Heritability and evolvability of fitness and non-fitness traits: lessons from livestock

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Abstract

Data from natural populations have suggested a disconnection between trait heritability (variance standardised additive genetic variance, V_A) and evolvability (mean standardised V_A) and emphasized the importance of environmental variation as a determinant of trait heritability but not evolvability. However, these inferences are based on heterogeneous and often small data sets across species from different environments. We surveyed the relationship between evolvability and heritability in >100 traits in farmed cattle, taking advantage of large sample sizes and consistent genetic approaches. Heritability and evolvability estimates were positively correlated ($r=0.37/0.54$ on untransformed/log scales) reflecting a substantial impact of V_A on both measures. Furthermore, heritabilities and residual variances were uncorrelated. The differences between this and previously described patterns may reflect lower environmental variation experienced in farmed systems, but also low and heterogeneous quality of data from natural populations. Similar to studies on wild populations, heritabilities for life history and behavioural traits were lower than for other traits. Traits having extremely low heritabilities and evolvabilities (17% of the studied traits) were almost exclusively life-history or behavioural traits, suggesting that evolutionary constraints stemming from lack of genetic variability are likely to be most common for classical 'fitness' (cf. life-history) rather than for 'non-fitness' (cf. morphological) traits.

Introduction

There has been considerable interest in comparing the magnitude of heritability (h^2), evolvability (I_A) and dominance variance (V_D) among different classes of traits across the last few decades (Mousseau and Roff 1987; Crnokrak and Roff 1995; Merilä and Sheldon 1999; Merilä et al. 2001; Blows and Hoffmann 2005; Charmantier and Garant 2005; Hansen et al. 2011). This interest has been driven by a number of hypotheses predicting differences in these parameters across different trait classes. These include predictions about directional selection eroding additive genetic variance leading fitness related traits to show low h^2 (Mousseau and Roff 1987) and elevated V_D (Crnokrak and Roff 1995), as well as the idea that limits to physiological processes may lead to low h^2 (Kellermann et al. 2009). However, as pointed out by Price and Schluter (1991) and Houle (1992), rather than reflecting low levels of additive genetic variance, low heritabilities of fitness-related traits may be explainable by them being subject to large amounts of environmental (V_E) and non-additive genetic variance (V_{NA}). The latter is intuitively understandable considering that the narrow-sense h^2 of a trait is defined as the ratio of additive genetic variance to phenotypic variance (V_A/V_P), where the $V_P = V_A + V_E + V_{NA}$. Hence, Houle (1992) suggested that the evolvability, defined as a ratio of V_A to trait mean (e.g., $I_A = 100 \times V_A / \text{mean}^2$; (Houle 1992)), might better reflect the extent to which a trait is capable of responding to directional selection.

Data from natural populations suggest that although traits closely associated with fitness tend to have low heritabilities, they tend to have high evolvabilities, whereas the opposite is true for traits less closely associated with fitness such as morphological traits (Houle 1992; Merilä and Sheldon 1999; Hansen et al. 2011). However, since both heritability and evolvability include V_A in the numerator, they converge at low levels of V_A , but in general, it has been suggested that the published estimates of heritability and evolvability are uncorrelated

(Hansen et al. 2011). This had led to the suggestion that evolvability may be a better measure of traits potential to respond to directional selection than heritability (Hansen et al. 2011).

A challenge in the evolutionary literature remains the imprecise nature of the heritability and evolvability estimates. For instance, in the supplementary material (their Supplementary appendix S1) to an influential review (Hansen et al. 2011), heritability estimates for animal studies for life history traits varied from -0.89 to 2.23 in contrast to expected values between 0 and 1, while evolvability estimates for this trait class varied from -0.07 to 190. The standard deviation of the heritability estimates exceeded the average or median heritabilities for different trait classes, and for evolvabilities this difference in relation to medians was even more marked. Part of the reason that very low and (in particular) very high values have been estimated from populations is that estimates are often highly imprecise with substantial standard errors, and there also tends to be a reporting bias particularly against low heritability estimates where sample sizes are small (Palmer 2000).

Imprecise estimates can be particularly problematical when only one or two classes of traits are characterized for a particular species, and then compared to traits from a different class characterized for another species exposed to different conditions, given the large impact of environmental conditions on heritability values (Hoffmann and Merilä 1999; Charmantier and Garant 2005). Moreover, when comparing traits falling in different classes, there is often no attempt to control the nature of the traits being compared – this means that data for a behavioural trait might reflect numerous estimates for a particular type of behaviour, rather than a sample of traits falling within a particular class. One solution is to restrict comparisons of trait classes to a species or a group of related species characterized in a similar environment, with only one representative estimate being used for a particular trait. Doing

that can lead to quite different conclusions about variation in genetic parameters across trait classes (Hoffmann 2000).

Because of the issues raised above, a comparison of evolvability and heritability for different trait classes based on a comparison of different sets of traits, species and environments is problematic. The tabled medians and SEs for different trait classes in the comprehensive survey of Hansen et al. (2011; their Supplementary appendix S1) indicates some interesting patterns but there is an enormous level of variability in the dataset. The tabled values also involve many tens of estimates for a particular trait class coming from a single paper and organism characterized under one set of conditions.

The very high values obtained for many estimates of I_A in Hansen et al. (2011) are particularly concerning because many of the studies reported use incorrect methods for calculating evolvabilities (Garcia-Gonzalez et al. 2012) or estimates are based on trait means that does not have an intrinsic biological meaning, leaving interpretation of evolvability estimates difficult (Visscher et al. 2008; Garcia-Gonzalez et al. 2012). We suggest that a way forward at least for normally distributed traits is to consider them on biological scales which tend to have positive values.

If variation in a trait is assumed to be normally distributed, there are limits to values of I_A that are likely to be meaningful. Evolvabilities will be large (and constraints low) when V_A in a trait is large relative to its mean value. If a trait has a mean of 3 and V_A of 1, its evolvability will be 1/9 or 11.1%. For a different trait scored on a different scale with a mean value of 30 and a V_A of 1, its evolvability will be 0.11%. A trait with a mean value near zero but a substantial V_A will have a high evolvability. However, for a biological scale to be meaningful when measuring evolvability, the vast majority of values for a normally distributed trait measured on a population of individuals should have values greater than zero: otherwise a

measure of evolvability where V_A is expressed relative to a trait's mean becomes hard to interpret, with evolvabilities increasing as a mean approaches zero and the trait's distribution encompasses negative as well as positive values. If it is assumed that at least 99.85% (i.e., 3 phenotypic SDs) of the individuals need to have trait values >0 for a trait's evolvability to have meaning, this sets a limit of 11.1% for evolvability assuming that $h^2 = 1$ (i.e., $V_P = V_A = SD = 1$, so that $\bar{x} = 3$ for a phenotypic distribution with a mean which is 3 SD removed from 0). If h^2 is less than one, the limit is reduced to maintain the same minimum level of V_P . On the other hand, a heritability of 10% implies a limit to the value of evolvability of 1.1% when the trait mean is 3 and V_P is 1. This points to a limit of I_A of $100 \times h^2/9$, or a less conservative limit with 97.5% of values (2 SD) exceeding 0 of $100 \times h^2/4$. It implies that trait means need to exceed zero by 2-3 phenotypic standard deviations to ensure that only a minority of values are less than zero, and an upper limit of around 10 for I_A when a trait has a very high heritability, but lower limits for traits with intermediate or low heritabilities ($V_A \ll V_P$).

A conservative upper limit of I_A defined by $100 \times h^2/9$ is exceeded quite often in estimates of evolvability (Supplementary appendix S1 in Hansen et al. (2011)). Focusing only on animal studies, for life history traits the evolvability limit is broken in 42% (59/142) of the cases in the data reviewed by Hansen et al. (2011), although the percentage is much lower for size traits (6%; 34/571). Clearly variance estimates for life history traits are often too large to make much biological sense of I_A estimates. This is perhaps not surprising given that life history traits are notoriously variable and show potential kurtosis, but it does make it challenging to undertake comparisons among trait groups.

One way of dealing with imprecise estimates of genetic parameters and comparisons of data sets from unrelated organisms scored in different environments is to focus on situations where accurate estimates of heritability and evolvability are available from a species or a set

of species measured in relatively similar environments. A particularly unique resource in this respect is provided by farmed livestock and particularly cattle, where there is a wealth of information on h^2 and V_A but much less on I_A or other measures of evolvability, with only a few exceptions (e.g. Sartori et al. 2015; Vallee et al. 2015). Livestock data are potentially valuable because animals are typically raised in rather homogenous production environments, genetic parameters (particularly for cattle data) are often estimated from thousands or even hundreds of thousands of individuals, and there are typically multiple studies from different researchers working in different countries providing consistent estimates that have been combined in reviews and meta-analyses (e.g. Bittante et al. 2012; Berry and Crowley 2013; Berry et al. 2014). Such comparisons will have their drawbacks because farmed animals represent artificially generated populations. Nevertheless, while acknowledging this constraint, we argue that livestock data provide interesting material for re-examination of connections between heritability and evolvability, as well as identifying potential problems with earlier analyses and conclusions from the data collected from natural populations.

The main aim of this study was to compare heritability and evolvability of different classes of traits leveraging the massive amounts of high-quality data available from the animal breeding literature. In particular, we were interested in addressing the following questions: Does the relationship between heritability and evolvability match that seen in data from natural populations, pointing to low V_A (low heritability and evolvability) in life history traits, but high $V_{NA} + V_E$ (low heritability but not necessarily evolvability) in these traits as well as behavioural traits when compared to morphological traits? Are estimates of heritability and evolvability correlated within different trait classes? Do heritabilities and evolvabilities converge at low levels, pointing to traits that are at evolutionary limits due to low V_A ? Do traits closely associated with fitness (cf. life-history traits) show lower heritabilities and evolvabilities than traits less closely associated with fitness (c.f. morphological traits)?

Materials and Methods

The survey

Because the massive cattle literature has been regularly reviewed for particular classes of traits, as well as being applied in commercial settings, we focused on two sources of information. The first comprises of reviews that often encompass many estimates of genetic parameters from very large studies, but for only a limited trait set. The second represents individual studies of traits that are not considered in reviews, but for which high-quality estimates are available. We initially undertook a literature search to identify reviews with useful heritability estimates for livestock traits using the terms “heritability”, “review” and the terms “dairy cow” or “cattle”. Our focus was on recent (post 2010) reviews which we used to identify estimates of heritability for particular classes of traits or (more rarely) across trait classes. Most of the livestock studies provided information on heritabilities based on literature compilations or meta-analyses. We made no attempt to distinguish between dairy and beef cattle studies, because reviews often considered both of these simultaneously and because genetic parameter estimates of comparable traits across these groups were similar for traits like weight and morphological measures even though means typically differed. Overall estimates of trait means, V_A and/or V_P required for computing evolvabilities were often not provided in the reviews (or many of the papers cited in the reviews). We therefore obtained estimates for these parameters from either a very recent study (with large sample sizes) or one of the papers cited in the review, as documented in Supplementary Table 1. However, heritabilities were always provided in the reviews and were therefore used; these were in any case rather similar to estimates provided in the papers used to extract other parameters. These

data were used to compile an initial list of heritabilities and evolvabilities in cattle for specific classes of traits (Supplementary Table 1). Only one estimate of a particular trait measure was considered to ensure that trait class comparisons were not biased by multiple estimates for the same trait class (Hoffmann 2000). For instance there are many hundreds of estimates for the heritability of milk yield but only one estimate (in this case from a review paper) was used. To increase the number of traits available for comparison, we then focused on studies reporting genetic parameters for individual traits not yet included in reviews. Many of these came from a paper highlighting new types of traits that were being measured in cattle (Egger-Danner et al. 2015) although some older papers on morphological or behavioural traits were also included. Our aim was not to be comprehensive in terms of number of studies to be included, but to collect information on a large number of traits while avoiding inclusion of different proxies of the same trait.

Trait definitions

We excluded traits that were measured on a binomial scale for which evolvabilities become difficult to interpret. For this reason, we excluded many estimates of cattle survival over a given time interval, or estimates based on the incidence of a disease. However we were able to include some quantitative traits that have been shown to be related to disease incidence, including body condition measured on a visual scale and some biochemical parameters. Ratios were also included where they were scored on individuals as percentages or proportions (e.g. % sperm that were motile) but not when they represented non-inclusive ratios where one of the terms was not contained within the other (e.g. feed conversion efficiency, a ratio of daily food intake and average daily weight gain). We divided traits into six categories based on evolutionary rather than agronomic considerations: life history (27 traits), growth (12 traits), morphology (23 traits), disease indicator (12 traits), behaviour (22

traits) and physiology (23 traits). The identities of traits included into each category can be found in Supplementary Table 1.

For traits with multiple estimates from a single study (e.g. across years, breeds), we averaged values to obtain a single estimate of h^2 , trait mean, V_P and V_A , and these average estimates were used to compute I_A . Evolvability was computed in only one study on cattle (Sartori et al. 2015) and estimates were therefore obtained from provided variance component estimates. We took two approaches. In one of these, based on the discussion above, we excluded traits whose mean value minus two standard deviations was less than zero, to ensure that the majority of a population (assuming a normal distribution) would have had positive values for the trait (103 traits). In the other approach we included all estimates, to allow a better comparison to Hansen et al. (2011) where all estimates were also included (119 traits).

Statistical analyses

Patterns among heritability, evolvability, CV_R (coefficient of residual variance which includes all terms apart from V_A) and other parameters were explored with a series of scatterplots. In visualizations of differences among trait classes, one carcass trait with a high heritability (0.8 – see Supplementary Table 1) was excluded from the plots, but not from the analyses. Associations between parameters (h^2 , I_A and CV_R) were explored with parametric and non-parametric correlation and regression analyses, with the parametric analyses run on untransformed and log transformed data. Correlations were examined for data pooled across trait classes and for the classes treated separately. To test for heterogeneity in parameter values among trait classes, we used linear models treating log-transformed parameter estimates (to reduce heterogeneity in variances) as response variables and trait class as fixed factor. We also ran contingency tests (using the likelihood ratio statistic with P values determined by a randomization test as implemented in SPSS Statistics version 22) to

investigate whether traits characterized as having a particularly low heritability (<0.1) and evolvability (<0.2) were randomly distributed across the trait classes.

Results

Overall patterns of heritability and evolvability

Heritability estimates included in the analyses varied from 0 to 0.8 and they were estimated usually with high accuracy as reflected by low standard errors (Supplementary Table 1). All I_A estimates were below 10. When considered across all 103 traits with means at least 2 SDs above zero, heritabilities and evolvabilities were positively correlated in both the original (Fig. 1a: $r = 0.371$, $P < 0.001$; r_s (Spearman rank correlation) = 0.550, $P < 0.001$) and log-transformed scales (Fig. 1b: $r = 0.540$, $P < 0.001$). A regression run to predict the evolvability based on trait heritability (log scale) produced an R^2 of 0.292 ($F_{1,102} = 41.60$, $P < 0.001$). When considered across all 119 traits, similar correlations were obtained for untransformed ($r = 0.300$, $P = 0.001$; $r_s = 0.504$, $P < 0.001$) and log-transformed scales ($r = 0.511$, $P < 0.001$) and the R^2 of 0.261 ($F_{1,117} = 41.31$, $P < 0.001$) was also similar.

Trait-class comparisons

A comparison of heritabilities among trait classes indicated significant heterogeneity ($F_{5,97} = 6.18$, $P < 0.001$). Life history traits, and to some extent also behavioural traits, tended to have lower heritabilities than other types of traits (Fig. 2a). A comparison of I_A also revealed significant heterogeneity among trait classes ($F_{5,97} = 2.50$, $P = 0.036$), with the life history

traits again showing the lowest values (Fig. 2b). In contrast, CV_R values were homogeneous across different trait classes ($F_{5,97}=1.4$, $P = 0.217$; Fig. 2c).

There was no relationship between CV_R and trait heritability (Fig. 1c; r_s (Spearman rank correlation) = -0.05, $P = 0.616$; $r = -0.117$, $P = 0.238$). In contrast, the I_A values were strongly positively correlated to CV_R (Fig. 1d: $r_s = 0.62$, $P < 0.001$) suggesting that evolvability to some extent reflects residual variance when standardised to the mean. We also examined the association between I_A and trait CV (ratio of the SD over the mean), and found that it was strongly positively correlated with I_A ($r_s = 0.701$, $P < 0.001$).

To gain some further insight on what kind of traits might have lowest evolutionary potential to respond to selection based on both heritabilities and evolvabilities, we focused on traits with $h^2 < 0.1$ and $I_A < 0.2$. For heritabilities < 0.1 , we ended up with 29 traits distributed heterogeneously across the trait classes ($G = 38.048$, $df = 5$, $P < 0.001$) with heritabilities for behavioural, disease indicator and life history traits tending to be low (Table 1). For I_A values < 0.2 , there were 27 estimates distributed heterogeneously across the trait classes ($G = 15.825$, $df = 5$, $P = 0.011$), with over representation of behavioural and life history traits (Table 1). Finally, 17 estimates meet both criteria of $h^2 < 0.1$ and $I_A < 0.2$, and these were distributed heterogeneously across the trait classes ($G = 25.96$, $df = 5$, $P < 0.001$): they were almost exclusively life history or behavioural traits (Table 1).

We considered the association between I_A and h^2 for individual trait classes to see if there was a consistent pattern across them, particularly when the different classes are more likely to be scored on similar scales. Figure 3 provides plots for the reduced data set which highlights particularly strong relationships for morphology and behaviour and somewhat weaker relationships for the other traits and particularly disease and growth, although the association

is in the same direction across trait classes, and the disease/growth classes were based on the fewest traits (i.e., 11/10 traits respectively, traits with means <2 SD from 0 excluded).

Discussion

This survey reinforces the notion that there is an enormous range of heritabilities and evolvabilities across traits, even though we have focused on one species living in a stable environment and for which highly accurate estimates of genetic parameters are available. We also found support for consistent differences in heritability across trait classes similar to those observed in earlier studies, suggesting low heritability of life history traits closely associated with fitness, and higher heritabilities of morphological traits less closely associated with fitness. However, in contrast to data from the natural populations, heritabilities and evolvabilities in the cattle data are positively correlated, contradicting the notion that heritability is weakly correlated to evolvability (Hansen et al. 2011). Furthermore, the view that low heritabilities would be driven by large environmental influences (as reflect by large CV_R – although this also includes non-additive genetic effects) was not supported by the data. In what follows, we will first discuss these findings and their interpretations by relating the results from cattle to those from studies of natural populations.

Lessons from livestock

Several patterns consistent with those observed in previous studies on natural populations emerged from our results. First, the proportion of traits showing low heritabilities appears to be high. For instance, 29% of the heritability estimates were < 0.1 when all traits in Supplementary Table 1 are considered, whereas the corresponding value in Hansen et al.'s

(2011) review of animal estimates was 19%. One reason why the estimate from farm animals is particularly high may be the publication bias towards high heritability estimates in organisms from natural populations as noted by Palmer (2000). In studies of natural populations or populations derived from natural populations, there is a strong tendency of studies with relatively small sample sizes (and hence large SEs around variance and heritability estimates) to exhibit high heritability values. However, this is less of an issue in cattle studies because of the large sample sizes involved in almost all studies leading to very low SEs (Supplementary Table 1). Estimates of evolvabilities also include many low values in both the current survey and the Hansen et al. (2011) study, with 21% of the cattle estimates being below 0.1% when all traits are considered. In Hansen et al. (2011) 37% of the estimates are < 0.1 . These patterns point to limited additive genetic variance present for many traits, suggesting that that selection responses and thereby genetic gains will often be minor. Genomic selection is expected to be especially important in changing these low heritability traits (Visscher et al. 2008).

Second, we find that heritabilities are lower for life history traits than for traits from other classes, consistent with previous patterns reported in reviews (Mousseau and Roff 1987; Hansen et al. 2011) and despite the fact that we only considered one set of estimates for each trait. There remains the issue that traits are not independent and many of those listed in Supplementary Table 1 will be correlated with other traits, but our comparisons at least do not involve the same traits being represented multiple times in a survey. Reviews of the livestock literature suggest that the genetic correlations between many of the traits falling into the same categories are not necessarily high (e.g. Bittante et al. 2012; Berry and Crowley 2013; Berry and Evans 2014; Egger-Danner et al. 2015; Haile-Mariam and Pryce 2015). Examples from dairy cattle breeds in the Nordic countries include carcass traits such as conformation and fat score with genetic correlations ranging from 0.15 to 0.35, fertility traits

where the genetic correlation between number of days from calving to first insemination and non-return rate is typically below 0.15, and genetic correlations between many disease traits that are not significantly different from zero (NAV 2013). Third, unlike in an earlier survey (Houle 1992), but consistent with a later survey (Hansen et al. 2011), we found a positive association between heritability and evolvability measures. The animal data considered by (Hansen et al. 2011) yielded a correlation between h^2 and I_A of 0.096 ($P = 0.003$) on an untransformed scale, lower than the value of around 0.3 for the cattle survey. However when the $100 \times h^2/4$ limit is applied to the Hansen et al. (2011) data, based on the arguments made in above on limits to I_A , several high I_A estimates are removed, and the correlation increases to 0.345 ($N = 891$, $P < 0.001$). Moreover, a Spearman rank correlation computed between these measures based on all the animal data from Hansen et al. (2011) yields a value of $r_s = 0.412$ ($N = 992$, $P < 0.001$) increasing to $r_s = 0.497$ ($N = 891$, $P < 0.001$) when the $100 \times h^2/4$ limit is applied. Both these values are similar to r_s values of around 0.5 for the cattle survey. In the cattle survey, heritability was not tightly linked to residual variance, which is commonly high for life history traits measured in natural populations due to large environmental effects on these traits (Falconer and Mackay 1996). However we did find that CV_R was highly variable for life history traits measured on cattle (Fig. 2c). Behavioural traits tended to show high CV_R values but this could be connected to low trait repeatabilities (Løvendahl and Munksgaard 2016). However for behavioural traits (and most other trait classes) we nevertheless find a strong positive association between heritability and evolvability (Fig. 3), reflecting trait variation in V_A relative to both means and variances. While we have focused on cattle where there are a very large number of accurate estimates available, it is anticipated that similar patterns would emerge from other livestock species. For instance, genetic parameter estimates for around 30 pig traits measured in the tropics reviewed by Akanno et al. (2013) indicates low heritability (and estimated evolvability) for

many life history traits associated with reproduction (litter size, weaning weight, farrowing interval etc.), whereas carcass and growth rates tended to have moderate heritabilities and evolvabilities. Estimates for Sabi sheep reviewed by Matika et al. (2003) also fit this pattern. Whether these patterns will also extend to natural populations once estimates become available for multiple traits scored for the same species held under similar conditions is still unclear. Admittedly rearing environments, selection intensities and methods, population sizes and population structuring often differ between domestic animals and natural populations. However, we argue that our results are still of strong relevance for natural populations based on several observations. Firstly, mean estimates of heritabilities (and evolvabilities) in different trait classes in livestock seem to fit well with those from studies on laboratory animals and wildlife (Mousseau and Roff 1987; Hansen et al. 2011). Secondly, the effective population sizes in most domesticated breeds are below a few hundred (Leroi et al. 2013). This is similar to estimates in many populations in nature (although obviously many natural populations are larger). Thirdly, there is little evidence that livestock populations are genetically depauperate (Kristensen et al. 2015); thus typically no signs of selection plateaus are observed and levels of genetic variation seem high in most breeds (Hill and Kirkpatrick 2010). Fourthly, heritabilities for milk yield, a trait that has been under intense directional selection in commercial dairy cattle breeds, is similar in beef cattle breeds where this trait has not been strongly selected for (Miller and Wilton 1999; Lee and Pollak 2002), suggesting that intense directional selection for some traits in some breeds has not changed heritabilities markedly.

Finally, we have found that two trait classes (behaviour, life history) have a high incidence of traits with very low adaptive potential regardless of whether this is scored through heritability or evolvability (Table 1). In the livestock literature, it is well recognized that traits with close connections to reproduction and development tend to have low heritabilities (e.g. Safari et al.

2005; Morris 2009; Hopkins et al. 2011; Lopez-Villalobos 2012; Akanno et al. 2013; Berry et al. 2014; Brien et al. 2014). In addition to the traits presented here, the heritabilities for other life history traits such as survival in cattle across a specific interval are also very low (Pritchard et al. 2013), with estimates ranging from 0.002 to 0.013 depending on the interval considered between 2 and 750 days (Pritchard et al. 2013). These are traits likely to be constrained genetically and unlikely to change much if directional selection is imposed on them. While mutation will continuously introduce new genetic variation and ensure that some level of V_A is maintained even if mutations are mostly deleterious (Turelli 1988), traits with very low V_A relative to means and variances may be at biophysical limits due to constraints imposed through metabolic processes, energetic requirements, membrane diffusion and so on (Barton and Partridge 2000; Blows and Hoffmann 2005; Hoffmann et al. 2013). Traits like heat loss, food conversion efficiency, metabolic rate and development time may be subjected to these types of constraints. Farmed animals provide an opportunity to explore such limits further given that genetic parameters can be estimated accurately and that information is available on biochemical and metabolic processes underlying production traits.

Lessons for livestock

Although there is a wealth of information on h^2 and V_A in livestock, with few notable exceptions (e.g. Sartori et al. 2015; Vallee et al. 2015), estimates of I_A or other measures of evolvability are scarce. Thus h^2 remains the preferred dimensionless population parameter used in animal breeding (Hill and Kirkpatrick 2010) which along with genetic correlations with other traits are used to predict the extent to which a trait is altered by selection. Reliance on h^2 is understandable in the view that in contrast to situation in the wild, the production environment is often considered relatively constant at least in regions of the world with large-

scale commercial farming. Selection responses (R) are considered through genetic gain or the breeder's equation, defined by $R = h^2 S$, where S is the selection differential reflecting the intensity of selection multiplied by V_P . Again this measure does not consider changes in the mean of a trait but changes measured in terms of trait standard deviations. Within a farming context, these measures can be translated into the economic benefits of particular selection regimes on traits as long as the association between the economic value of changes in trait standard deviations is known (Hill and Kirkpatrick 2010; Visscher et al. 2008). In evolutionary biology, the equivalent measure might be regarded as fitness, but the exact way in which changes in trait means or standard deviations map onto fitness is usually unknown, and in any case will be highly variable across seasons and years, given that selection in natural populations varies and even changes in sign (Kingsolver et al. 2001).

Can low heritabilities and evolvabilities inform animal breeding? There is little evidence that directional selection for milk yield and other agronomic traits has exhausted genetic variation for these traits as there is a history of ongoing genetic gain in most economically important agronomic traits (e.g. Chikhi et al. 2004; Hill and Kirkpatrick 2010; NAV 2013). However there is an increasing interest in selecting on "new" traits that are suited to changing market conditions, environmental considerations and so on (Egger-Danner et al. 2015). For instance, there has recently been interest in selecting cattle for increased heat resistance and reduced methane production to adapt to an increasing frequency of heat waves and to meet environmental concerns. In cattle, it appears possible to select for heat resistance which has a moderate heritability when considered on its own (Dikmen et al. 2012), but a negative interaction between production and resistance may reduce the V_A left in the desired direction of artificial selection (Dikmen et al. 2012; Santana et al. 2015). In some pig breeds however, it appears that heat resistance has a very low heritability (close to 0) with a low V_A (Bloemhof et al. 2012) and I_A (computed from data in this reference), so relatively little

progress may be possible within breeds. Where both evolvabilities and heritabilities are low, only little genetic gain may be obtained when selecting on such traits, and if the traits represent limits it may be hard to overcome them. Several behavioural and life-history traits fall into this category (Table 1) and estimating both h^2 and I_A (when meaningful) might better enable animal breeders to identify traits that are evolutionary constrained. Information on both measures may also be useful in situations where a trait has both high h^2 and I_A which suggest that the trait is likely to respond fast to selection across variable environments and in herds with different means. Thus, biologically meaningful estimates of I_A can inform also animal breeders.

Conclusions

Similarly to data from the wild, the results of this study suggest that life history and behavioural traits have lower heritabilities than morphological traits in cattle. However, in contrast to data from natural populations, this is also true in the case of evolvabilities, and evolvabilities and heritabilities across the investigated traits in cattle were positively correlated. It is not clear if the patterns established here for livestock would hold up in studies of natural populations because there are differences both in data quality and levels of environmental variability experienced by natural populations. A useful way forward would involve larger studies of natural populations of a single species or set of related species across multiple trait sets, particularly for sets of traits that are normally distributed. Both evolvability and heritability remain important genetic parameters for predicting evolutionary potential and constraints in ecologically important traits.

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Fig 1. Associations between (a-b) heritability and evolvability (I_A), between (c) the coefficient of residual variance (CV_R) and heritability and (d) between CV_R and I_A for cattle traits (with means >2 SD from 0). The association between heritability and evolvability is plotted both (a) without transformation and (b) with log transformation of both parameters. Traits belonging to different trait classes are plotted in different colours.

Fig. 2. Box plots for comparison of (a) heritabilities, (b) evolvabilities and (c) CV_R values across trait classes. Outlier data points are included in the graph (indicated by dots and asterisks)

Fig. 3. Association between heritability and evolvability (both log transformed) plotted for trait classes separately (based on traits with means >2 SD from 0) along with R^2 values.

Trait class	Heritability		Evolvability		Both	
	Low	Not Low	Low	Not Low	Low	Not Low
behaviour	12	8	9	11	8	12
disease indicator	6	5	1	10	0	11
growth	0	10	0	10	0	10
life history	11	6	8	9	7	10
morphology	2	20	4	18	1	21
physiology	2	21	5	18	1	22

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