

RESEARCH ARTICLE

Regression dilution in energy management patterns

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ABSTRACT

Analysis of some experimental biology data involves linear regression and interpretation of the resulting slope value. Usually, the x -axis measurements include noise. Noise in the x -variable can create regression dilution, and many biologists are not aware of the implications: regression dilution results in an underestimation of the true slope value. This is particularly problematic when the slope value is diagnostic. For example, energy management strategies of animals can be determined from the regression slope estimate of mean energy expenditure against resting energy expenditure. Typically, energy expenditure is represented by a proxy such as heart rate, which adds substantive measurement error. With simulations and analysis of empirical data, we explore the possible effect of regression dilution on interpretations of energy management strategies. We conclude that unless the coefficient of determination r^2 is very high, there is a good possibility that regression dilution will affect qualitative interpretation. We recommend some ways to contend with regression dilution, including the application of alternative available regression approaches under certain circumstances.

KEY WORDS: Energy expenditure, Heart rate, Metabolic rate, Regression bias

INTRODUCTION

In experimental biology, the results of linear regressions are usually interpreted in terms of whether the relationship differs from the usual null hypothesis of 0, or by predicting values of y from x . Interpretation is less often based on the regression slope value. It is perhaps for this reason that many researchers are not aware of some of the problems arising from bias in linear regression slope estimates, which occurs due to random measurement noise in the x -axis. This bias in slope estimates is termed ‘regression dilution’ or ‘attenuation bias’, and results in an underestimate of the true slope value when the regression slope is calculated using the ordinary least squares (OLS) approach, which assumes that the x -axis values are error free (Frost and Thompson, 2000; Smith, 2009). Regression dilution occurs because lower values of x tend to include a disproportionate number of values that are underestimates while higher values of x tend to include a disproportionate number of values that are overestimates (MacMahon et al., 1990) (for further explanation, see Fig. 1). The result is an increase in the x -value range, serving to spuriously attenuate the slope gradient towards 0. Measurement noise occurs as a result of any variation that causes the observed values to be randomly different to the ‘true’ values (McArdle, 2003), such as inaccuracies during the recording of the x -value variable, sampling error and/or when the x -value variable is being used as a proxy.

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Although some comparative physiologists have highlighted the regression dilution problem (e.g. Green, 2001; Herrera, 1992; LaBarbera, 1989; McNerny and Purves, 2011; White, 2011; White and Kearney, 2014), there is value in revisiting this issue through application to an en vogue subfield of comparative physiology.

An area of comparative physiology for which analysis is based on interpretation of the gradient of linear regression slopes is energy management modelling. The amount of energy that animals can use to fuel their lives is finite and thus we expect animals to be strategic with their energy expenditure. One aspect of this energetics strategy is represented by patterns of energy management, which indicate the broad relationships between the energy an animal spends on ‘background’ processes such as cell growth and immune function against the energy it spends on ‘auxiliary’ processes such as locomotion (Halsey et al., 2019). The slope of the relationship between daily energy expenditure and background energy expenditure provides quick and easy insight into animals’ energy management (Mathot and Dingemanse, 2015; Ricklefs et al., 1996). Slope estimates <1 indicate the constraint pattern of energy management whereby an animal compensates during periods when auxiliary energy expenditure is high by decreasing background energy expenditure, and vice versa, thus constraining daily energy expenditure. A slope estimate of 1 is predicted by the independent pattern whereby variations in auxiliary energy expenditure do not correlate with variations in background energy expenditure (i.e. there is a lack of constraint of energy expenditure). Slope estimates >1 indicate the performance pattern of energy management whereby greater auxiliary energy expenditure is associated with greater background energy expenditure. For a visual representation of this explanation, see Fig. 2. Hence, this analytical process for categorising energy expenditure into one of three management strategies based on the relationship between daily and background energy expenditure is reliant on interpreting the gradient of the linear regression line. However, the x -value variable in analyses of energy management patterns from linear regression is prone to multiple sources of noise, particularly when a proxy for energy expenditure, such as heart rate, has been measured (Portugal et al., 2016).

These interpretations of slope estimates can strongly influence how we perceive animals respond to variations in their daily activity levels. For example, where the slope estimate <1 , animals appear to be trading off the energy they expend on background metabolic costs with that which they expend on auxiliary costs, indicating a clear limit to their energy expenditure. In the case of humans, if they exhibit the constraint pattern then prescribed increases in exercise may be less effective at reducing weight than currently presumed; this is particularly pertinent for modern-living human populations in the midst of an obesity epidemic. It is therefore important that the slope estimates are accurate, yet the phenomenon of regression dilution may be causing inaccuracies and in turn encouraging a misinterpretation of the data.

We investigated the possibility of regression dilution affecting the slope estimates interpreted in the context of energy management

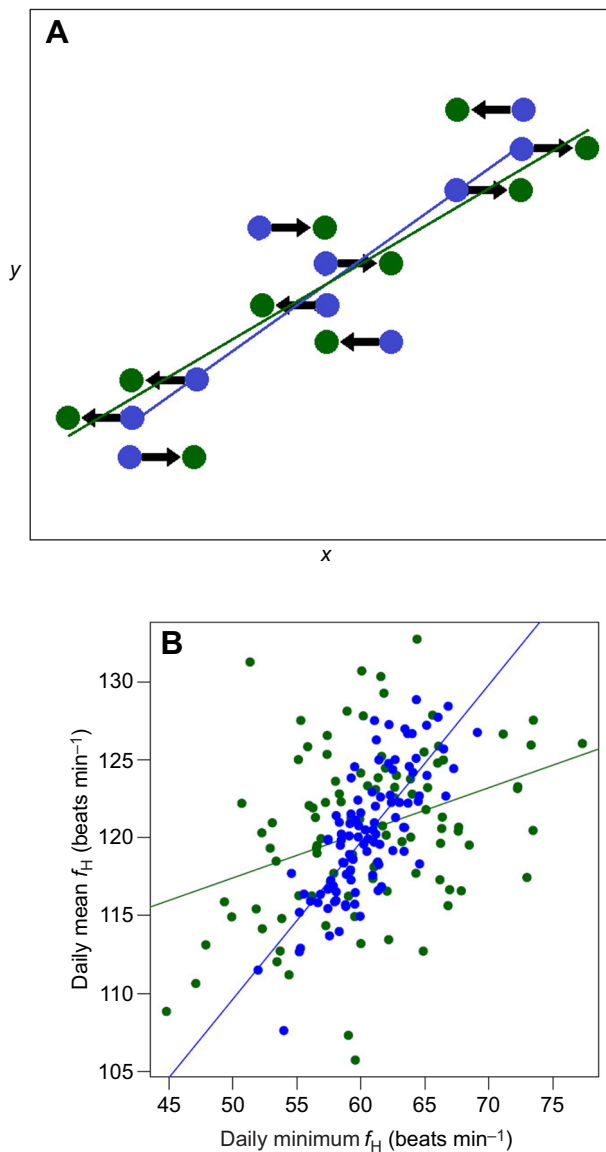


Fig. 1. Regression dilution. Regression dilution arises as a consequence of measurement noise in the x -axis variable and results in an attenuation of the regression line towards 0, which is depicted visually as the line flattening out. (A) Where values of x are measured without noise ('true values'; blue circles), ordinary least squares (OLS) regression returns the regression represented by the blue line. Where values of x include random noise, then the 'observed values' are different to the true values (denoted by each blue circle moving in the direction shown by its associated arrow to positions on the x axis represented by green circles). While the mean of the central x values tends to remain stable in the presence of random noise, because of the cancelling out of under-measured and over-measured data points, this is not the case at particularly low or high values. Particularly low observed values of x are either truly low values or have been under-measured; the latter are not cancelled out by even lower true values that are over-measured, because such extremely low true values do not exist in the population. The reciprocal is true for particularly high observed values of x . This results in an extended range of x values (the range of the green circles is greater than the range of the blue circles) and consequently the OLS regression returns a flatter line (lower slope estimate; green line, fitted through the green circles). (B) A simulation of ecologically valid heart rate (f_H) data, presented as daily mean heart rate against daily minimum heart rate. The blue data points represent noise-free values, and the blue line represents the OLS regression of those data. The green data points represent the same data but with measurement noise induced to the x -axis variable (daily minimum heart rate); the green line represents the equivalent regression. Note that the x -axis range of the green data points is greater while the y range is unchanged, and thus the regression has an attenuated slope.

patterns by: (1) running simulations of ecologically valid randomised samples of heart rate measurements to elucidate how different levels of measurement noise variance affect the slope estimate; and (2) revisiting some of the data presented in Halsey et al. (2019) and comparing the slope estimates of simple linear regressions fitted to those data by different approaches, and then quantifying how the strength of the relationship appears to relate to the degree of regression dilution.

MATERIALS AND METHODS

Four approaches to linear regression were applied in the analyses of the present study: ordinary least squares, OLS; and three major axis approaches: major axis, MA; standard major axis, SMA; and ranged major axis, RMA (note this is not reduced major axis regression). While the OLS approach assumes that measurement noise only exists in the y -axis values, major axis approaches accept measurement noise in both axes, but each approach assumes different ratios in the magnitude of that noise between y and x (Legendre and Legendre, 1998; Quinn and Keough, 2002). This ratio is termed lambda (λ), and thus in the current study lambda is calculated as the ratio of measurement noise in daily mean heart rate and measurement noise in daily minimum heart rate.

Through analysis of both simulated data and empirical data, we investigated the regression dilution caused by different values of lambda. The analyses were conducted in R v.3.4.0, and the various regression approaches were applied using the package `lmodel2()`.

Simulations

To investigate the effects of different measurement noise ratios of daily mean heart rate and daily minimum heart rate (lambda), simulations were run involving 1000 iterations of datasets generated to represent ecologically valid ranges of heart rate values (beats min^{-1}). Each iteration was based on 100 values of daily mean heart rate, each associated with a value of daily minimum heart rate. Daily minimum heart rate values were randomly drawn from a distribution with mean 60 and standard deviation between 0 and 5 (see below). Daily mean heart rate is the summation of daily minimum heart rate and daily auxiliary heart rate (Halsey et al., 2019); thus, 100 values of daily auxiliary heart rate were generated by drawing randomly from a distribution also with mean 60 and standard deviation 3. This process provided 100 values of true (i.e. without measurement noise) daily mean heart rate and daily minimum heart rate generated according to the independent energy expenditure pattern (no correlation between the two variables). Measurement noise was induced into the values of daily mean heart rate by randomly drawing values of noise from a normal distribution of mean 0 and standard deviation 3. Measurement noise was induced into the values of daily minimum heart rate also by randomly drawing from a normal distribution of mean 0; however, the magnitude of the standard deviation was varied for each simulation in order to affect lambda.

Six simulations were run, the first with a standard deviation for the distribution of daily minimum heart rate of 0, and each subsequent simulation incorporating a unitary increase in that value, producing lambda values for each simulation of infinity (∞), 3, 1.5, 1, 0.75 and 0.6. For each iteration of each simulation, daily mean heart rate was regressed against daily minimum heart rate using four approaches to linear regression. By plotting each simulation separately and including the average slope estimates across all iterations, along with the average correct value across all iterations (very close to 1), it is possible to infer which approaches to the regression of daily mean heart rate against daily minimum heart rate are most accurate at various values of lambda.

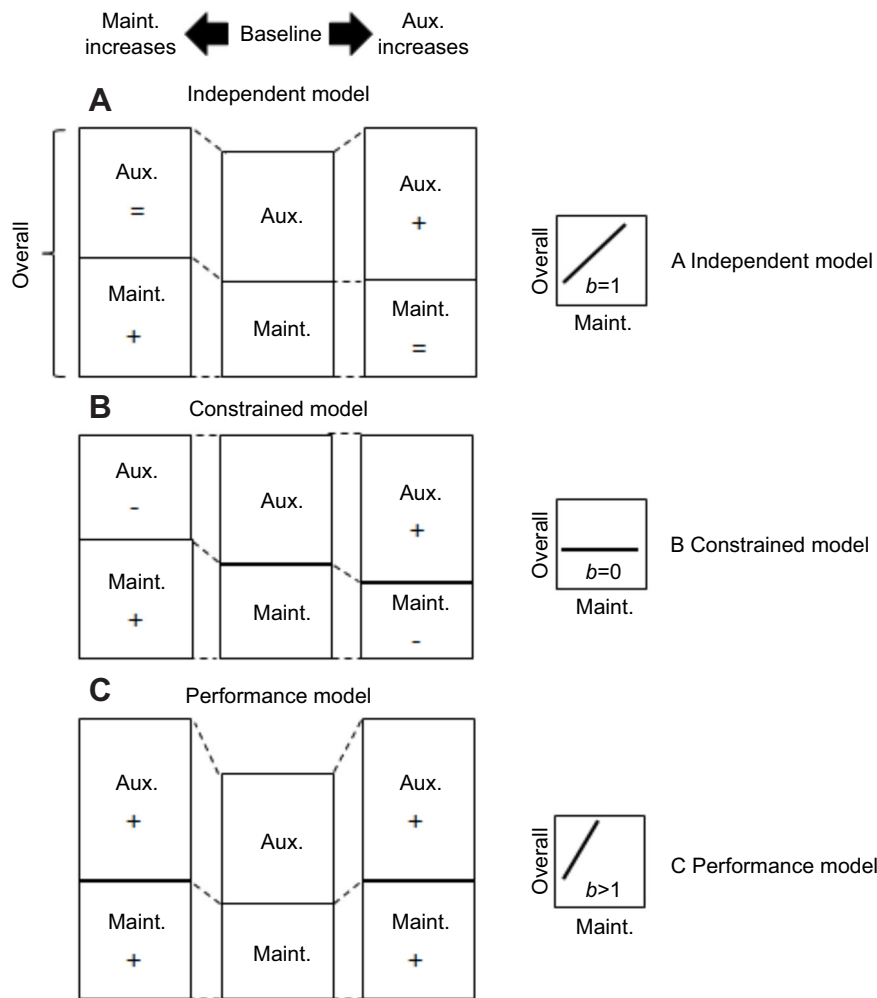


Fig. 2. Hypothetical representations of three energy management patterns. Modified from Careau (2017), where a full explanation is given. Comparing the middle versus right stacks shows the effect of an increase in auxiliary energy expenditure on daily energy expenditure and maintenance energy expenditure. Comparing the middle versus left stacks shows the effect of an increase in maintenance energy expenditure on daily energy expenditure and auxiliary energy expenditure. The right-hand panel shows the predicted relationship between daily energy expenditure and maintenance energy expenditure, along with the predicted slope (b) of the relationship, as suggested by Mathot and Dingemans (2015). (A) The independent pattern, where maintenance and auxiliary energy expenditure are independent of each other. (B) The constrained pattern, where increases in maintenance energy expenditure are associated with decreases in auxiliary energy expenditure and vice versa. (C) The performance pattern, defined by increases in maintenance energy expenditure in response to increases in auxiliary energy expenditure and vice versa.

Empirical data

Empirical data were taken from the dataset presented in Halsey et al. (2019), which represents daily mean and minimum heart rate values for multiple individuals of each of 16 vertebrate species. To account for temporal autocorrelation in the data, for each species the dataset was reduced to every fifth data point. Certain species were then removed from the dataset because of typically small sample sizes per individual. For the remaining 11 species (represented by 12 datasets), a single individual was randomly selected (with the stipulation that the selected individual represented at least 20 data points, which is arguably important for SMA regression; Jolicoeur, 1990) and daily mean heart rate was linearly regressed against daily minimum heart rate using the four regression approaches stated above. This process resulted in a single coefficient of determination (r^2) value and slope estimate calculated from each regression approach per species. Finally, to investigate whether the correlations between daily mean heart rate and daily minimum heart rate with lower r^2 values are subjected to greater regression dilution, the difference between the OLS slope estimate and each of the major axis fitted slope estimates was regressed against r^2 .

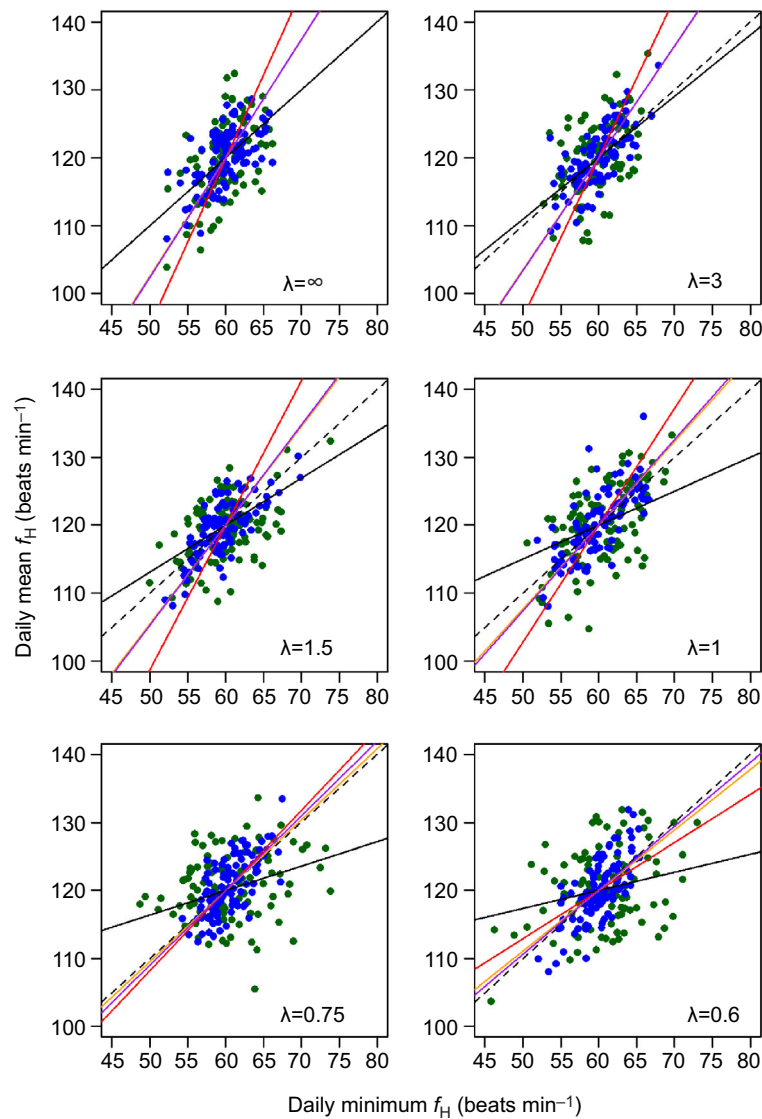
RESULTS

Simulations

The outputs from the six simulations are presented in Fig. 3, in both graphical and tabulated forms. When there is no noise in the

measurements of daily minimum heart rate (the x -axis variable), $\lambda = \infty$ and the strength of the correlation (measured by r^2) is high, as would be expected. As the measurement noise in the x -axis variable is increased (and λ decreases), r^2 decreases. While all four regression approaches exhibit a decrease in slope estimate as λ decreases, thus arguably all showing regression dilution, different regression approaches provide the most accurate slope estimate at different λ values.

When $\lambda = \infty$, the OLS slope estimate is almost identical to the correct slope of 1. The other regression approaches (MA, SMA and RMA) all return substantially greater slope estimates. The case is similar at $\lambda = 3$, where the noise variance in the measures of daily minimum heart rate is one-third the magnitude of the noise variance in the measures of daily mean heart rate. At $\lambda = 1.5$, all major axis regression approaches somewhat overestimate the slope while OLS somewhat underestimates it. At $\lambda = 1$, indicating the same magnitude of noise variance in the two heart rate variables, OLS no longer provides the most accurate slope estimate, and SMA and RMA are both quite close to the true value of 1. In the last two simulations, where the noise variance in daily mean heart rate is larger than the noise variance in daily minimum heart rate ($\lambda = 0.75$ and 0.6), all three major axis regression approaches provide at least reasonably accurate slope estimates while OLS returns a considerable underestimate. In all simulations, the MA approach provides a less accurate slope estimate than either SMA or RMA.



λ	OLS slope	MA slope	SMA slope	RMA slope	r^2
∞	1.00	2.46	1.74	1.75	0.57
3	0.88	2.34	1.63	1.65	0.54
1.5	0.69	2.14	1.45	1.47	0.48
1	0.50	1.72	1.23	1.28	0.41
0.75	0.37	1.14	1.03	1.08	0.35
0.6	0.26	0.70	0.89	1.61	0.30

Empirical data

The r^2 value for the regression of each single individual representing each species, along with the simple linear regression slope estimate determined by each regression approach, is presented in Table 1. r^2 was typically high (>0.7 for 8 of the 11 datasets), suggesting that the correlation between daily mean heart rate and daily minimum heart rate is often strong for these types of data. For every species, the slope estimate calculated from the OLS regression approach was lower than the slope estimate calculated for all of the major axis approaches. The difference between the OLS slope estimate and each of the major axis slope estimates covaried negatively with the r^2 value of the relationship (Fig. 4).

Fig. 3. The ratio of noise variance in daily mean heart rate to noise variance in daily minimum heart rate (lambda) influences which regression approach provides the most accurate slope estimate. Each panel represents a different value of lambda. The blue data points represent the true values of daily mean heart rate (f_H) and daily minimum f_H , while the green values represent the observed values, i.e. including measurement noise. Note that where lambda is greater than 0, noise variance is present in the x-axis and this results in the range of observed values of the x-variable (daily minimum f_H) being greater than the range of true values. The dashed line (slope=1 in every panel) represents the correct slope value for the true dataset. Each full line represents the slope estimate returned by each of the regression approaches (black: OLS; red: major axis, MA; orange: standard major axis, SMA; purple: ranged major axis, RMA). The mean slope estimates and coefficient of determination (r^2) for each value of lambda plotted are tabulated below the panels. All data presented are means of 1000 iterations.

DISCUSSION

The energy management patterns exhibited by animals can be inferred from the slope estimates of linear regressions between daily mean heart rate and daily minimum heart rate. The present study examined how noise variance in heart rate measures could affect the accuracy of these regression slope estimates.

The simulations (Fig. 3) show that when the noise variance in daily minimum heart rate is either non-existent or at least low compared with the noise variance in daily mean heart rate (thus lambda is high), OLS regression provides an accurate slope estimate; there is no appreciable regression dilution. This slope estimate is more accurate than the estimates returned from

Table 1. r^2 and slope estimates calculated from the simple linear regression fits, for daily mean heart rate against daily minimum heart rate of single individuals from a range of vertebrate species

Species	r^2	OLS	MA	SMA	RMA	Mean MA	n
Barnacle goose	0.77	1.02	1.18	1.16	1.16	1.17	73
Greylag goose	0.72	0.74	0.85	0.87	0.86	0.86	79
Great cormorant	0.23	0.69	2.06	1.45	1.37	1.63	21
Australasian gannet	0.47	1.09	1.9	1.58	1.54	1.67	40
Little penguin	0.64	0.97	1.28	1.22	1.24	1.25	39
Macaroni penguin	0.77	1.09	1.28	1.24	1.25	1.26	56
Eider duck	0.26	0.48	0.88	0.93	1.08	0.96	42
Przewalski's horse	0.95	1.04	1.07	1.07	1.07	1.07	41
Alpine ibex	0.8	1.46	1.71	1.63	1.65	1.66	31
Red deer (dataset 1)	0.93	0.97	1.01	1.01	1.01	1.01	95
Red deer (dataset 2)	0.82	1.19	1.35	1.31	1.33	1.33	122
Roe deer	0.71	1.32	1.7	1.57	1.49	1.59	25
Mean	0.67	1	1.36	1.25	1.25	1.29	55.3
1 s.e.m.	0.02	0.02	0.03	0.02	0.02	0.02	2

OLS, ordinary least squares; MA, major axis; SMA, standard major axis; RMA, ranged major axis. Mean MA is the mean of the MA, SMA and RMA values.

other regression approaches, which overestimate. However, once the noise variance in daily minimum heart rate is at least as large as that in daily mean heart rate (i.e. $\lambda < 1$), the OLS slope estimate attenuates considerably, thus becoming an inaccurate underestimate, while in contrast certain other regression approaches provide an accurate slope estimate. This is to be expected because whereas OLS regression assumes that the y -axis variable, but not the x -axis variable, is measured with noise (Quinn and Keough, 2002), the various major axes regression approaches (MA, SMA, RMA) accept noise in both variables (Herrera, 1992).

There is of course noise in real measurements of daily minimum heart rate, and thus $\lambda \neq \infty$. Lambda might be estimated at ~ 1 as both daily mean and minimum heart rate are likely to incur the same forms of measurement noise: measurement technique imperfections, sampling variation and being used as a proxy for energy expenditure (but see Smith, 2009). Moreover, minimum heart rate possibly has even greater noise variance than mean heart rate because while estimates of mean heart rate remain centred on the real value independently of the sample used for the estimation, estimates of minimum heart rate are affected by the duration of time over which minimum heart rate is calculated. The simulations indicate that if indeed $\lambda \approx 1$ or $\lambda < 1$, OLS is not a viable regression analysis for interpreting energy management patterns.

Regression dilution will be greater when the r^2 value is smaller, because measurement noise is here defined as any deviation from a perfect fit between the y - and x -variables (Smith, 2009). This phenomenon was confirmed by the simulations, and we also showed this in the empirical heart rate datasets (Fig. 4); a higher r^2 value for a species is associated with a higher slope estimate calculated using OLS regression. This suggests that lambda is sufficiently low in some of these regressions that regression dilution is clearly apparent. Of course, we do not know the true value of each regression slope of empirical data. However, comparing the reduction in the OLS slope estimate with the three other regression approaches (Fig. 3), it appears that when $r^2 > 0.8$ the difference in slope estimate is minimal (< 0.1), while r^2 values of around 0.6 have a slope estimate difference of around 0.3, and substantially smaller r^2 values have differences that are considerably larger.

How might regression dilution affect previous reports of energy management based on analysis of the regression slope estimate of daily mean heart rate against daily minimum heart rate? Here, we consider three published papers as brief case studies.

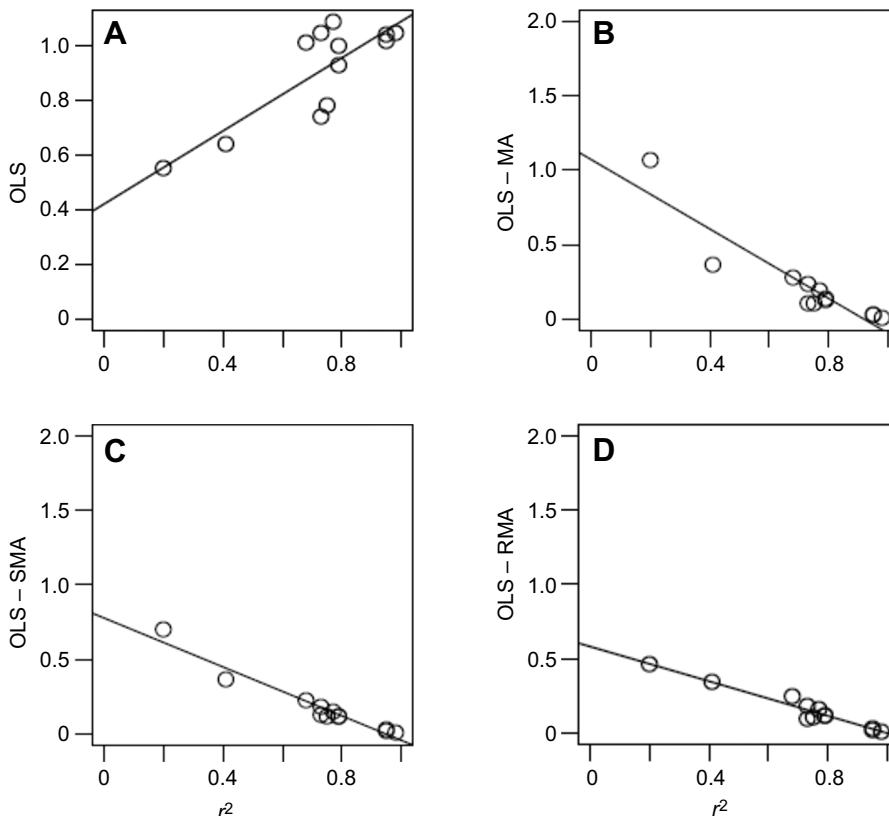


Fig. 4. Regression dilution of single linear relationships between daily mean f_H and daily minimum f_H of empirical multi-species data increases as r^2 of the relationship decreases. This is evidenced by (A) the positive relationship between OLS slope estimate and r^2 , and also by the negative relationships between the difference in slope estimate calculated using OLS simple linear regression and a major axis method (B: MA; C: SMA; D: RMA).

Vézina et al. (2006) report a slope of 1.1 for captive, non-breeding zebra finches, with an r^2 for the OLS regression of 0.35. This relatively low r^2 value might suggest that the true slope value is somewhat higher than 1.1, which in turn could move interpretation of the energy management pattern exhibited by these birds from an independent pattern to a performance pattern. Careau (2017) reports that people training for a half-marathon exhibit an among-individuals slope of 2.60 ($r^2=0.39$). Again, this r^2 value is sufficiently low that we might be concerned the analysis includes a substantial degree of regression dilution. However, in this case, the qualitative interpretation made of the slope estimate is perhaps unlikely to be affected because the among-individuals slope is already $\gg 1$ (performance pattern).

Third, Halsey et al. (2019) argue that the species they analysed predominantly exhibit either the independent (slope=1) or performance (slope>1) pattern at the across-individuals level; the evidence for this claim would be strengthened if regression dilution was not present as slope estimates would be higher. They also suggest that at the within-individual level there is a general tendency for species to exhibit an element of the compensation pattern (slope<1). For some species this interpretation is likely to be robust as the r^2 values associated with the slope estimates are very high (e.g. red deer, $r^2=0.96$; grey seals, $r^2=0.83$; Halsey et al., 2019). For other species, however, where the r^2 values are relatively low, regression dilution might falsely indicate that individual animals are exhibiting an element of energy compensation (e.g. Australasian gannets, $r^2=0.40$; human beings, $r^2=0.64$; Halsey et al., 2019). Halsey et al. (2019) also make the claim that there is generally a 'left shunt' in slope estimates from the across-individuals level to the within-individual level (see fig. 3 in Halsey et al., 2019). This observation should be robust because the slope estimate confidence intervals are always larger at the across-individuals level (and hence measurement noise is greater), suggesting that the regression dilution is probably attenuating the size of this left shunt. Finally, the regression dilution in these analyses did not hide the insightful negative correlations found between slope value and mean heart rate per month (see fig. 3 in Halsey et al., 2019), which suggest that species exhibit more energetic constraints during periods when daily energy expenditure is higher.

How should we conduct energy management regressions?

It is not the case that OLS should be substituted for an alternative approach simply because daily minimum heart rate includes noise variance. If the noise variance associated with daily minimum heart rate is fairly small compared with the daily mean heart rate noise variance (i.e. lambda is large), our simulations confirm the advice of McArdle (1988) that OLS is appropriate (see also White, 2011). Smith (2009) argues it is usually the case in regression analyses of biological data that lambda is large. In turn, he suggests that OLS is appropriate when the x -variable is thought to be affecting the y -variable, which is indeed the case in regressions of daily mean heart rate against daily minimum heart rate. However, at low r^2 values, OLS can underestimate the slope considerably; indeed, low slope estimates associated with a low r^2 are suggestive of an inappropriate regression model (LaBarbera, 1989). Yet, in this situation, major axes methods can overestimate the slope (Fig. 3; see also Kimura, 1992). Unfortunately, for datasets associated with energy expenditure such as heart rate or rate of oxygen consumption, the noise associated with measurement inaccuracies, with the use of these variables as proxies of energy expenditure and given that sampling is always imperfect, cannot easily be quantified. Therefore, it is difficult to ascertain whether lambda is sufficiently large that OLS is a better approach than other methods (Smith, 2009). Based on the simulation results,

and in agreement with McArdle (1988), one rule of thumb worth considering, however, is that if the major axis approach is taken then SMA or RMA may provide more accurate slope estimates than MA.

Where the slope estimate is the focus of data interpretation and r^2 is anything less than very high, researchers are advised to consider presenting their data using more than one regression approach. However, modelling approaches more complicated than single linear regression are usually based on OLS (Smith, 2009). In these situations, we would suggest that some simple linear regressions are also conducted, using a range of fitting approaches, to gain some insight into the potential impact of regression dilution on the slope estimates.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: L.H.; Methodology: L.H.; Software: L.H., A.P.; Validation: A.P.; Formal analysis: L.H., A.P.; Investigation: L.H.; Data curation: L.H.; Writing - original draft: L.H.; Writing - review & editing: L.H., A.P.

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