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Of Uberfleas and Krakens:
Detecting Trade-offs Using Mixed Models

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Synopsis

All animals experience performance trade-offs as they complete tasks such as capturing prey, defending territories, acquiring mates, and escaping predators. Why then, is it so hard to detect performance trade-offs at the whole-organismal level? Why do we sometimes even obtain positive correlations between two performance traits that are predicted to be negatively associated? Here we explore two plausible explanations. First, most analyses are based on individual maximal values (i.e., personal best), which could introduce a bias in the correlation estimates. Second, phenotypic correlations alone may be poor indicators of a trade-off when contrasting processes occur at the among- vs. within-individual levels. One such scenario is the "big houses big cars" model developed in life-history theory to explain the existence of "uberfleas" that are superior in all regards (because they acquire more resources than others). We highlight that the exact opposite scenario might occur for performance trade-offs, where among-individual trade-offs may be masked by within-individual changes in physical condition. One of the best ways to test the alternative scenarios is to collect repeated pairs of performance traits and analyse them using multivariate mixed models (MMMs). MMMs allow straightforward and simultaneous examination of trait correlations at the among- and within-individual levels. We use a simple simulation tool (SQuID package in R) to create a population of Krakens, a mythical giant squid-like sea creature whose morphology generates a performance trade-off between swimming speed and ability to sink ships. The simulations showed that using individual maximum values introduces a bias that is particularly severe when individuals differ in the number of repeated samples (n_{trial}). Finally, we show how MMMs can help detect performance (or any other type of) trade-offs and offer additional insights. We hope researchers will adopt MMMs when exploring trade-offs in whole-animal performances.

Why are whole-organism performance trade-offs so hard to detect?

The concept of trade-offs is key to many research fields such as evolutionary biology, physiology, behavioral ecology, and functional morphology (Agrawal and others 2010; Garland 2014). Performance trade-offs occur when characteristics that enhance one aspect of performance necessarily decrease another type of performance. For example, greater proportions of slow-twitch oxidative muscle fibers should enhance stamina, whereas more fast-twitch glycolytic fibers would facilitate sprinting abilities (Dohm and others 1996; Garland 1988; Sorci and others 1995). The mechanistic bases of many performance trade-offs are well described and accepted (Esbjornsson and others 1993; Komi 1984; Wilson and James 2004; Wilson and others 2004). Yet evidence for their existence at the whole-animal level is far from convincing (Ford and Shuttlesworth 1986; Garland 1988; Garland and Else 1987; Herrel and Bonneaud 2012; Huey and others 1990; Jayne and Bennett 1990; Sorci and others 1995; Tsuji and others 1989; Wilson and others 2002). Many studies exploring trade-offs at the whole-animal level find that high performers in one task are also high performers in other tasks, or find no trade-off between tasks at all (Garland and Else 1987; Huey and others 1990; Jayne and Bennett 1990; Tsuji and others 1989). Given the intuitive physiological basis of many performance trade-offs, the paucity of studies showing them in whole animals is puzzling.

Among-individual variation in “quality”

Van Damme and others (2002) and Wilson and others (2014) have suggested that individual variation in overall “quality” can mask within-individual trade-offs in performance. Because individuals vary in health, physical fitness, nutrition, developmental stage or genetics, some individuals perform better or worse across all types of performance tasks than others. This means that when researchers try to understand *intra*-individual functional trade-offs using *inter*-individual variation in performance, then trade-offs that do occur within individuals can be masked by among-individual variation in overall "quality" (Lailvaux and Kasumovic 2011). Previous studies have shown that correcting for quality can reveal functional trade-offs between motor tasks such as speed, power, and endurance that would otherwise be missed (Van Damme and others 2002; Wilson and others 2014). However, how to how to unambiguously define and account for quality remains controversial (Walker and Caddigan 2015).

Uberfleas and the "big houses big cars" scenario

The pattern described above is essentially the same as the classic Y-model of life-history evolution in which inter-individual variation in acquisition can mask allocation trade-offs (van Noordwijk and de Jong 1986). In other words, some individuals can circumvent an apparent trade-off in allocation of resources by acquiring more resources. Reznick and others (2000) referred to this situation as the "big houses big cars" scenario: because the resources available for families to spend on both a house and a car are finite, the more a family spends on their car then the less they have available for their house (*vice versa*). However, some families can have both big houses and flashy cars if they have more resources (money) available to them. It is quite easy to see how this situation could apply to animals. For example, limits to energy stores and/or maternal abdominal volume (e.g., Du and others 2005) can yield a trade-off between egg size and number (Roff 1992; Stearns 1992). However, some female "uberfleas" (superior in all regards) may be able to lay many large eggs because they are able to obtain more energy and nutrients and have larger abdominal volume than "unterfleas" (inferior in all regards) (Reznick and others 2000). In such a scenario (Fig. 1A), the relative amount of variance in allocation vs.

acquisition will dictate whether egg size and number are correlated negatively (i.e., trade-off revealed) or positively (inverse of a trade-off) at the phenotypic level (Fig. 1A).

Trade-offs within energy budget

One implication of the “big houses big cars” scenario is that studies based at a single level of variation – or those aggregating repeated measures to reduce the hierarchical nature of the data and facilitate statistical analysis – may fail to detect an association between two traits even when they are connected through processes occurring at different levels and cancelling each other out (Dingemanse and Dochtermann 2013; Downs and Dochtermann 2014). This situation is illustrated by a recent re-analysis of data in humans, where individuals differed in their total energy intake, but nevertheless had to allocate energy to maintenance vs. locomotor activity (Fig. 2, taken from Careau (2017)). Westerterp and others (1992) collected data on sedentary men and women between the ages of 28–41 years old as they followed a training program to run a half marathon (four sessions per week, increasing running time to 10-30 min, 20-60 min and 30-90 min per training session after 8, 20 and 40 weeks respectively). Westerterp and others (1992) quantified energy intake (self-reported) and basal metabolic rate (respirometry) on four occasions for each individual. Reanalysis of this dataset using multivariate mixed models revealed that while surplus energy intake and basal metabolic rate tended to be positively correlated at the among-individual level, there was a negative correlation at the within-individual level (Fig. 2).

Reverse scenario: trade-offs at the among-individual level

In general, it is intuitive to think of allocation trade-offs as processes occurring *within* individuals. In the case of performance trade-offs, however, one may expect situations in which trade-offs occur *among* individuals (Fig. 1B). For example, if individuals consistently differ in many morphological (e.g., gear ratio) and physiological (muscle fiber types) traits that enhance their performance in certain tasks (e.g., speed) while hindering performance in others (e.g., endurance), then the trade-off should be apparent at the among-individual level (Fig. 1B). We may also intuitively expect that within-individual changes in general physical condition will simultaneously affect all performance traits, thus generating positive correlations among performance traits within individuals (Fig. 1B). Although this scenario is the exact opposite as the “big houses big cars” scenario, we argue it is equally likely in the case of performance trade-offs. We refer to this scenario as the “sink or swim” scenario (explained below).

How to detect trade-offs?

When contrasting processes occur at the among- vs. within-individuals, how should one go about verifying the presence of a trade-off? To ensure one does not miss out on information regarding the alternative “big houses big cars” (Fig. 1A) and “sink or swim” (Fig. 1B) scenarios, we suggest the best strategy is to use multivariate mixed models (MMMs). Otherwise, it is likely that the calculated phenotypic correlation (r_P) will be a poor indicator of the presence of trade-offs (Fig. 3). We argue that the use of r_Ps calculated on individual maximum values – rather than using MMMs – is one of the reasons that whole-animal performance trade-offs are rarely detected, and even spurious positive correlations are sometimes obtained.

Simulating a performance trade-off in a legendary sea monster

We used the SQuID package in R (Allegue and others 2017) to simulate a population of 100 individual organisms that experience a trade-off between two performance traits. We used the legendary giant squids known as Krakens (https://en.wikipedia.org/wiki/Kraken) for our simulation. Krakens are mythical creatures, which live off the coast of Norway, made famous in various fictional works that depict them attacking ships at sea. Let us for a moment imagine that Krakens experience a trade-off between swimming speed and their ability to sink a ship and swallow all the seamen (hence the “sink or swim” scenario). We expect this trade-off is related to an individual’s size and shape; such that slimmer squids can swim faster while bulkier squids can overpower ships. This trade-off occurs at the among-individual level as depicted by the black dots and lines in Fig. 3A. Moreover, we simulated a positive relationship between speed and strength occurring within individuals, as depicted by thin lines in Fig. 3A. This positive relationship occurring within individuals could be due to correlated plasticity as function of variation in an unknown factor (e.g., temperature, age, and training). Now imagine we can only catch a Kraken once in its lifetime to obtain a single measure of speed and strength for each individual (n_{trial}=1). Only a single measure per animal would yield a random sample like in Fig. 3B, in which the phenotypic correlation (r_{P}) is not significantly different from zero even at N=100. This is because the r_{P} reflects a mixture of the processes occurring at the among- and within-individual levels (like in Fig. 1B).

Phenotypic correlations based on average values

Had one access to all 20 repeated measures of performances for each Kraken, how should one go about verifying if there is a trade-off as simulated? One easy solution is to calculate r_{P} based on the individual mean values, which has the advantage of facilitating statistical analysis by reducing the hierarchical nature of the data. Although this approach proves effective at detecting the trade-off (Fig. 3C), the r_P based on individual mean values tend to be attenuated (i.e., biased toward zero). As pointed out by Head and others (2012), it has been known since Spearman (1904) that attenuation is proportional to within-individual variance (as in here) and measurement error (assumed to be 5% here).

Phenotypic correlations based on maximum values

An alternative approach to analysing the data would be to select the best performance for each individual among the 20 measurement trials and then calculate r_P on the resulting 100 "personal best" samples. However, due to the undesirable properties of the sampling distribution of extreme values (Head and others 2012), maximum values can actually conceal performance trade-offs (Fig. 3D). Surprisingly still, retaining individual maximum values is common practice in studies of organismal performance (Adolph and Pickering 2008).

Multivariate mixed models to the rescue

To obtain an unbiased estimate of the strength of the "sink or swim" trade-off in Krakens, we need to quantify the among-individual correlation (r_{ind}) separately from the within-individual (or residual) correlation (r_e). Whenever two traits are repeatedly measured for a set of individuals, we can estimate r_{ind} and r_e in one step using MMMs (Dingemanse and Dochtermann 2013). MMMs are now relatively easy to learn thanks to several "how to" papers (Dingemanse and Dochtermann 2013; Roche and others 2017) and widely available software like ASReml (Butler and others 2009), SAS, and the R package MCMCglmm (Hadfield 2010). Using a MMM we successfully detected the trade-off as indicated by the negative r_{ind} (-0.41±0.09), which is close to the simulated value of -0.5.

Implications of a within-individual correlation

We generated a positive r_e by simulating an environmental gradient that simultaneously affected both speed and strength, and assumed the environmental factor was unknown. Such a factor could be temperature, for example, as it could positively affect both speed and strength. Another factor could be age (Krakens can live up to 100 years and become terrible sea creatures as they grow and get both faster and stronger). By modelling random intercepts only, individual (co)variation in plasticity ended up in the r_e (Brommer 2013a), which was 0.43±0.02. To fully capture the among-individual correlation in phenotypic plasticity of speed and strength, we must run a bivariate random regression model [see Careau and others (2014) for a recent application of this method for detecting correlated thermal sensitivities]. A bivariate random regression model would capture correlated plasticity and model it separately from the residuals, which should yield a r_e close to zero (unless there is correlated measurement error). Note that changes in performance in response to training is a form of phenotypic plasticity, such that correlated plasticity would describe a very likely situation in which two or more performance traits increase in response to training.

Magnitude of bias using individual maximum performance

To make a more convincing case against using maximum values – and a more convincing case for using MMMs – we simulated 100 populations of Krakens and tested the 3 methods on each population (MMMs, using individual means, and using individual maxima). Moreover, we tested each method with all 20 repeated measures per individual (equal n_{trial}) and once again after we deleted a randomly varying number of observations for each individual (unequal n_{trial}). As expected, MMMs were not sensitive to variable n_{trial} (Fig. 4). Although mean values yield acceptable r_{P}s in most populations when n_{trial} was equal, there was a clear bias when n_{trial} was unequal among individuals (Fig. 4). Finally, there was a clear bias when using individual maximum values, which was especially severe when n_{trial} is variable among individuals (Fig. 4).

Conclusions

We hope researchers studying performance trade-offs will heed the call made by Adolph and colleagues (Adolph and Hardin 2007; Adolph and Pickering 2008; Head and others 2012), as our simulation exemplifies the magnitude of the bias introduced by using sample maxima. Still, the correction factor developed by Adolph and Hardin (2007) may yield a biaised r_{ind} because it assumes that r_e is zero (Dingemanse and others 2012). As shown by Downs and Dochtermann (2014), this correction factor of Adolph and Hardin (2007) can result in an underestimation of r_{ind} when there is a positive r_e (as in the case in our simulation of speed and strength in Krakens). Thus, researchers should pay greater attention to processes occuring at the within-individual level, such as correlated phenotypic plasticity and correlated measurement error. In the presence of a significant r_e then random regression models can be used to separate potential individual differences in plasticity from the residuals (Brommer 2013a; 2013b). Most importantly, partitionnig performance trade-offs at the within- and among-individual levels is required to discern between scenarios like those occuring in mythical organisms like uberfleas ("big houses big cars"; Fig. 1A) and Krakens ("sink or swim"; Fig. 1B). Finally, we note that while using MMMs to estimate r_{ind} and r_e is informative in its own right, it is only the first step towards identifying genetic and environmental associations among performance traits through larger-scale quantitative genetics studies (e.g., Dohm and others 1996; Garland 1988).

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Supplementary Data

All of the R codes necessary to reproduce these results were made available to editors and reviewers upon initial submission and are available as supplementary material available at ICB online.

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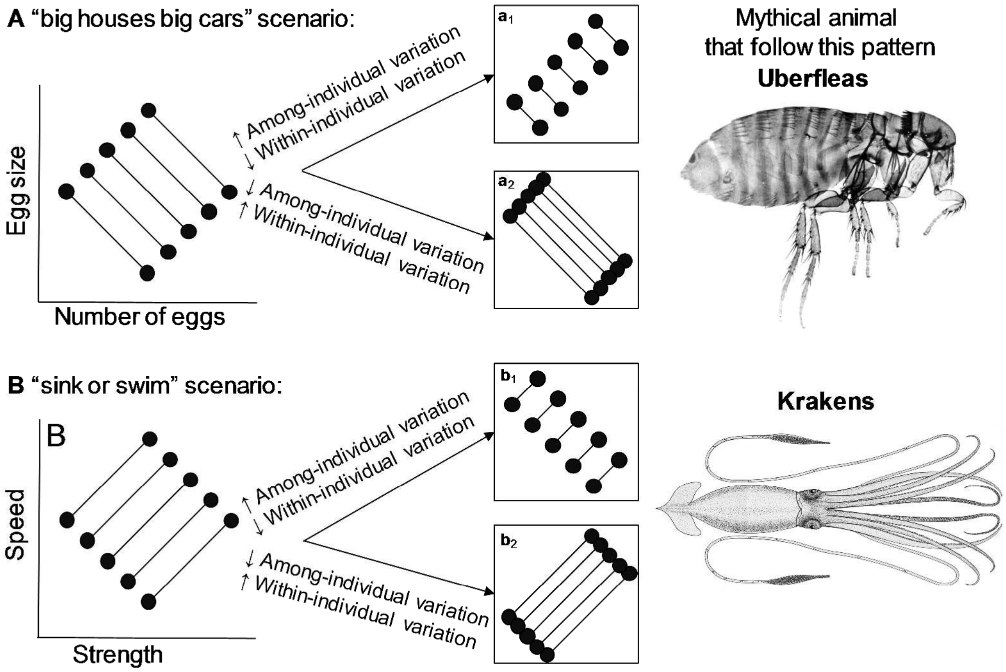

Fig. 1. Schematic representations of trade-offs and facilitation processes simultaneously occurring at the among- vs within-individual levels. (**A**) the classic "big houses big cars" scenario (Reznick and others 2000; van Noordwijk and de Jong 1986) where individuals differ in the amount of resources (energy, time, or space) that they allocate to competing demands (egg size vs. quantity). Repeated pairs of measurements on each individual are represented by dots connected by a line. Thus, some female *uberfleas* appear to always have more resources than others, but on any given reproduction event they nevertheless face the same quantity vs. quality trade-off. Whenever acquisition and allocation processes respectively occur at the among- and within-individual levels, the relative amount of among- vs. within-individual variance in the two traits (i.e., their geometric mean repeatability) will dictate whether the resulting phenotypic correlation will be positive (panel $\mathbf{a}_1$) or negative (panel $\mathbf{a}_2$). (**B**) Another scenario where individuals consistently differ in morphology (e.g., gear ratio) or physiology (e.g., muscle fiber type) such that, on average, strong individuals are slower. However, whenever individuals train to increase their overall physical condition, their performance is enhanced for both strength and speed. Such a situation would yield a negative correlation at the among-individual level (trade-off), but a positive correlation at the within-individual level (training effect), as in the simulated population of Krakens (see Fig. 3 and 4). Because Krakens face a trade-off between swimming speed and the ability to sink ships, we refer to this scenario as the "sink or swim" scenario. Note that Wilson and others (2014) applied the "big houses big cars" scenario (**A**) to performance trade-offs, suggesting that *among*-individual differences in "quality" can mask *within*-individual trade-offs. Here we suggest that the "sink or swim" scenario (**B**) is equally likely to apply to performance trade-offs (i.e., that *among*-individual differences in trade-offs can be masked *within*-individual changes in condition). Multivariate mixed models can be used to test these alternative scenarios and quantify the relative importance of the acquisition vs. allocation processes (see Fig. 2 for an example).

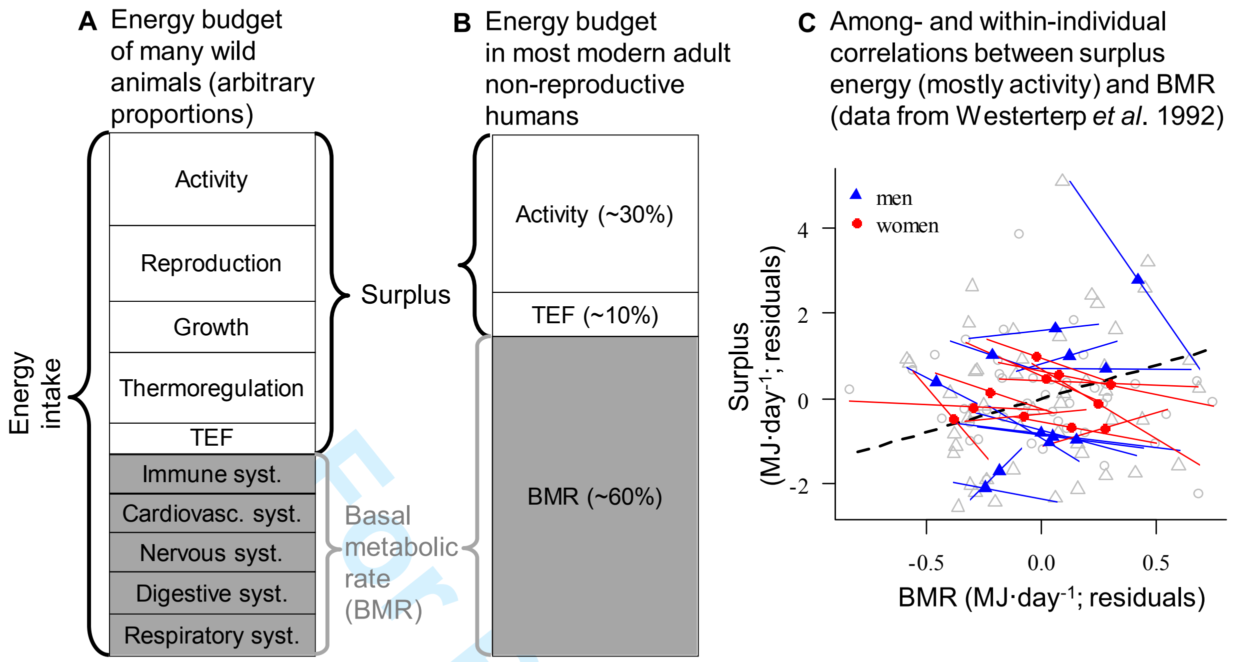

Fig. 2. Trade-offs among and within energy budgets. (**A**) Representation of the total energy intake of most wild animals as the sum of the energy invested in locomotor activity, reproduction, growth, thermoregulation, digestion (thermic effect of food; TEF), and basal metabolic rate (BMR). BMR represent the minimum amount of energy required for the functioning (e.g., breathing) and the maintenance (e.g., tissue turnover) of maintain vital systems. Proportions are arbitrary and can change depending on the age, season, and life-history stage of animals. Any source of energy expenditure above BMR can be grouped into the "surplus energy". (**B**) Energy budget in most modern non-reproductive adult humans, in which there are no cost of growth and reproduction. The cost of thermoregulation is assumed to be negligible (people wearing appropriate clothing at room temperature do not have any extra energy expenditure to maintain body temperature). In this simplified energy budget, a large proportion (~60%) is taken BMR and most of the surplus energy is devoted to activity. (**C**) Among- and within-individual correlations between surplus energy and BMR in 12 and 11 adult men (triangles) and women (circles) measured 4 times each during a long-term training program in preparation for running a half marathon [data from Westerterp and others (1992) and figure taken from Careau (2017)]. BMR and surplus energy are shown as residuals (open symbols) from multiple regression models including several fixed effects (testing sequence, age, sex, body mass, and fat mass). Solid symbols indicate the mean residual values for each individual, and the thick black line illustrates the positive *among*-individual relationship. Thin lines show separate linear regression for each individual, thus illustrating the *within*-individual relationship. A bivariate mixed model applied to these data revealed a positive among-individual correlation (0.49±0.27; $P = 0.113$) and a negative within-individual correlation (-0.32±0.11; $P = 0.007$), providing support for a "big houses big cars" scenario depicted in Fig 1A.

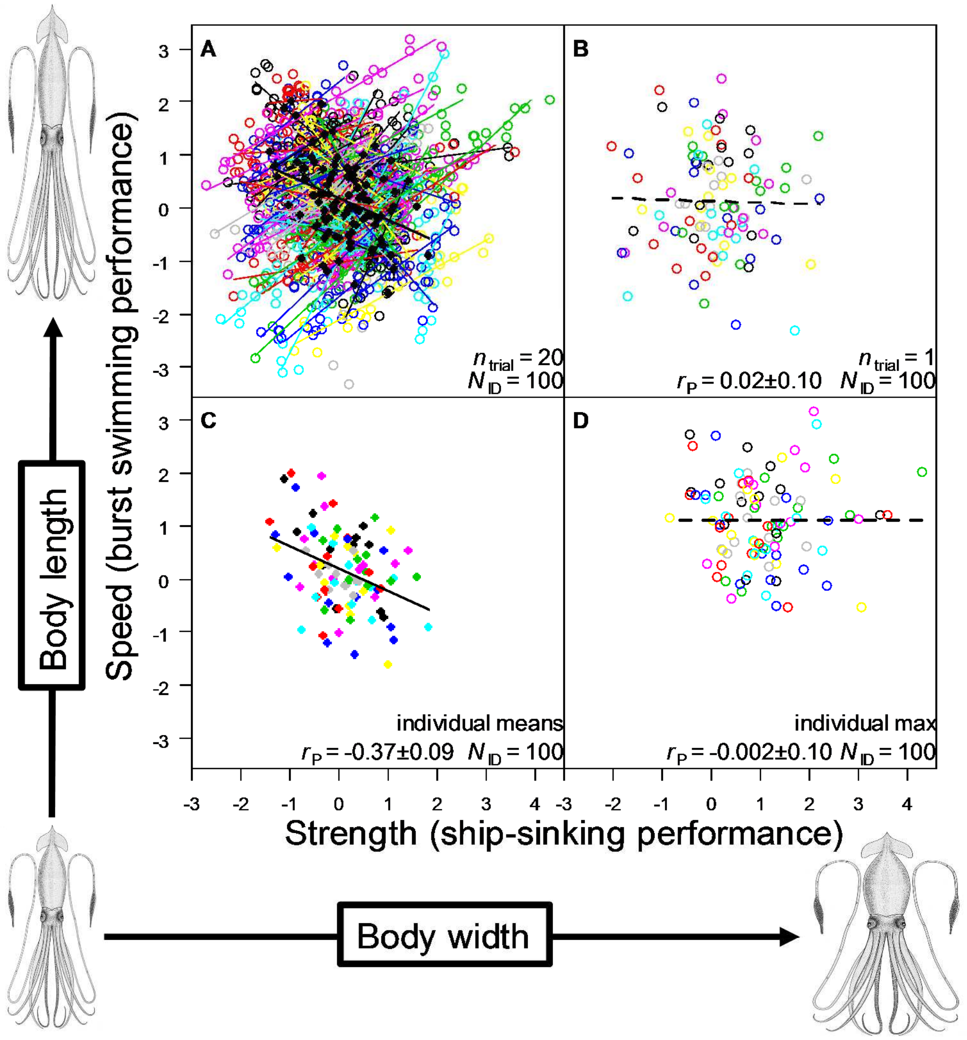

Fig. 3. Trade-off between swimming speed vs. ship-sinking performance in a simulated population of N=100 Krakens (sea monsters of giant size dwelling off the Norwegian sea). (**A**) Each legendary giant squid was sampled 20 times (n_{trial}=20) for speed and strength, which were part of trade-off at the among-individual level because of morphological differences (a slender body is good for swimming speed, but a wider body confers strength needed to sink ships). Black dots indicate mean values for each individual and the thick line illustrates the negative among-individual correlation (r_{ind}; simulated value = -0.5). Thin lines show separate linear regression for each individual, thus illustrating the facilitation effects occurring through within-individual correlated phenotypic plasticity in response to an unknow factor (e.g., temperature, age, or training). (**B**) After randomly sampling each Kraken once (N=100; n_{trial}=1), the phenotypic correlation (r_{P}) shows no relationship at all and can vary wildly depending on the random sampling of the original dataset in **A**. Phenotypic correlations (r_{P}) calculated using (**C**) individual mean (same as black dots in A) and (**D**) individual maximum values. This figure shows how interesting contrasting processes can go undetected when n_{trial} is low (**B**) and using individual maximum values (**D**). The data was simulated using SQuID package in R (Allegue and others 2017).

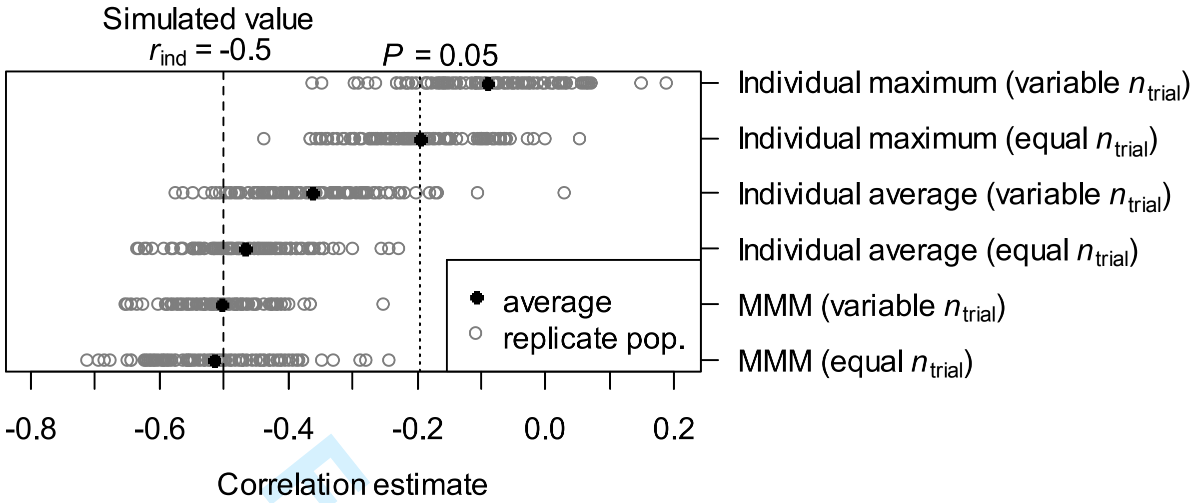

Fig. 4. Attenuated and biased correlations, or not. We used the SQuID package in R (Allegue and others 2017) to simulate 100 populations of Krakens like in Fig. 3 in which there is a negative among-individual correlation of -0.5 (dashed line). For each population, we calculated correlations using the full dataset (equal n_{trial}) and again after deleting a randomly different number of observations for each individual (variable n_{trial}). We first calculated the among-individual correlation (r_{ind}) using a multivariate random mixed model (MMM) in which the among- and within-individual (co)variances were properly modelled. Although the MMM is not sensitive to variable n_{trial}, it is not the case for phenotypic correlations (r_{P}) estimated using individual mean and maximum values. Indeed, individual mean values yield relatively unbiased r_{P}s when n_{trial} is equal, but the r_{P}s become slightly biased when n_{trial} is variable among individuals. The bias is clearly worst when using individual maximum values. For equal n_{trial}, we successfully detected the trade-off in only ~50% of populations (with N=100, $P < 0.05$ for all $|r_{\mathrm{P}}|>0.197$, dotted line). The bias with individual maxima is much more severe when n_{trial} is variable among individuals – only a few of the negative r_{P}s were significant and even positive r_{P}s are obtained.