

1 **Evolutionary quantitative genetics of juvenile body size in a population of feral horses**
2 **reveals sexually antagonistic selection**

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4 Charlotte E. Regan^{1†}, Laura Tuke^{2†}, Julie Colpitts¹, Philip D. McLoughlin¹, Alastair J. Wilson² and
5 Jocelyn Poissant^{3*}

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7 ¹ Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK S7N 5E2,
8 Canada

9 ² College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, Penryn, TR10
10 9FE, UK

11 ³ Department of Ecosystem and Public Health, University of Calgary, 3280 Hospital Drive, Calgary, AB
12 T2N 4N1, Canada

13 †These authors contributed equally to this work

14 ***Corresponding author:** Jocelyn Poissant: Department of Ecosystem and Public Health, University of
15 Calgary, 3280 Hospital Drive, Calgary, AB T2N 4N1, Canada; Phone +1(403) 210-6734; Fax +1(403)
16 210-9740; jocelyn.poissant@ucalgary.ca

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25

26 **Abstract**

27 Inter-individual variation in juvenile body size can have important consequences for individual
28 fitness, population dynamics, and adaptive evolution. In wild vertebrate populations, larger
29 juvenile size is usually expected to be selected for. However, understanding how such selection
30 may translate into adaptive evolution requires an understanding of the genetic underpinnings of
31 early development and the factors modulating selection. In this study, we characterised the
32 genetic basis of and selection pressures acting upon juvenile body size in a large insular
33 population of feral horses on Sable Island, Canada, to gain insights into the evolution of juvenile
34 body size in wild vertebrate populations. We used pedigree-based quantitative genetic ‘animal
35 models’ to quantify the sources of phenotypic variation in withers-knee length, and assessed the
36 influence of maternal age, sex, and temporal (birth year) and spatial environmental heterogeneity
37 in modulating overwinter survival selection. We found that withers-knee length is moderately
38 heritable and that there was a significant positive genetic correlation between males and females.
39 There was no indication of directional selection in a pooled-sex analysis, but we did find
40 evidence for significant sexually antagonistic selection, with a tendency for smaller body size to
41 be favoured in males and larger body size to be favoured in females. These results suggest that
42 juvenile body size has the potential to evolve in this population, and that selection on juvenile
43 size may play an important role in modulating sex-specific contributions to population dynamics.
44 However, our results also suggest that there is unlikely to be evolutionary change in the mean
45 body size of Sable Island foals.

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48

49 **Introduction**

50 Wild animal populations are characterised by inter-individual variation, from differences in
51 physiological (e.g., hormonal responses [Jenkins et al. 2014]) and morphological traits (e.g., horn
52 length [Coltman et al. 2005]), to differences in behaviour (Dingemanse et al. 2012) and life-
53 history traits (e.g., age at first reproduction [Jorgenson et al. 1993]). Such variation is crucial for
54 enabling effective responses to changes in environmental conditions, whether through plasticity,
55 dispersal, or evolutionary change. Thus, researchers have long been interested in understanding
56 the processes that maintain variation in phenotypic traits within wild populations and modulate
57 responses to changing conditions (Hendry 2017).

58

59 Juvenile body size is a trait that varies considerably in populations of wild vertebrates and is
60 closely associated with individual fitness (e.g., Rollinson and Rowe 2015; Kruuk 2017; Bonnet
61 et al. 2017) due to its association with early survival, development, and subsequent reproduction
62 (Clutton-Brock et al. 1987). This strong association between inter-individual variation in juvenile
63 body size and fitness is likely to have significant consequences for population and evolutionary
64 dynamics (Clutton-Brock et al. 1987; Ronget et al. 2018). Indeed, changes in juvenile body size
65 have been linked with changes in population size through their effects on juvenile fitness
66 components, such as survival (Clutton-Brock et al. 1987; Clutton-Brock et al. 1992). Therefore,
67 understanding the determinants of inter-individual variation in juvenile body size and the
68 consequences of such variation for population dynamics and evolutionary processes has been,
69 and continues to be, a focus of research in evolutionary and population ecology.

70

71 Previous studies have shown that a number of factors contribute to variance in juvenile body size
72 and so, presumably to fitness. These include environmental conditions early in life, such as
73 climate (Forchhammer et al. 2001) and population density (Toïgo et al. 2006), as well as
74 maternal characteristics, such as age (Bowen et al. 1994; Derocher and Stirling 1998) and
75 dominance rank (Altmann and Alberts 2005; Michel et al. 2015). However, adaptive evolution of
76 juvenile body size requires that it has a genetic basis of variation (i.e., significant heritability)
77 and that it is under directional selection. Body size traits have been consistently shown to be
78 moderately heritable (Postma 2014) and significant heritability for juvenile body size has been
79 found on a number of occasions (e.g., Garant et al. 2004; Wilson et al. 2005b; Wilson et al. 2007;
80 Postma 2014). Due to large juvenile size being expected to increase fitness, selection for larger
81 juvenile body size is also anticipated in wild vertebrate populations. Indeed, a large number of
82 studies have demonstrated a positive relationship between juvenile body size and survival in wild
83 vertebrate populations (summarised in Ronget et al. 2018).

84
85 Despite the common occurrence of both (directional) selection and heritable variation, previous
86 studies have frequently been unable to detect changes in the phenotypic distribution of juvenile
87 body size over time. Several hypotheses have been put forward to explain this so-called ‘paradox
88 of stasis’. These include cryptic evolution, where fluctuating environmental conditions mask
89 genetic change at the phenotypic level (Merilä et al. 2001), antagonistic selection, for example
90 between offspring size and parental investment (Rollinson and Rowe 2015), or between the sexes
91 (Cox and Calsbeek 2009), and the effect of skewed phenotypic distributions on natural selection
92 and its estimation (Bonamour et al. 2017). Nevertheless, little consensus over the importance of
93 these potential explanations has been reached; hence, we still do not fully understand when

94 adaptive evolutionary change in juvenile body size is to be expected. Greater diversity in studies
95 of the evolutionary ecology of juvenile body size will help facilitate improved understanding of
96 the conditions leading to evolution of this trait in wild populations. This is because both
97 heritability estimates and selection pressures are context specific. For example, heritability
98 estimates depend on factors including migration, previous selection, inbreeding, and the
99 importance of non-genetic sources of trait variation (Visscher et al. 2008), whilst selection
100 pressures are driven by the biotic and abiotic environment, which is specific to a given
101 population at a particular time.

102

103 In this study, we investigate the genetic basis of, and selection on, juvenile body size in the
104 isolated feral horse population (*Equus ferus caballus*) of Sable Island, Canada between 2012 and
105 2016. This population is a valuable system in which to study the evolutionary potential of
106 juvenile body size in a wild ungulate because it differs considerably from other ungulate
107 populations that are more frequently the subject of quantitative genetic study. For example, the
108 population is confined to an island that lacks both predators and other terrestrial competitors.
109 Furthermore, horses are not sexually dimorphic and exhibit a social system that is unique among
110 ungulates, forming stable social groups that consist of multiple unrelated adult females, their
111 immature offspring, and one or more adult males (Cameron et al. 2003). Thus, this system
112 provides an opportunity to examine the evolutionary potential of juvenile body size in a
113 population that is likely to be experiencing different selection pressures to other previously
114 studied ungulate populations. To examine the evolutionary potential of juvenile body size (in our
115 cases juveniles are defined as foals – individuals less than one year of age) in the Sable Island
116 population, we start by decomposing the variance in juvenile body size into genetic and

117 environmental components. We then assess the strength and form of selection on juvenile body
118 size and identify intrinsic/extrinsic factors modulating selection by using data on foal over-winter
119 survival.

120

121 **Materials and Methods**

122 **Study area and population**

123 Sable Island National Park Reserve is a crescent-shaped sandbar situated approximately 275 km
124 southeast of Halifax, Nova Scotia, Canada (43°55'N, 60°00'W). The island is ~50 km long, 1.25
125 km wide at its widest point, and features a strong habitat gradient, with greater availability of
126 freshwater and important forage species in the west compared to the east (Contasti et al. 2012). It
127 is home to a population of up to 550 feral horses (population size has ranged from ~150 to ~550
128 horses since 2007) that was founded by introductions during the mid-1700s (Plante et al. 2007).
129 Since 2013, the island has been managed as a National Park Reserve, where the horses are
130 recognised by Parks Canada Agency as a naturalised species (Laforge et al. 2016). Given the
131 isolation of the population and the lack of introgression since the early 20th century (Welsh 1975)
132 the population does experience inbreeding (Lucas et al. 2009), though we currently have little
133 information regarding the degree of inbreeding depression. From 2007, individuals have been
134 followed as part of an ongoing long-term individual-based study, enabling individual life-
135 histories to be tracked and the collection of additional data (Debeffe et al. 2016, 2017; Cabrera et
136 al. 2017), including morphological measures, such as body size (Weisgerber et al. 2015).

137

138 The majority of individual data is collected through systematic whole-island censuses each
139 summer (typically from mid-July to early September) coinciding with the mid- to late-breeding

140 season. To conduct censuses, we split the island into seven sections, as this allows a section to be
141 surveyed by researchers on foot each day and therefore whole-island coverage in one week (and
142 this is repeated multiples times during a field season). When horses are encountered, we record
143 their locations using a handheld global positioning system (GPS), and note individual
144 characteristics, such as sex, group membership, and age group (foal, yearling, or adult). We also
145 take photographs of each horse from multiple angles to enable later individual identification. The
146 summer censuses account for >99% of horses each year; therefore, individuals are presumed
147 dead if they are not observed in a given census year.

148

149 **Body size measures**

150 Alongside the summer censuses, we measure individual body size using non-invasive digital
151 photogrammetry, based on a standardised method outlined in Weisgerber et al. (2015). From a
152 distance of 5–10 m, we take photographs of each horse using a laser standard, with two lasers
153 projected horizontally onto the horse's barrel. The laser standard consists of a rectangular frame
154 mounted with a digital camera and two parallel fixed laser sights (19.05 cm apart; calibrated each
155 day). From these photographs, we take multiple measures of skeletal body size (Fig. 1) using the
156 ImageJ image processing software (Schneider et al. 2012). We measure the pixel length distance
157 between the appropriate points on the body and convert this into centimetres using the laser
158 standard distance (19.05 cm).

159

160 This study focuses on the body size of 287 foals born between 2012 and 2016 ($n=86, 16, 69, 59,$
161 and 57, respectively), with foals defined as individuals aged <1 year. Multiple body size
162 measurements were generally obtained for each foal in each field season (on separate days)

163 ranging from one to seven measures per individual ($\bar{x} = 2.06$, $SD = 1.25$) resulting in 593
164 measurements in total. We originally considered three measures of skeletal body size (heart
165 depth [HD], withers-knee length [WK], and sternum-pin length [SP]) as these have been shown
166 to be the most reliable predictors of overall horse body size (Weisgerber et al. 2015). However,
167 we present analyses using only withers-knee length because all three measures were strongly
168 correlated ($r=0.89$, $t_{591}=48.30$, $p<0.001$ for HD-WK; $r=0.91$, $t_{591}=54.61$, $p<0.001$ for HD-SP; and
169 $r=0.86$, $t_{591}=41.90$, $p<0.001$ for WK-SP), had similar repeatabilities (WK: 0.73 ± 0.11 [SE]; HD:
170 0.76 ± 0.11 ; SP: 0.80 ± 0.11), and withers height is a commonly used measure of horse size that
171 is correlated with composite measures of horse body size (Brooks et al. 2010).

172

173 **Statistical analysis**

174 **Heritability estimation**

175 We fitted a type of linear mixed-effects model, known as an ‘animal model’, in ASReml 4.1
176 (Gilmour et al. 2015) to partition the phenotypic variance in juvenile body size into genetic and
177 environmental components. To do this, we used a pedigree compiled from field observations
178 spanning 2007 to 2016, with maternal identities inferred from suckling behaviour and paternal
179 identities assumed based on the identity of the band stallion at the time of breeding (i.e., the
180 previous summer). Analyses presented herein were based on a pruned version of the full
181 pedigree only containing individuals contributing to the estimation of quantitative genetic
182 parameter for juvenile body size. This pruned pedigree contained 599 individuals, with 346
183 maternal links and 398 paternal links (from 120 distinct dams and 202 distinct sires), and 123
184 and 665 pairs of full- and half-siblings, respectively. Incorrect assignment of pedigree
185 relationships due to the use of social information may be expected to influence quantitative

186 genetic parameter estimates. However, studies suggest that results from analyses using social
187 pedigrees may be relatively robust and that incorrect assignment of paternity is likely to result in
188 a more conservative estimate of trait heritability (Charmantier and Réale 2005; Firth et al. 2015).
189 The degree to which males other than the dominant band stallion sire offspring in feral horses
190 varies considerably, ranging from as low as 15% (Kaseda and Khalil 1996) to approximately
191 50% (Gray et al. 2012). Therefore, although we do not yet know the degree of error in Sable
192 Island horse paternity assignments, there may be a small change in parameter estimates if a
193 genetic pedigree was available.

194

195 In the animal models, we included fixed effects of birth year (five-level factor [2012 – 2016]), to
196 account for potential cohort effects, Julian date (covariate), to account for growth over the
197 summer, maternal age (three-level factor [3, 4, and 5+ years]), to account for differences in
198 maternal investment with age, and an interaction between birth year and Julian date. This fixed
199 effect structure (which excluded individual summer median location) was selected as the most
200 appropriate by comparing linear mixed-effects models with different combinations of fixed
201 effect terms prior to animal model analysis (see supporting information for details). We started
202 by fitting a model that included foal additive genetic merit (to partition the additive genetic
203 variance, V_A) and a permanent environment effect (i.e., among-individual differences arising
204 from environmental conditions or non-additive genetic effects, V_{PE}) as random effects. We then
205 constructed an additional model containing a maternal identity term (V_M) to understand the
206 importance of maternal effects in generating variation in juvenile body size and avoid potential
207 upward bias in the heritability estimate (Wilson et al. 2005a). To get an estimate of the cross-sex
208 genetic correlation, we also fitted a bivariate animal model with male and female juvenile body

209 sizes treated as different traits. This model included the same fixed effects as above, as well as
210 additive genetic and permanent environment random effects (models including a maternal effect
211 term would not converge), allowing us to estimate sex-specific V_A and V_{PE} , as well as the cross-
212 sex genetic covariance for V_A . Note that because individuals are either male or female and can
213 therefore only have a measurement for either the female or male size trait, the cross-sex
214 covariance for V_{PE} and the residual component are not estimable.

215

216 We used likelihood ratio tests to determine the significance of random effects, assuming the test
217 statistic was distributed as a 50:50 mix of χ^2 distributions with zero and one degrees of freedom
218 (Self and Liang 1987). To test whether the additive genetic correlation between male and female
219 juvenile body size was significantly different from zero or one, we used a likelihood ratio test
220 (assuming a χ^2 distribution with one degree of freedom) to compare a model where the
221 covariance was estimated to models where the covariance was fixed at zero or correlation fixed
222 to one. We also tested for a difference in the magnitude of sex-specific additive genetic variances
223 by comparing a model where sex-specific additive genetic variances were allowed to vary with
224 one where they were constrained to be equal (with significance tested using a likelihood ratio test
225 assuming a χ^2 distribution with two degrees of freedom). We calculated narrow-sense heritability
226 (h^2) as the ratio of additive genetic variance to phenotypic variance (i.e., V_P , the sum of all
227 estimated components): $h^2 = V_A / V_P$, with similar ratios obtained for permanent environment
228 effects (pe^2), maternal effects (m^2), and residual error (r^2). We estimated the cross-sex additive
229 genetic correlation (r_{Amf}) as:

230
$$r_{Amf} = \frac{Cov_{Amf}}{\sqrt{V_{Am} \times V_{Af}}}$$

231 where V_{Am} and V_{Af} are the male- and female-specific V_A , respectively. It is important to note that
232 estimates are ‘conditioned’ on the fixed effects included within each model (Wilson 2008). To
233 allow comparison with other studies, we also calculated coefficients of additive genetic variation
234 using the formula (Houle 1992):

$$235 \quad CV = 100 \times \frac{\sqrt{\text{variance}}}{\text{sample mean}}$$

236

237 **Selection analysis**

238 For selection analyses, we only considered 230 of the 287 foals in these analyses because the
239 fates of individuals born in 2016 were unknown at the time of analysis. As a first step, we tested
240 if selection on withers-knee length was modulated by intrinsic (sex) and extrinsic (maternal age,
241 location (median summer longitude to assess the effect of the island resource gradient – no
242 individuals use the entire island, with within-summer movements averaging only 8000 m
243 [Marjamäki et al. 2013]), and birth year) factors using generalised linear models (GLMs) with
244 over-winter survival as the response variable. To avoid the problems associated with performing
245 such analyses on best linear unbiased predictions (BLUPs, often used to standardise
246 measurements to a specific moment in time) (Hadfield et al. 2010; Houslay and Wilson 2017),
247 we used non-parametric bootstrapping (1000 bootstraps in the ‘boot’ package [Canty and Ripley
248 2017]) to establish 95% confidence intervals around the coefficients from two different GLMs
249 using data where individuals were each represented only once. The first model contained linear
250 and quadratic withers-knee length terms (scaled prior to incorporation so that both terms are
251 interpretable) as well as birth year (four-level factor [2012–2015]), maternal age (three-level
252 factor [3, 4, and 5+ years]), location (covariate), and foal sex (two-level factor). The second
253 contained a first-order interaction between withers-knee length and one of the above

254 intrinsic/extrinsic factors as well as main effects of all the remaining intrinsic/extrinsic factors.
255 We found that the clearest effect of any of the interactions was that between sex and withers-
256 knee length (Table 3), suggesting that, of the variables we considered, sex was the key one
257 modulating selection.

258

259 Given strong evidence for selection to be modulated by sex, we then proceeded to obtain formal
260 estimates of selection differentials for all foals, and for males and females separately. For this,
261 we used bivariate linear mixed models in MCMCglmm (Hadfield 2010) with relative over-winter
262 survival (survival divided by mean survival) as the fitness component and wither-knee length as
263 the phenotypic trait (standardised to $\bar{x} = 0$ and $SD = 1$) for all foals as well as males and females
264 separately. We assumed a Gaussian distribution for both relative survival and withers-knee
265 length to provide interpretable selection differentials. For the survival trait, we included fixed
266 effects of foal birth year (four-level factor [2012–2015]), and for withers-knee length, we also
267 included the Julian date of the body size measurement (covariate) and the interaction between
268 birth year and Julian date as fixed effects. All models included foal ID as the single random
269 effect, with the individual-level covariance between body size and survival providing an estimate
270 of the variance-standardised selection differentials. In both cases, the residual variance for
271 survival was fixed at 0.0001 as it is not estimable. However, because the distribution of relative
272 survival is not Gaussian, the resulting credible intervals are not exact and cannot be used to
273 denote significance. Thus, to assess significance, we also repeated the models using the threshold
274 family to model survival as a binary trait (constraining the latent variables to be between ± 7 to
275 prevent under/overflow) and assumed a Gaussian distribution for the body size measure(s).
276 These models did not have any random effects for survival, but the residual survival effect was

277 allowed to covary with the ID effect on foal withers-knee length, using the ‘covu = TRUE’
278 command in the first residual structure specified in the prior (see section 1 in the supporting
279 information from Thomson et al. (2017) for more detail on this approach). These models also
280 included the same fixed effects as the models used to estimate differentials described above.
281 Selection differentials from the first set of models were assumed to be statistically significant if
282 the 95% credible intervals from the latter threshold models did not overlap zero. Similarly, we
283 assessed whether the posterior distribution of male and female selection differentials were
284 significantly different from each other by subtracting one from the other (from the threshold
285 models) and examining whether this distribution overlapped zero. In all cases, we used the
286 default priors for the fixed effects, and an inverse-Wishart prior with low degree of belief
287 parameter (0.002) for the residual and random effect terms. All models were run for 1,100,000
288 iterations (burn-in = 30,000 and thin = 1000) as these resulted in low autocorrelation between
289 retained samples (<0.10). We also ran the analysis twice and checked model convergence using
290 the Gelman-Rubin convergence diagnostic (Gelman and Rubin 1992) in the R package ‘coda’
291 (Plummer et al. 2006).

292

293 **Results**

294 **Heritability estimation**

295 Foal withers-knee length ranged from 41.5–76.7 cm, with a mean of 62.1 cm (SD = 5.3 cm). The
296 fixed effects portion of the animal model indicated that older mothers had foals with larger
297 withers-knee lengths, that foal withers-knee lengths increased over the summer, and that the
298 degree of increase across the summer varied between years (Table 1). We also found some
299 evidence for significant additive genetic variance in foal withers-knee length ($\chi^2_{(0,1)} = 17.34, p$

300 <0.001). Incorporating the maternal effect term did not improve model fit ($\chi^2_{(0,1)} = 0.69, p =$
301 0.20), suggesting that maternal effects (both environmental and genetic) did not account for a
302 significant proportion of the phenotypic variance in juvenile body size. However, adding the
303 maternal effect term did result in a decline in the estimated heritability from 0.54 (± 0.15 [SE]) to
304 0.38 (± 0.22 ; Table 2), with the additive genetic component being marginally non-significant in
305 this model ($\chi^2_{(0,1)} = 2.40, p = 0.06$). The coefficient of additive genetic variation for withers-knee
306 length was 6.18 in the model excluding maternal effects and 5.14 in the model including a
307 maternal effect term. Using the bivariate animal model, we also found a positive genetic
308 correlation between male and female juvenile body size that was significantly different from zero
309 ($r_{Amf} = 0.77 \pm 0.34, \chi^2_{(1)} = 4.61, p = 0.03$), but not from one ($\chi^2_{(1)} = 0.37, p = 0.54$). An equivalent
310 model in MCMCglmm produced comparable results (posterior mean = 0.75, 95 % credible
311 interval: 0.09, 0.99). There was also no evidence to suggest that the additive genetic variance for
312 withers-knee length differed between the sexes ($\chi^2_{(2)} = 0.86, p = 0.65$).

313

314 **Selection analysis**

315 Between 2012 and 2015, foal over-winter survival was 71% and our GLMs indicated that
316 relative survival was not associated with withers-knee length when considering all foals (95% CI
317 for linear withers-knee length term: $-0.07, 0.19$). Similarly, we found no evidence for quadratic
318 selection (95% CIs: $-0.07, 0.10$). Furthermore, survival selection did not appear to vary given
319 maternal age, or birth year (except for 2013), as the 95% CIs for these effects crossed zero
320 (Table 3). However, we did find weak support for interactions between withers-knee length and
321 location (Table 3), and between withers-knee length and sex (95% CI = $-0.79, -0.32$ [female =
322 reference level]). This latter effect suggested that male foals with larger withers-knee lengths had

323 reduced survival relative to those with smaller withers-knee lengths, whilst the opposite was true
324 for females (see Table S1 for CIs for all effects).

325

326 We found no evidence for significant directional selection on withers-knee length in our analysis
327 considering all individuals and all phenotypic measurements in a bivariate mixed model ($S = -$
328 0.009 , 95% CI from a model using the threshold family for survival overlapped zero: $-0.13,$
329 0.19 , Fig. 2). However, when we treated male and female body size as separate traits, we found
330 that males with larger withers-knee lengths tended to have lower survival ($S = -0.09$, 95% CI
331 from a model using the threshold family for survival overlapped zero: $-0.42, 0.03$, Fig. 2), whilst
332 the opposite was true for females ($S = 0.07$, 95% CI from a model using the threshold family for
333 survival *did not* overlap zero, indicating significance: $0.01, 0.49$; Fig. 2). Finally, male and
334 female selection differentials were significantly different from each other (95% CI for difference
335 between sex-specific covariances from a model using the threshold family for survival *did not*
336 overlap zero: $-0.74, -0.09$; Fig. 2).

337

338 **Discussion**

339 We found evidence that the body size of Sable Island foals, measured as withers-knee length, is
340 moderately heritable, and therefore has the potential to undergo adaptive evolutionary change.
341 While we found no evidence for consistent directional selection when either combining both
342 sexes or treating them separately, selection differentials differed significantly and were of
343 opposite sign between the sexes, suggesting the presence of sexually antagonistic selection, a
344 phenomenon that may constrain change in mean juvenile body size within this population.

345

346 Much recent work has centred on trying to explain the lack of phenotypic change in wild
347 populations, particularly in cases where traits have a substantial genetic component and are
348 associated, or expected to associate, with individual fitness (e.g., Merilä et al. 2001; Kruuk et al.
349 2002). One process that may preclude adaptive evolutionary change in wild populations is
350 antagonistic selection, which may occur between traits expressed in the same individual at the
351 same point in ontogeny (Gratten et al. 2008), between traits expressed at different life stages
352 (Charmantier et al. 2006; Lemaître et al. 2015) or generations (Mainguy et al. 2009; Rollinson
353 and Rowe 2015), or between the sexes (Foerster et al. 2007; Mills et al. 2012), as suggested by
354 our results. Thus, our work provides an additional example of a mechanism that may be an
355 important barrier to evolutionary change in natural systems. Indeed, attention has previously
356 been drawn to the lack of studies investigating the presence of sexually antagonistic selection in
357 the wild, possibly because there may be a tendency for studies of highly sexually dimorphic traits
358 to focus on trait expression in a single sex, and for studies of monomorphic traits to study both
359 sexes simultaneously (Cox and Calsbeek 2009). There are also few studies that estimate both
360 selection and cross-sex quantitative genetic parameters simultaneously (Cox and Calsbeek 2009;
361 Poissant et al. 2010).

362

363 Studies examining sex-specific selection often report sexually antagonistic selection (Cox and
364 Calsbeek 2009). For example, a study on great reed warblers, *Acrocephalus arundinaceus*, found
365 that male wing length was under positive directional selection ($S = 0.18$, $p = 0.02$) whilst female
366 wing length was under negative direction selection ($S = -0.12$, $p = 0.03$; Tarka et al. 2014).
367 Similarly, a study on Soay sheep, *Ovis aries*, found significant positive selection on horn size in
368 males ($S = 0.07$) and non-significant negative selection on females ($S = -0.04$), with an

369 interaction between sex and horn size providing evidence for sexually antagonistic selection
370 (Robinson et al. 2006). The difference between male and female selection reported here (0.16) is
371 somewhat lower than the median value of 0.30 reported in other studies (Cox and Calsbeek
372 2009). However, a difference of 0.16 appears substantial when compared only to traits showing
373 little sexual dimorphism (Figure 4A in Cox and Calsbeek [2009]). In addition, evidence for
374 statistically significant sexually antagonistic selection, as reported here, is rare (Cox and
375 Calsbeek 2009), and recent work by Morrissey (2016) suggests that previous informal meta-
376 analyses (Cox and Calsbeek 2009) that have assessed the presence of sexually antagonistic
377 selection using the absolute difference between male and female coefficients have likely
378 overstated its presence due to substantial covariation between male and female selection
379 coefficients.

380

381 Sexually antagonistic selection can have different consequences, depending on the specific
382 context. It may lead to sexual dimorphism in the trait in question, or to suboptimal mean
383 phenotype in both sexes (Lindenfors 2002; Cox and Calsbeek 2009). The result depends on a
384 complex interplay of factors, including the fitness component considered, the degree to which
385 trait expression in the sexes shares the same genetic architecture (Poissant and Coltman 2009;
386 Poissant et al. 2010), and the existence and strength of pleiotropic constraints as genes that
387 control multiple phenotypic traits are likely to be under very complex selection and thus may be
388 unable to respond to sex-specific selection (Mank et al. 2008; Poissant et al. 2016). Thus,
389 establishing the evolutionary consequences of antagonistic selection is complex, particularly in
390 wild systems (but see Poissant et al. 2016), and further work will be necessary to ascertain the
391 potential consequences of our finding that male and female Sable Island horses experience

392 differential selection early in life (this is discussed in greater detail below). Nevertheless, the
393 strong genetic correlation between male and female juvenile body size found here may hinder the
394 evolution of increased sexual dimorphism in juveniles of this population (Lande 1980; Poissant
395 et al. 2010).

396

397 In this study, we only considered viability selection on juvenile body size, but it is possible that
398 relationships between juvenile body size and other fitness components, for example reproductive
399 success, may influence the total selection on juvenile body size. This is particularly likely if
400 juvenile body size influences other traits, such as age at sexual maturity and adult body size, that
401 may influence reproductive performance. Such associations have been shown in other wild
402 systems (e.g., correlations between juvenile size and age at maturity/first reproduction [Albon et
403 al. 1987; Jorgenson et al. 1993], and correlations between age-specific traits [Wilson et al.
404 2005b]) and thus may also be present in our study system. The evolution of body size in the
405 sexes is believed to be driven by different types of selection, with fecundity selection being the
406 predominant driver of larger body size in females and sexual selection expected to be the major
407 driver of larger body size in males (Blanckenhorn 2000). Due to their unusual mating system,
408 where males defend harems year round (Linklater et al. 1999), horses may prove an interesting
409 system in which to test this idea. For example, there is little evidence to suggest that larger male
410 body size is associated with factors such as male dominance when in a multi-stallion band
411 (Linklater and Cameron 2000), the length of a male's tenure as band stallion, or a male's
412 reproductive success (Feh 1990). Thus, if body size in male horses is correlated at different
413 points during life, then the fact that larger body size is not advantageous in terms of reproductive
414 success may also mean there is little selection for males to be larger as juveniles (Wilson et al.

415 2005b). Therefore, although viability selection is likely to be the most important selection type
416 acting upon juvenile body size, an understanding of body size evolution in populations such as
417 the Sable Island horses will require an understanding of the inter-dependence of body size traits
418 at different points in ontogeny and the differing selection types acting on these traits. As the
419 long-term study continues and data availability increases, we will not only be able to explore
420 correlations between the same trait expressed at different life stages (Poissant and Coltman
421 2009), but will be able to investigate the importance of genetic correlations between body size
422 and other traits for constraining or accelerating evolutionary change.

423

424 Over and above the potential evolutionary consequences, our work raises some interesting
425 questions about the role of body size in determining fitness in the Sable Island horse population
426 and other similar populations. The lack of a clear and consistent signal of positive directional
427 selection in both sexes was unexpected, given that larger juvenile body size is generally expected
428 to confer a survival advantage. Indeed, this finding contrasts to results from other ungulates, such
429 as bighorn sheep, *Ovis canadensis* (Festa-Bianchet et al. 1997), roe deer, *Capreolus Capreolus*
430 (Gaillard et al. 2000) and red deer, *Cervus elaphus* (Loison et al. 1999). Sable Island horses, by
431 nature of being an island population may be expected to show different trends in juvenile body
432 size due to differences in the environment they experience, including the common lack of
433 predation and inter-specific competition, and severe intra-specific competition. For example,
434 research suggests that larger species confined to islands tend to evolve smaller body size
435 (Foster's Island Rule; Foster 1964), perhaps due to heightened competition for resources
436 (Lomolino 2005). Therefore, smaller body size may be advantageous on Sable Island due to the
437 pronounced seasonal resource shortages. However, no such trend has been found in a similar

438 island population, the St. Kilda Soay sheep (Ozgul et al. 2009), and it is unclear how the sex-
439 difference indicated in our results fits with the idea of insular dwarfism.

440

441 Sex-biased maternal investment is perhaps one of the most likely explanations for the sex-
442 specific selection on juvenile body size we observed in our study population. Horses have a long
443 period of maternal investment, with offspring receiving post-natal care in the form of lactation,
444 but also prolonged social support before natal dispersal at between two and three years of age
445 (Cameron et al. 2003). Despite the lack of sexual dimorphism in horses, research suggests that
446 females invest more into daughters than sons when in poor condition (Cameron and Linklater
447 2000). Given that winters on Sable Island are harsh and females experience severe drops in body
448 condition, it is possible that smaller males, by virtue of being less costly to their mothers, receive
449 more adequate levels of care than larger male foals, and therefore are more likely to survive their
450 first winter. To establish whether this is the case, future research should aim to understand the
451 condition-dependent investment decisions of females in this population and the knock-on effects
452 for their offspring.

453

454 In summary, we found some evidence for sexually antagonistic viability selection on a heritable
455 juvenile body size trait in Sable Island horses. We suggest that the tendency for larger male foals
456 to have lower over-winter survival probability is likely to be mediated by mothers providing
457 suboptimal care to large males when in poor condition over the winter. However, further
458 research would be needed to confirm this. The consequences of potential sexually antagonistic
459 selection on foals in the Sable Island horse population will become more apparent with the
460 integration of between-trait genetic correlations and multivariate selection analysis (Poissant et

461 al. 2016), but it is likely that a strong genetic correlation between the sexes and equal genetic
462 variances in males and females for foal body size will limit the evolution of sexual dimorphism
463 in this population (Lande 1980; Poissant et al. 2010). Equids exhibit a unique mating/social
464 system among ungulates, and thus the selection pressures imposed on male body size are likely
465 to differ substantially from other well-studied systems. Research on body size variation in wild
466 equids, such as Sable Island horses, will provide valuable insights to our understanding of eco-
467 evolutionary dynamics in the wild.

468

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Appendix

1. Details on model comparisons to determine the fixed effect structure of animal models

We fitted linear mixed-effects models using the R-package ‘lme4’ (Bates *et al.* 2015), to test the influence of intrinsic and extrinsic variables on the withers-knee length and thus identify an appropriate fixed effects structure for subsequent animal models. We did this by comparing models with all combinations of the following fixed effects and their first-order interactions. We considered fixed effect of sex (2-level factor) to account for any sex differences in size, birth year (5-level factor [2012-2016]) to account for cohort effects, Julian date (centred covariate) to account for growth over a census period, maternal age (3-level factor [3-5+ years]) to account for age-mediated differences between mothers, and the individuals median summer location (covariate) to account for individual differences in birth date and/or development along the island’s environmental gradient. We included foal identity as a random effect in all models to account for repeated measures. We used Akaike’s Information Criterion (AIC) to determine the best fixed effects structure, with the model with the lowest AIC being denoted the best model (see table below for AIC values for the top ten models). This model included birth year, Julian date, maternal age, and an interaction between birth year and Julian date.

Akaike Information Criterion values for the top ten best models for foal withers-knee length.

Model structure	AIC	ΔAIC	ωAIC
Birth.year + Julian.date + maternal.age + birth.year*Julian.date	3202.208	0.000	0.085
Birth.year + Julian.date + maternal.age + location + birth.year*Julian.date	3202.504	0.296	0.073
Birth.year + Julian.date + maternal.age + location + birth.year*Julian.date + birth.year*location	3203.074	0.866	0.055

Birth.year + Julian.date + maternal.age + sex + birth.year*Julian.date	3203.564	1.357	0.043
Birth.year + Julian.date + location + maternal.age + sex + birth.year*Julian.date	3203.875	1.667	0.037
Birth.year + Julian.date + maternal.age + location + birth.year*Julian.date + location*maternal.age	3204.270	2.062	0.030
Birth.year + Julian.date + maternal.age + sex + birth.year*Julian.date + Julian.date*sex	3204.317	2.109	0.029
Birth.year + Julian.date + maternal.age + location + birth.year*Julian.date + Julian.date*location	3204.586	2.378	0.026
Birth.year + Julian.date + location + maternal.age + sex + birth.year*Julian.date + birth.year*location	3204.647	2.439	0.025
Birth.year + Julian.date + location + maternal.age + sex + birth.year*Julian.date + location*sex	3204.674	2.466	0.024

Tables

Table 1. Fixed effect estimates, standard errors, and z ratios, from the withers-knee length animal model with maternal effect term. The analyses were conducted using 593 measures of body size from 287 individual Sable Island foals born between 2012 and 2016.

Parameter	Coefficient	SE	z
Intercept	61.16	1.14	53.57
Julian date	0.30	0.04	8.36
Birth year (2013)	9.62	5.29	1.82
Birth year (2014)	-3.39	0.77	-4.36
Birth year (2015)	-2.98	0.81	-3.67
Birth year (2016)	-0.42	0.85	-0.50
Maternal age (4-year-old)	1.46	1.29	1.13
Maternal age (5+ year-old)	3.73	1.09	3.43
Julian date: Birth year (2013)	-1.06	0.42	-2.52
Julian date: Birth year (2014)	-0.09	0.04	-2.43
Julian date: Birth year (2015)	-0.17	0.04	-4.60
Julian date: Birth year (2016)	-0.17	0.04	-3.89

Table 2. Variance component estimates (both the raw estimate and expressed as a proportion of the total phenotypic variance) from univariate and bivariate animal models for withers-knee length in Sable Island foals. The variance components are the additive genetic variance (V_A), permanent environment variance (V_{PE}), maternal effect variance (V_M), and residual variance (V_R).

Model	N_{ind} (N_{obs})	Mean (SD)	V_A	V_{PE}	V_M	V_R	h^2	r_{Amf}	CV_a
Univariate - no maternal effect	287 (593)	62.05 (5.49)	14.70 (4.60)	8.58 (3.86)	-	3.76 (0.31)	0.54 (0.15)	-	6.18
Univariate - with maternal effect	287 (593)	62.05 (5.49)	10.17 (6.23)	10.23 (4.03)	2.67 (3.09)	3.76 (0.31)	0.38 (0.22)	-	5.14
Males	141 (287)	62.01 (5.60)	21.27 (2.99)	1.50×10^{-5} (0)*	-	4.15 (0.49)	0.84 (0.03)	0.77 (0.34)	7.44
Bivariate Females	146 (306)	62.10 (5.39)	15.33 (7.77)	10.07 (7.04)	-	3.35 (0.38)	0.74 (0.13)	0.77 (0.34)	6.30

*the permanent environment term for male wither-knee length got stuck at the boundary (0) and therefore standard errors were not provided.

Table 3. Non-parametric bootstrapped 95% confidence intervals for terms from Generalised Linear Models (GLMs) with the survival of Sable Island foals as the response variable. These models were used to establish whether the relationship between withers-knee length and survival was dependent on the individual's birth year, the age of an individual's mother, their location on the island, or their sex. GLMs were run 1000 times, each with a different sample of the dataset that contained only one withers-knee length measure per foal.

Term	Lower 95% CI	Upper 95% CI
Withers-knee length	-0.07	0.19
Withers-knee length ²	-0.07	0.10
Withers-knee length*Maternal age [4 years]	-1.83	0.29
Withers-knee length*Maternal age [5+ years]	-2.10	0.03
Withers-knee length*Birth year [2013]	0.28	0.63
Withers-knee length*Birth year [2014]	-0.46	0.07
Withers-knee length*Birth year [2015]	-0.07	0.44
Withers-knee length*Location	0.01	0.19
Withers-knee length*Sex [Male]	-0.79	-0.32

Figures

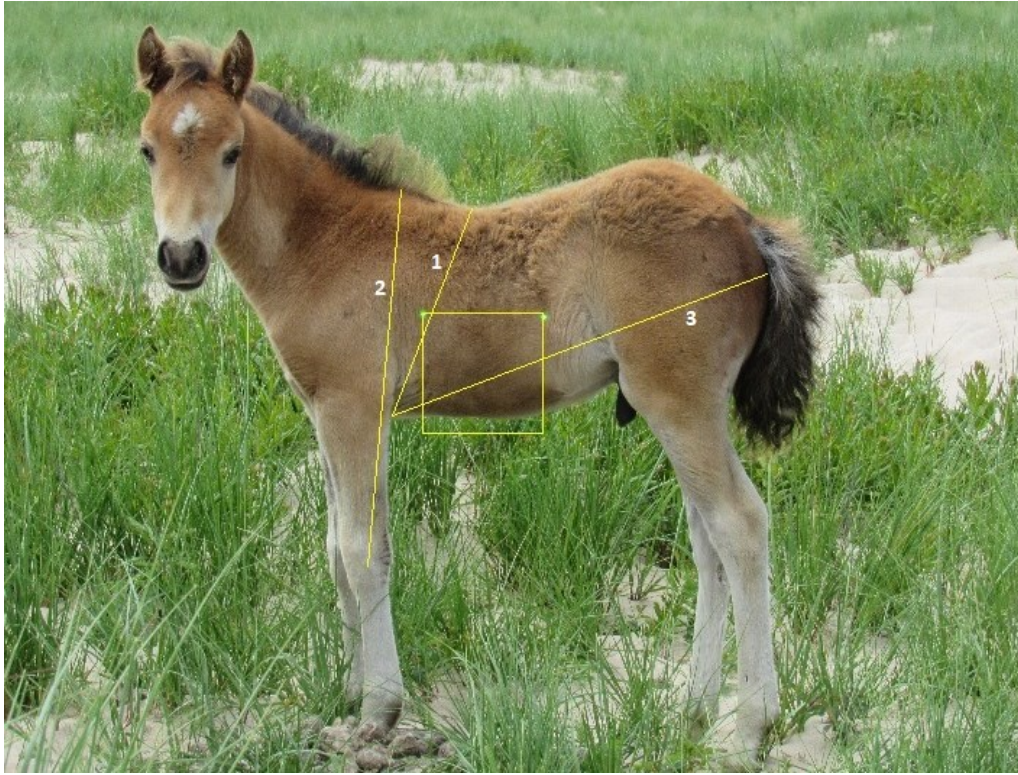


Figure 1. Body size measurements (1) heart depth, (2) withers-knee length, and (3) sternum-pin length, and standard area (square), as measured on a Sable Island foal. Green laser points at the top two corners of the square were spaced 19.05cm apart. Yellow body size measurement lines were drawn using ImageJ.

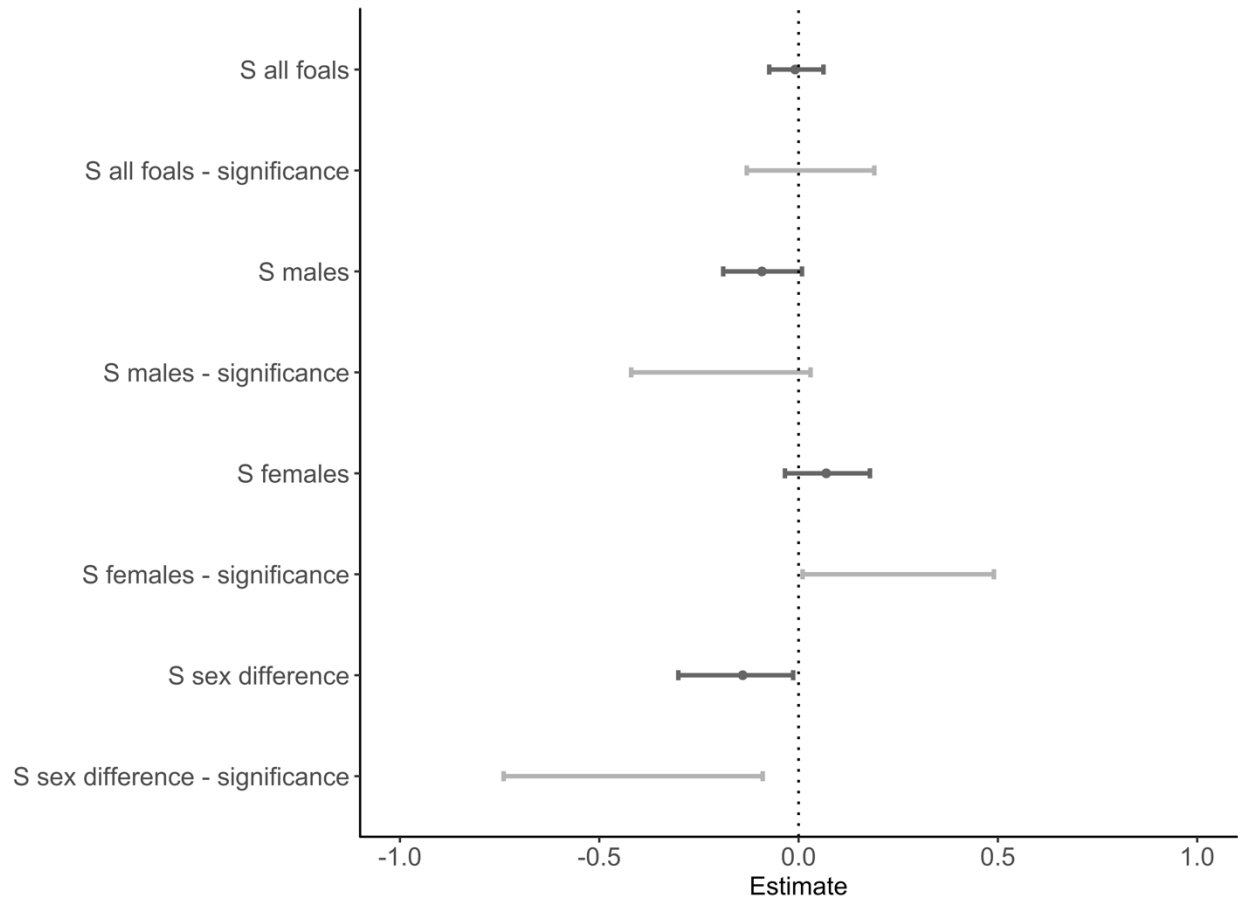


Figure 2. Estimated variance-standardised selection differentials (S) and credible intervals from bivariate mixed models using data for all foals and each sex separately. S were obtained from linear mixed models using the Gaussian family for both size and relative survival and are therefore correct, but credible intervals should be interpreted with caution. Significance was tested separately using a more appropriate generalised linear mixed models with the threshold family used for relative survival (see Methods for details) and credible intervals from these analyses are presented using light grey bars.