution.—III. Regression, heredity, and panmixia. *Philosophical Transactions of the Royal Society of London. Series A*, **187**, 253–318.
Pélabon, C., Hilde, C.H., Einum, S. & Gamelon, M. (2020) On the use of the coefficient of variation to quantify and compare trait variation. *Evolution Letters*, **4**, 180–188.
Simmons, L.W. & Kotiaho, J.S. (2002) Evolution of ejaculates: patterns of phenotypic and genotypic variation and condition dependence in sperm competition traits. *Evolution*, **56**, 1622–1631.
Zulian, V. & Youngflesh, C. (2025) Geography, environmental conditions and life history shape patterns of within-population phenotypic variation in North American birds. *Ecology Letters*, **28**, e70244.