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

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Abstract

21   Data from natural populations have suggested a disconnection between trait heritability

22   (variance standardised additive genetic variance, V_A) and evolvability (mean standardised

23   V_A) and emphasized the importance of environmental variation as a determinant of trait

24   heritability but not evolvability. However, these inferences are based on heterogeneous and

25   often small data sets across species from different environments. We surveyed the

26   relationship between evolvability and heritability in >100 traits in farmed cattle, taking

27   advantage of large sample sizes and consistent genetic approaches. Heritability and

28   evolvability estimates were positively correlated (r=0.37/0.54 on untransformed/log scales)

29   reflecting a substantial impact of V_A on both measures. Furthermore, heritabilities and

30   residual variances were uncorrelated. The differences between this and previously described

31   patterns may reflect lower environmental variation experienced in farmed systems, but also

32   low and heterogeneous quality of data from natural populations. Similar to studies on wild

33   populations, heritabilities for life history and behavioural traits were lower than for other

34   traits. Traits having extremely low heritabilities and evolvabilities (17% of the studied traits)

35   were almost exclusively life-history or behavioural traits, suggesting that evolutionary

36   constraints stemming from lack of genetic variability are likely to be most common for

37   classical 'fitness' (cf. life-history) rather than for 'non-fitness' (cf. morphological) traits.

38

Introduction

40 There has been considerable interest in comparing the magnitude of heritability (h^2),

41 evolvability (I_A) and dominance variance (V_D) among different classes of traits across the last

42 few decades (Mousseau and Roff 1987; Crnokrak and Roff 1995; Merilä and Sheldon 1999;

43 Merilä et al. 2001; Blows and Hoffmann 2005; Charmantier and Garant 2005; Hansen et al.

44 2011). This interest has been driven by a number of hypotheses predicting differences in

45 these parameters across different trait classes. These include predictions about directional

46 selection eroding additive genetic variance leading fitness related traits to show low h^2

47 (Mousseau and Roff 1987) and elevated V_D (Crnokrak and Roff 1995), as well as the idea

48 that limits to physiological processes may lead to low h^2 (Kellermann et al. 2009). However,

49 as pointed out by Price and Schluter (1991) and Houle (1992), rather than reflecting low

50 levels of additive genetic variance, low heritabilities of fitness-related traits may be

51 explainable by them being subject to large amounts of environmental (V_E) and non-additive

52 genetic variance (V_{NA}). The latter is intuitively understandable considering that the narrow-

53 sense h^2 of a trait is defined as the ratio of additive genetic variance to phenotypic variance

54 (V_A/V_P,), where the $V_P = V_A + V_E + V_{NA}$. Hence, Houle (1992) suggested that the

55 evolvability, defined as a ratio of V_A to trait mean (e.g., $I_A = 100 \times V_A/\text{mean}^2$; (Houle 1992)),

56 might better reflect the extent to which a trait is capable of responding to directional

57 selection.

58 Data from natural populations suggest that although traits closely associated with fitness tend

59 to have low heritabilities, they tend to have high evolvabilities, whereas the opposite is true

60 for traits less closely associated with fitness such as morphological traits (Houle 1992; Merilä

61 and Sheldon 1999; Hansen et al. 2011). However, since both heritability and evolvability

62 include V_A in the numerator, they converge at low levels of V_A, but in general, it has been

63 suggested that the published estimates of heritability and evolvability are uncorrelated

64 (Hansen et al. 2011). This had led to the suggestion that evolvability may be a better measure

65 of traits potential to respond to directional selection than heritability (Hansen et al. 2011).

66 A challenge in the evolutionary literature remains the imprecise nature of the heritability and

67 evolvability estimates. For instance, in the supplementary material (their Supplementary

68 appendix S1) to an influential review (Hansen et al. 2011), heritability estimates for animal

69 studies for life history traits varied from -0.89 to 2.23 in contrast to expected values between

70 0 and 1, while evolvability estimates for this trait class varied from -0.07 to 190. The standard

71 deviation of the heritability estimates exceeded the average or median heritabilities for

72 different trait classes, and for evolvabilities this difference in relation to medians was even

73 more marked. Part of the reason that very low and (in particular) very high values have been

74 estimated from populations is that estimates are often highly imprecise with substantial

75 standard errors, and there also tends to be a reporting bias particularly against low heritability

76 estimates where sample sizes are small (Palmer 2000).

77 Imprecise estimates can be particularly problematical when only one or two classes of traits

78 are characterized for a particular species, and then compared to traits from a different class

79 characterized for another species exposed to different conditions, given the large impact of

80 environmental conditions on heritability values (Hoffmann and Merilä 1999; Charmantier

81 and Garant 2005). Moreover, when comparing traits falling in different classes, there is often

82 no attempt to control the nature of the traits being compared – this means that data for a

83 behavioural trait might reflect numerous estimates for a particular type of behaviour, rather

84 than a sample of traits falling within a particular class. One solution is to restrict comparisons

85 of trait classes to a species or a group of related species characterized in a similar

86 environment, with only one representative estimate being used for a particular trait. Doing

87   that can lead to quite different conclusions about variation in genetic parameters across trait

88   classes (Hoffmann 2000).

89   Because of the issues raised above, a comparison of evolvability and heritability for different

90   trait classes based on a comparison of different sets of traits, species and environments is

91   problematic. The tabled medians and SEs for different trait classes in the comprehensive

92   survey of Hansen et al. (2011; their Supplementary appendix S1) indicates some interesting

93   patterns but there is an enormous level of variability in the dataset. The tabled values also

94   involve many tens of estimates for a particular trait class coming from a single paper and

95   organism characterized under one set of conditions.

96   The very high values obtained for many estimates of I_A in Hansen et al. (2011) are

97   particularly concerning because many of the studies reported use incorrect methods for

98   calculating evolvabilities (Garcia-Gonzalez et al. 2012) or estimates are based on trait means

99   that does not have an intrinsic biological meaning, leaving interpretation of evolvability

100   estimates difficult (Visscher et al. 2008; Garcia-Gonzalez et al. 2012). We suggest that a way

101   forward at least for normally distributed traits is to consider them on biological scales which

102   tend to have positive values.

103   If variation in a trait is assumed to be normally distributed, there are limits to values of I_A that

104   are likely to be meaningful. Evolvabilities will be large (and constraints low) when V_A in a

105   trait is large relative to its mean value. If a trait has a mean of 3 and V_A of 1, its evolvability

106   will be 1/9 or 11.1%. For a different trait scored on a different scale with a mean value of 30

107   and a V_A of 1, its evolvability will be 0.11%. A trait with a mean value near zero but a

108   substantial V_A will have a high evolvability. However, for a biological scale to be meaningful

109   when measuring evolvability, the vast majority of values for a normally distributed trait

110   measured on a population of individuals should have values greater than zero: otherwise a

111   measure of evolvability where V_A is expressed relative to a trait's mean becomes hard to

112   interpret, with evolvabilities increasing as a mean approaches zero and the trait's distribution

113   encompasses negative as well as positive values. If it is assumed that at least 99.85% (i.e., 3

114   phenotypic SDs) of the individuals need to have trait values >0 for a trait's evolvability to

115   have meaning, this sets a limit of 11.1% for evolvability assuming that $h^2 = 1$ (i.e., $V_P = V_A =$

116   SD = 1, so that $\bar{x} = 3$ for a phenotypic distribution with a mean which is 3 SD removed from

117   0). If h^2 is less than one, the limit is reduced to maintain the same minimum level of V_P. On

118   the other hand, a heritability of 10% implies a limit to the value of evolvability of 1.1% when

119   the trait mean is 3 and V_P is 1. This points to a limit of I_A of 100 x $h^2/9$, or a less conservative

120   limit with 97.5% of values (2 SD) exceeding 0 of 100 x $h^2/4$. It implies that trait means need

121   to exceed zero by 2-3 phenotypic standard deviations to ensure that only a minority of values

122   are less than zero, and an upper limit of around 10 for I_A when a trait has a very high

123   heritability, but lower limits for traits with intermediate or low heritabilities ($V_A << V_P$).

124   A conservative upper limit of I_A defined by $100*h^2/9$ is exceeded quite often in estimates of

125   evolvability (Supplementary appendix S1 in Hansen et al. (2011)). Focusing only on animal

126   studies, for life history traits the evolvability limit is broken in 42% (59/142) of the cases in

127   the data reviewed by Hansen et al. (2011), although the percentage is much lower for size

128   traits (6%; 34/571). Clearly variance estimates for life history traits are often too large to

129   make much biological sense of I_A estimates. This is perhaps not surprising given that life

130   history traits are notoriously variable and show potential kurtosis, but it does make it

131   challenging to undertake comparisons among trait groups.

132   One way of dealing with imprecise estimates of genetic parameters and comparisons of data

133   sets from unrelated organisms scored in different environments is to focus on situations

134   where accurate estimates of heritability and evolvability are available from a species or a set

135   of species measured in relatively similar environments. A particularly unique resource in this

136   respect is provided by farmed livestock and particularly cattle, where there is a wealth of

137   information on h^2 and V_A but much less on I_A or other measures of evolvability, with only a

138   few exceptions (e.g. Sartori et al. 2015; Vallee et al. 2015). Livestock data are potentially

139   valuable because animals are typically raised in rather homogenous production environments,

140   genetic parameters (particularly for cattle data) are often estimated from thousands or even

141   hundreds of thousands of individuals, and there are typically multiple studies from different

142   researchers working in different countries providing consistent estimates that have been

143   combined in reviews and meta-analyses (e.g. Bittante et al. 2012; Berry and Crowley 2013;

144   Berry et al. 2014). Such comparisons will have their drawbacks because farmed animals

145   represent artificially generated populations. Nevertheless, while acknowledging this

146   constraint, we argue that livestock data provide interesting material for re-examination of

147   connections between heritability and evolvability, as well as identifying potential problems

148   with earlier analyses and conclusions from the data collected from natural populations.

149   The main aim of this study was to compare heritability and evolvability of different classes of

150   traits leveraging the massive amounts of high-quality data available from the animal breeding

151   literature. In particular, we were interested in addressing the following questions: Does the

152   relationship between heritability and evolvability match that seen in data from natural

153   populations, pointing to low V_A (low heritability and evolvability) in life history traits, but

154   high $V_{NA} + V_E$ (low heritability but not necessarily evolvability) in these traits as well as

155   behavioural traits when compared to morphological traits? Are estimates of heritability and

156   evolvability correlated within different trait classes? Do heritabilities and evolvabilities

157   converge at low levels, pointing to traits that are at evolutionary limits due to low V_A? Do

158   traits closely associated with fitness (cf. life-history traits) show lower heritabilities and

159   evolvabilities than traits less closely associated with fitness (c.f. morphological traits)?

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161

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

184 data were used to compile an initial list of heritabilities and evolvabilities in cattle for specific

185 classes of traits (Supplementary Table 1). Only one estimate of a particular trait measure was

186 considered to ensure that trait class comparisons were not biased by multiple estimates for the

187 same trait class (Hoffmann 2000). For instance there are many hundreds of estimates for the

188 heritability of milk yield but only one estimate (in this case from a review paper) was used.

189 To increase the number of traits available for comparison, we then focused on studies

190 reporting genetic parameters for individual traits not yet included in reviews. Many of these

191 came from a paper highlighting new types of traits that were being measured in cattle (Egger-

192 Danner et al. 2015) although some older papers on morphological or behavioural traits were

193 also included. Our aim was not to be comprehensive in terms of number of studies to be

194 included, but to collect information on a large number of traits while avoiding inclusion of

195 different proxies of the same trait.

196 *Trait definitions*

197 We excluded traits that were measured on a binomial scale for which evolvabilities become

198 difficult to interpret. For this reason, we excluded many estimates of cattle survival over a

199 given time interval, or estimates based on the incidence of a disease. However we were able

200 to include some quantitative traits that have been shown to be related to disease incidence,

201 including body condition measured on a visual scale and some biochemical parameters.

202 Ratios were also included where they were scored on individuals as percentages or

203 proportions (e.g. % sperm that were motile) but not when they represented non-inclusive

204 ratios where one of the terms was not contained within the other (e.g. feed conversion

205 efficiency, a ratio of daily food intake and average daily weight gain). We divided traits into

206 six categories based on evolutionary rather than agronomic considerations: life history (27

207 traits), growth (12 traits), morphology (23 traits), disease indicator (12 traits), behaviour (22

208   traits) and physiology (23 traits). The identities of traits included into each category can be

209   found in Supplementary Table 1.

210   For traits with multiple estimates from a single study (e.g. across years, breeds), we averaged

211   values to obtain a single estimate of h^2, trait mean, V_P and V_A, and these average estimates

212   were used to compute I_A. Evolvability was computed in only one study on cattle (Sartori et al.

213   2015) and estimates were therefore obtained from provided variance component estimates.

214   We took two approaches. In one of these, based on the discussion above, we excluded traits

215   whose mean value minus two standard deviations was less than zero, to ensure that the

216   majority of a population (assuming a normal distribution) would have had positive values for

217   the trait (103 traits). In the other approach we included all estimates, to allow a better

218   comparison to Hansen et al. (2011) where all estimates were also included (119 traits).

219   *Statistical analyses*

220   Patterns among heritability, evolvability, CV_R (coefficient of residual variance which

221   includes all terms apart from V_A) and other parameters were explored with a series of

222   scatterplots. In visualizations of differences among trait classes, one carcass trait with a high

223   heritability (0.8 – see Supplementary Table 1) was excluded from the plots, but not from the

224   analyses. Associations between parameters (h^2, I_A and CV_R) were explored with parametric

225   and non-parametric correlation and regression analyses, with the parametric analyses run on

226   untransformed and log transformed data. Correlations were examined for data pooled across

227   trait classes and for the classes treated separately. To test for heterogeneity in parameter

228   values among trait classes, we used linear models treating log-transformed parameter

229   estimates (to reduce heterogenity in variances) as response variables and trait class as fixed

230   factor. We also ran contingency tests (using the likelihood ratio statistic with P values

231   determined by a randomization test as implemented in SPSS Statistics version 22) to

232   investigate whether traits characterized as having a particularly low heritability (<0.1) and

233   evolvability (<0.2) were randomly distributed across the trait classes.

234

235   **Results**

236

237   *Overall patterns of heritability and evolvability*

238   Heritability estimates included in the analyses varied from 0 to 0.8 and they were estimated

239   usually with high accuracy as reflected by low standard errors (Supplementary Table 1). All

240   I_A estimates were below 10. When considered across all 103 traits with means at least 2 SDs

241   above zero, heritabilities and evolvabilities were positively correlated in both the original

242   (Fig. 1a. $r = 0.371$, P < 0.001; r_s (Spearman rank correlation) = 0.550, P < 0.001) and log-

243   transformed scales (Fig. 1b: $r = 0.540$, P < 0.001). A regression run to predict the evolvability

244   based on trait heritability (log scale) produced an R^2 of 0.292 ($F_{1,102} = 41.60$, P < 0.001).

245   When considered across all 119 traits, similar correlations were obtained for untransformed (r

246   = 0.300, P = 0.001; $r_s = 0.504$, P < 0.001) and log-transformed scales ($r = 0.511$, P < 0.001)

247   and the R^2 of 0.261 ($F_{1,117} = 41.31$, P < 0.001) was also similar.

248

249   *Trait-class comparisons*

250   A comparison of heritabilities among trait classes indicated significant heterogeneity ($F_{5,97} =$

251   6.18, P < 0.001). Life history traits, and to some extent also behavioural traits, tended to have

252   lower heritabilities than other types of traits (Fig. 2a). A comparison of I_A also revealed

253   significant heterogeneity among trait classes ($F_{5,97} = 2.50$, P = 0.036), with the life history

254   traits again showing the lowest values (Fig. 2b). In contrast, CV_R values were homogeneous

255   across different trait classes ($F_{5,97}$=1.4, P = 0.217; Fig. 2c).

256   There was no relationship between CV_R and trait heritability (Fig. 1c; r_s (Spearman rank

257   correlation) = -0.05, P = 0.616; r = -0.117, P = 0.238). In contrast, the I_A values were strongly

258   positively correlated to CV_R (Fig. 1d: r_s = 0.62, P < 0.001) suggesting that evolvability to

259   some extent reflects residual variance when standardised to the mean. We also examined the

260   association between I_A and trait CV (ratio of the SD over the mean), and found that it was

261   strongly positively correlated with I_A (r_s = 0.701, P < 0.001).

262   To gain some further insight on what kind of traits might have lowest evolutionary potential

263   to respond to selection based on both heritabilities and evolvabilities, we focused on traits

264   with $h^2 < 0.1$ and $I_A < 0.2$. For heritabilities < 0.1, we ended up with 29 traits distributed

265   heterogeneously across the trait classes (G = 38.048, df = 5, P < 0.001) with heritabilities for

266   behavioural, disease indicator and life history traits tending to be low (Table 1). For I_A values

267   < 0.2, there were 27 estimates distributed heterogeneously across the trait classes (G =

268   15.825, df = 5, P = 0.011), with over representation of behavioural and life history traits

269   (Table 1). Finally, 17 estimates meet both criteria of $h^2 < 0.1$ and $I_A < 0.2$, and these were

270   distributed heterogeneously across the trait classes (G = 25.96, df = 5, P < 0.001): they were

271   almost exclusively life history or behavioural traits (Table 1).

272   We considered the association between I_A and h^2 for individual trait classes to see if there

273   was a consistent pattern across them, particularly when the different classes are more likely to

274   be scored on similar scales. Figure 3 provides plots for the reduced data set which highlights

275   particularly strong relationships for morphology and behaviour and somewhat weaker

276   relationships for the other traits and particularly disease and growth, although the association

277 is in the same direction across trait classes, and the disease/growth classes were based on the

278 fewest traits (i.e., 11/10 traits respectively, traits with means <2 SD from 0 excluded).

279

280 **Discussion**

281 This survey reinforces the notion that there is an enormous range of heritabilities and

282 evolvabilities across traits, even though we have focused on one species living in a stable

283 environment and for which highly accurate estimates of genetic parameters are available. We

284 also found support for consistent differences in heritability across trait classes similar to those

285 observed in earlier studies, suggesting low heritability of life history traits closely associated

286 with fitness, and higher heritabilities of morphological traits less closely associated with

287 fitness. However, in contrast to data from the natural populations, heritabilities and

288 evolvabilities in the cattle data are positively correlated, contradicting the notion that

289 heritability is weakly correlated to evolvability (Hansen et al. 2011). Furthermore, the view

290 that low heritabilities would be driven by large environmental influences (as reflect by large

291 CV_R – although this also includes non-additive genetic effects) was not supported by the data.

292 In what follows, we will first discuss these findings and their interpretations by relating the

293 results from cattle to those from studies of natural populations.

294

295 *Lessons from livestock*

296 Several patterns consistent with those observed in previous studies on natural populations

297 emerged from our results. First, the proportion of traits showing low heritabilities appears to

298 be high. For instance, 29% of the heritability estimates were < 0.1 when all traits in

299 Supplementary Table 1 are considered, whereas the corresponding value in Hansen et al.'s

300 (2011) review of animal estimates was 19%. One reason why the estimate from farm animals

301 is particularly high may be the publication bias towards high heritability estimates in

302 organisms from natural populations as noted by Palmer (2000). In studies of natural

303 populations or populations derived from natural populations, there is a strong tendency of

304 studies with relatively small sample sizes (and hence large SEs around variance and

305 heritability estimates) to exhibit high heritability values. However, this is less of an issue in

306 cattle studies because of the large sample sizes involved in almost all studies leading to very

307 low SEs (Supplementary Table 1). Estimates of evolvabilities also include many low values

308 in both the current survey and the Hansen et al. (2011) study, with 21% of the cattle estimates

309 being below 0.1% when all traits are considered. In Hansen et al. (2011) 37% of the estimates

310 are < 0.1. These patterns point to limited additive genetic variance present for many traits,

311 suggesting that that selection responses and thereby genetic gains will often be minor.

312 Genomic selection is expected to be especially important in changing these low heritability

313 traits (Visscher et al. 2008).

314 Second, we find that heritabilities are lower for life history traits than for traits from other

315 classes, consistent with previous patterns reported in reviews (Mousseau and Roff 1987;

316 Hansen et al. 2011) and despite the fact that we only considered one set of estimates for each

317 trait. There remains the issue that traits are not independent and many of those listed in

318 Supplementary Table 1 will be correlated with other traits, but our comparisons at least do

319 not involve the same traits being represented multiple times in a survey. Reviews of the

320 livestock literature suggest that the genetic correlations between many of the traits falling into

321 the same categories are not necessarily high (e.g. Bittante et al. 2012; Berry and Crowley

322 2013; Berry and Evans 2014; Egger-Danner et al. 2015; Haile-Mariam and Pryce 2015).

323 Examples from dairy cattle breeds in the Nordic countries include carcass traits such as

324 conformation and fat score with genetic correlations ranging from 0.15 to 0.35, fertility traits

325 where the genetic correlation between number of days from calving to first insemination and

326 non-return rate is typically below 0.15, and genetic correlations between many disease traits

327 that are not significantly different from zero (NAV 2013). Third, unlike in an earlier survey

328 (Houle 1992), but consistent with a later survey (Hansen et al. 2011), we found a positive

329 association between heritability and evolvability measures. The animal data considered by

330 (Hansen et al. 2011) yielded a correlation between h^2 and I_A of 0.096 (P = 0.003) on an

331 untransformed scale, lower than the value of around 0.3 for the cattle survey. However when

332 the 100 x $h^2/4$ limit is applied to the Hansen et al. (2011) data, based on the arguments made

333 in above on limits to I_A, several high I_A estimates are removed, and the correlation increases

334 to 0.345 (N = 891, P < 0.001). Moreover, a Spearman rank correlation computed between

335 these measures based on all the animal data from Hansen et al. (2011) yields a value of r_s =

336 0.412 (N = 992, P < 0.001) increasing to r_s = 0.497 (N = 891, P < 0.001) when the 100 x $h^2/4$

337 limit is applied. Both these values are similar to r_s values of around 0.5 for the cattle survey.

338 In the cattle survey, heritability was not tightly linked to residual variance, which is

339 commonly high for life history traits measured in natural populations due to large

340 environmental effects on these traits (Falconer and Mackay 1996). However we did find that

341 CV_R was highly variable for life history traits measured on cattle (Fig. 2c). Behavioural traits

342 tended to show high CV_R values but this could be connected to low trait repeatabilities

343 (Løvendahl and Munksgaard 2016). However for behavioural traits (and most other trait

344 classes) we nevertheless find a strong positive association between heritability and

345 evolvability (Fig. 3), reflecting trait variation in V_A relative to both means and variances.

346 While we have focused on cattle where there are a very large number of accurate estimates

347 available, it is anticipated that similar patterns would emerge from other livestock species.

348 For instance, genetic parameter estimates for around 30 pig traits measured in the tropics

349 reviewed by Akanno et al. (2013) indicates low heritability (and estimated evolvability) for

350   many life history traits associated with reproduction (litter size, weaning weight, farrowing

351   interval etc.), whereas carcass and growth rates tended to have moderate heritabilities and

352   evolvabilities. Estimates for Sabi sheep reviewed by Matika et al. (2003) also fit this pattern.

353   Whether these patterns will also extend to natural populations once estimates become

354   available for multiple traits scored for the same species held under similar conditions is still

355   unclear. Admittedly rearing environments, selection intensities and methods, population sizes

356   and population structuring often differ between domestic animals and natural populations.

357   However, we argue that our results are still of strong relevance for natural populations based

358   on several observations. Firstly, mean estimates of heritabilities (and evolvabilities) in

359   different trait classes in livestock seem to fit well with those from studies on laboratory

360   animals and wildlife (Mousseau and Roff 1987; Hansen et al. 2011). Secondly, the effective

361   population sizes in most domesticated breeds are below a few hundred (Leroi et al. 2013).

362   This is similar to estimates in many populations in nature (although obviously many natural

363   populations are larger). Thirdly, there is little evidence that livestock populations are

364   genetically depauperate (Kristensen et al. 2015); thus typically no signs of selection plateaus

365   are observed and levels of genetic variation seem high in most breeds (Hill and Kirkpatrick

366   2010). Fourthly, heritabilities for milk yield, a trait that has been under intense directional

367   selection in commercial dairy cattle breeds, is similar in beef cattle breeds where this trait has

368   not been strongly selected for (Miller and Wilton 1999; Lee and Pollak 2002), suggesting that

369   intense directional selection for some traits in some breeds has not changed heritabilities

370   markedly.

371   Finally, we have found that two trait classes (behaviour, life history) have a high incidence of

372   traits with very low adaptive potential regardless of whether this is scored through heritability

373   or evolvability (Table 1). In the livestock literature, it is well recognized that traits with close

374   connections to reproduction and development tend to have low heritabilities (e.g. Safari et al.

375   2005; Morris 2009; Hopkins et al. 2011; Lopez-Villalobos 2012; Akanno et al. 2013; Berry et

376   al. 2014; Brien et al. 2014). In addition to the traits presented here, the heritabilities for other

377   life history traits such as survival in cattle across a specific interval are also very low

378   (Pritchard et al. 2013), with estimates ranging from 0.002 to 0.013 depending on the interval

379   considered between 2 and 750 days (Pritchard et al. 2013). These are traits likely to be

380   constrained genetically and unlikely to change much if directional selection is imposed on

381   them. While mutation will continuously introduce new genetic variation and ensure that some

382   level of V_A is maintained even if mutations are mostly deleterious (Turelli 1988), traits with

383   very low V_A relative to means and variances may be at biophysical limits due to constraints

384   imposed through metabolic processes, energetic requirements, membrane diffusion and so on

385   (Barton and Partridge 2000; Blows and Hoffmann 2005; Hoffmann et al. 2013). Traits like

386   heat loss, food conversion efficiency, metabolic rate and development time may be subjected

387   to these types of constraints. Farmed animals provide an opportunity to explore such limits

388   further given that genetic parameters can be estimated accurately and that information is

389   available on biochemical and metabolic processes underlying production traits.

390

391   *Lessons for livestock*

392   Although there is a wealth of information on h^2 and V_A in livestock, with few notable

393   exceptions (e.g. Sartori et al. 2015; Vallee et al. 2015), estimates of I_A or other measures of

394   evolvability are scarce. Thus h^2 remains the preferred dimensionless population parameter

395   used in animal breeding (Hill and Kirkpatrick 2010) which along with genetic correlations

396   with other traits are used to predict the extent to which a trait is altered by selection. Reliance

397   on h^2 is understandable in the view that in contrast to situation in the wild, the production

398   environment is often considered relatively constant at least in regions of the world with large-

399   scale commercial farming. Selection responses (R) are considered through genetic gain or the

400   breeder's equation, defined by R = h^2S, where S is the selection differential reflecting the

401   intensity of selection multiplied by V_P. Again this measure does not consider changes in the

402   mean of a trait but changes measured in terms of trait standard deviations. Within a farming

403   context, these measures can be translated into the economic benefits of particular selection

404   regimes on traits as long as the association between the economic value of changes in trait

405   standard deviations is known (Hill and Kirkpatrick 2010; Visscher et al. 2008). In

406   evolutionary biology, the equivalent measure might be regarded as fitness, but the exact way

407   in which changes in trait means or standard deviations map onto fitness is usually unknown,

408   and in any case will be highly variable across seasons and years, given that selection in

409   natural populations varies and even changes in sign (Kingsolver et al. 2001).

410   Can low heritabilities and evolvabilities inform animal breeding? There is little evidence that

411   directional selection for milk yield and other agronomic traits has exhausted genetic variation

412   for these traits as there is a history of ongoing genetic gain in most economically important

413   agronomic traits (e.g. Chikhi et al. 2004; Hill and Kirkpatrick 2010; NAV 2013). However

414   there is an increasing interest in selecting on "new" traits that are suited to changing market

415   conditions, environmental considerations and so on (Egger-Danner et al. 2015). For instance,

416   there has recently been interest in selecting cattle for increased heat resistance and reduced

417   methane production to adapt to an increasing frequency of heat waves and to meet

418   environmental concerns. In cattle, it appears possible to select for heat resistance which has a

419   moderate heritability when considered on its own (Dikmen et al. 2012), but a negative

420   interaction between production and resistance may reduce the V_A left in the desired direction

421   of artificial selection (Dikmen et al. 2012; Santana et al. 2015). In some pig breeds however,

422   it appears that heat resistance has a very low heritability (close to 0) with a low V_A

423   (Bloemhof et al. 2012) and I_A (computed from data in this reference), so relatively little

424   progress may be possible within breeds. Where both evolvabilities and heritabilities are low,

425   only little genetic gain may be obtained when selecting on such traits, and if the traits

426   represent limits it may be hard to overcome them. Several behavioural and life-history traits

427   fall into this category (Table 1) and estimating both h^2 and I_A (when meaningful) might better

428   enable animal breeders to identify traits that are evolutionary constrained. Information on

429   both measures may also be useful in situations where a trait has both high h^2 and I_A which

430   suggest that the trait is likely to respond fast to selection across variable environments and in

431   herds with different means. Thus, biologically meaningful estimates of I_A can inform also

432   animal breeders.

433

434   **Conclusions**

435   Similarly to data from the wild, the results of this study suggest that life history and

436   behavioural traits have lower heritabilities than morphological traits in cattle. However, in

437   contrast to data from natural populations, this is also true in the case of evolvabilities, and

438   evolvabilities and heritabilities across the investigated traits in cattle were positively

439   correlated. It is not clear if the patterns established here for livestock would hold up in studies

440   of natural populations because there are differences both in data quality and levels of

441   environmental variability experienced by natural populations. A useful way forward would

442   involve larger studies of natural populations of a single species or set of related species across

443   multiple trait sets, particularly for sets of traits that are normally distributed. Both

444   evolvability and heritability remain important genetic parameters for predicting evolutionary

445   potential and constraints in ecologically important traits.

446

Acknowledgments

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564   Fig 1. Associations between (a-b) heritability and evolvability (I_A), between (c) the coefficient of

565   residual variance (CV_R) and heritability and (d) between CV_R and I_A for cattle traits (with means >2 SD

566   from 0). The association between heritability and evolvability is plotted both (a) without

567   transformation and (b) with log transformation of both parameters. Traits belonging to different

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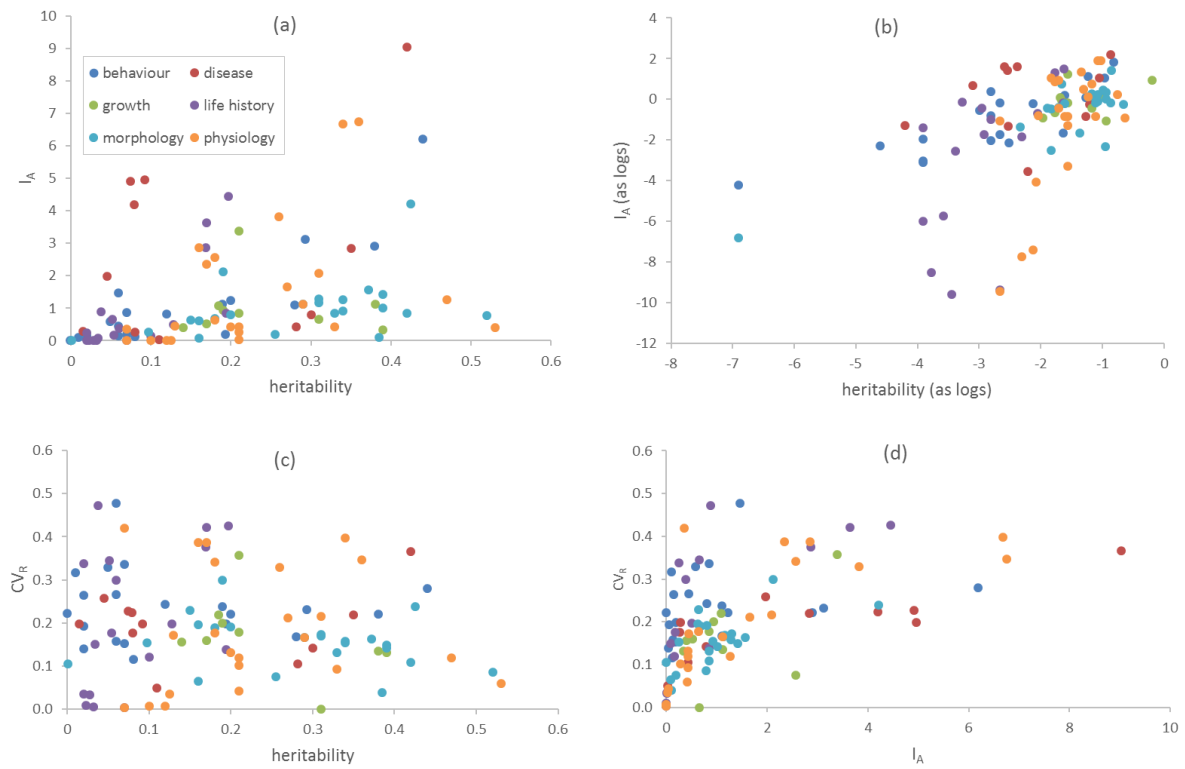
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571   Fig. 2. Box plots for comparison of (a) heritabilities, (b) evolvabilities and (c) CV_R values across trait
572   classes. Outlier data points are included in the graph (indicated by dots and asterisks)

(a)

(b)

(c)
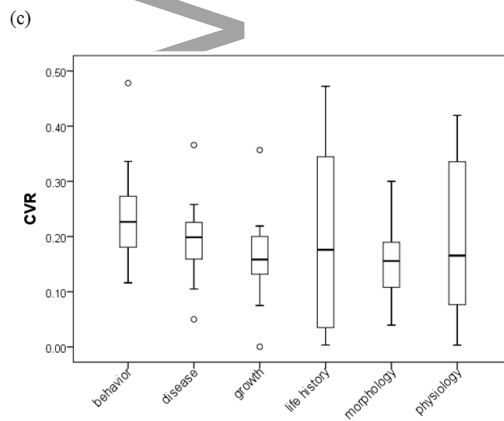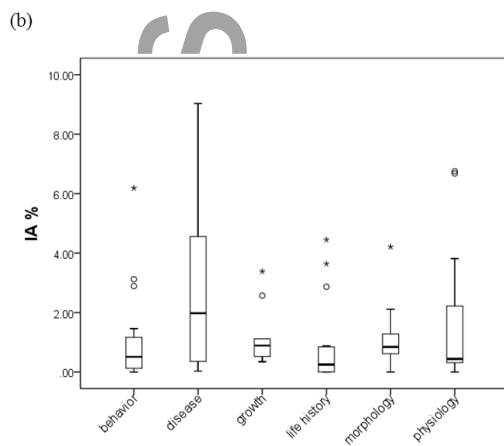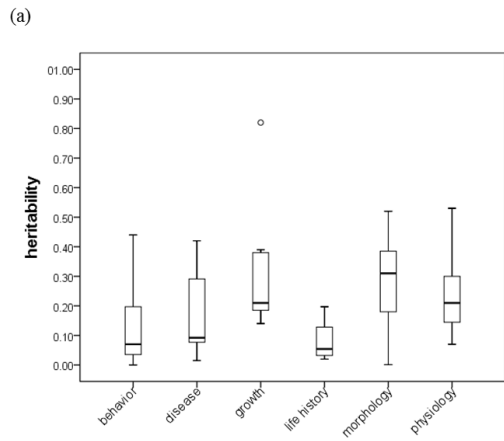
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575   Fig. 3. Association between heritability and evolvability (both log transformed) plotted for trait
576   classes separately (based on traits with means >2 SD from 0) along with R_2 values.
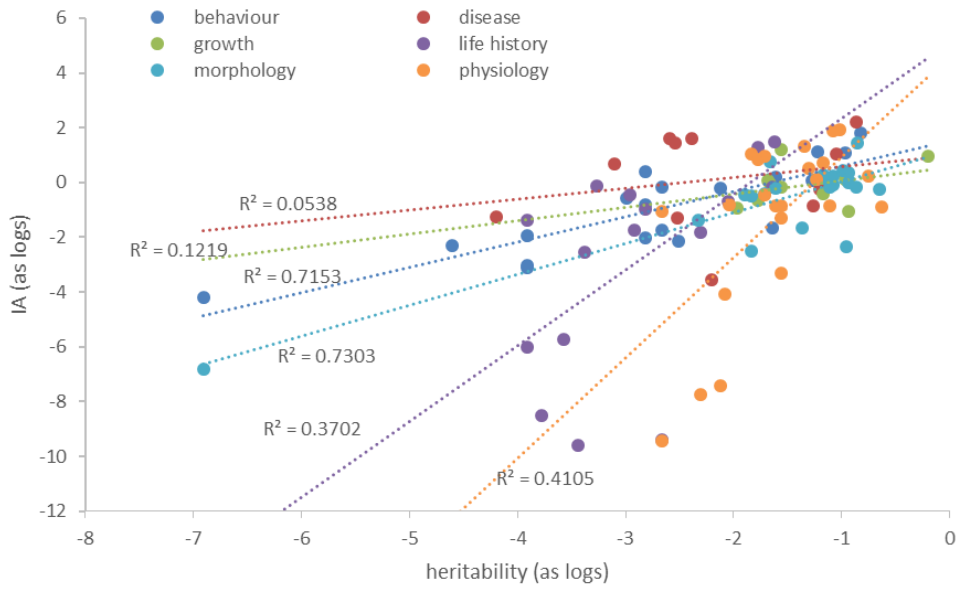
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Trait class	Heritability		Evolvability		Both	
	Low	Not Low	Low	Not Low	Low	Not Low
behaviour	12	8	9	11	8	12
disease indicator	6	5	1	10	0	11
growth	0	10	0	10	0	10
life history	11	6	8	9	7	10
morphology	2	20	4	18	1	21
physiology	2	21	5	18	1	22

581

582