

# Gene flow from domesticated escapes alters the life history of wild Atlantic salmon

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**Interbreeding between domesticated and wild animals occurs in several species. This gene flow has long been anticipated to induce genetic changes in life-history traits of wild populations, thereby influencing population dynamics and viability. Here, we show that individuals with high levels of introgression (domesticated ancestry) have altered age and size at maturation in 62 wild Atlantic salmon *Salmo salar* populations, including seven ancestral populations to breeding lines of the domesticated salmon. This study documents widespread changes to life-history traits in wild animal populations following gene flow from selectively bred, domesticated conspecifics. The continued high abundance of escaped, domesticated Atlantic salmon thus threatens wild Atlantic salmon populations by inducing genetic changes in fitness-related traits. Our results represent key evidence and a timely warning concerning the potential ecological impacts of the globally increasing use of domesticated animals.**

Gene flow from domesticated animals into wild conspecific populations is widespread, and documented examples include American mink<sup>1</sup>, wolves<sup>2</sup>, wild boars<sup>3</sup>, wild cats<sup>4</sup>, bison<sup>5</sup> and Atlantic salmon<sup>6,7</sup>. Domestication commonly entails selection for economically important traits and genetic homogenization due to low effective population sizes<sup>8</sup>. Domesticated organisms have therefore altered the genetic composition underlying functional traits, and theoretical models predict that gene flow from domesticated organisms into wild populations is detrimental for population growth and viability<sup>9,10</sup>. In plants, the effects of hybridization between domesticated and wild conspecifics include evolution of weeds, increased or new invasiveness, and increased risk of extinction for wild species<sup>11</sup>. In animals, experimental studies have documented genetic differentiation in phenotypic traits between domesticated organisms and their wild conspecifics, with hybrids often at intermediate values. The animal literature is dominated by studies on salmonid fishes, and particularly on Atlantic salmon.

The domestication process of the Atlantic salmon in Norway involved a large-scale national breeding programme beginning in the 1970s, based on several wild populations from Norway, with selection on increased growth and avoidance of early sexual maturation<sup>12,13</sup>. Later, the breeding goal included other traits such as disease resistance, flesh colour and fat content<sup>12–14</sup>. Common garden experiments show that domesticated salmon and hybrids have altered phenotypes, compared with wild salmon. This includes growth<sup>15,16</sup>, predator avoidance and aggression<sup>17</sup>, life-history traits and phenology<sup>18</sup>, and probability of precocious male maturation<sup>19,20</sup>. Three large-scale experiments using different rivers controlled by fish traps showed that domesticated introgression can alter the age at seaward migration (smolt age) and the sea age at maturity, and lead to reduced survival and reproductive fitness<sup>21–24</sup>. This literature leaves little doubt that domesticated introgression is expected to impact the wild Atlantic salmon in a way that is most probably detrimental to population demography. However, the experimental

settings and limited number of whole-river experiments do not necessarily represent the extent or scale of the impact of domesticated introgression on natural populations.

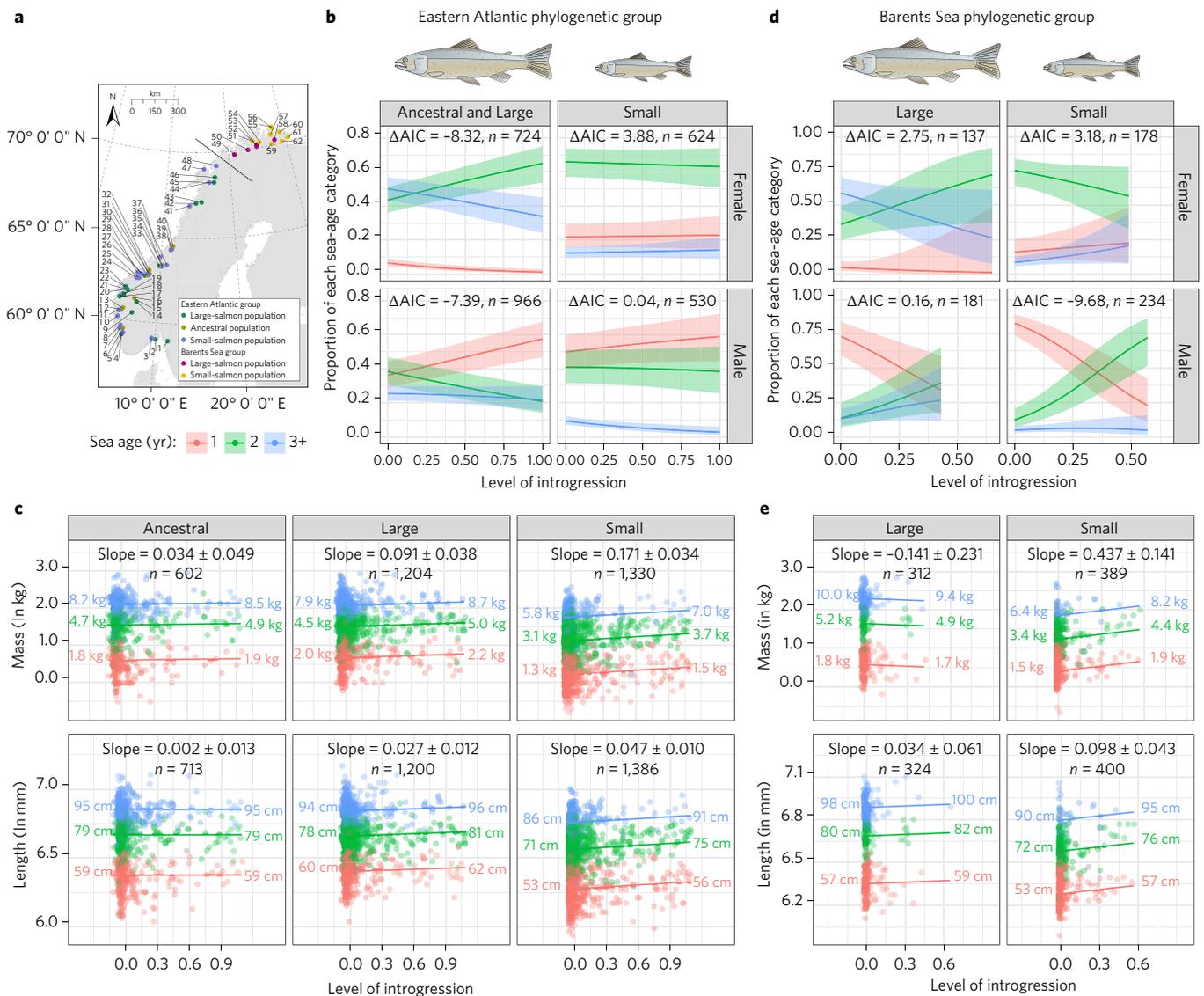
The effects of introgression on life-history traits, such as age and size at maturation, are of particular concern because of their close connection to fitness and demography<sup>25</sup>. In Atlantic salmon, the time spent at sea before maturation, called sea age, is closely related to their size at maturity<sup>26,27</sup>. An Atlantic salmon returning to the river to spawn after three winters at sea is 3–5 times heavier than one returning after one winter. Because size is strongly related to reproductive success<sup>28</sup> and the survival at sea is low<sup>29</sup>, the sea age at maturity represents a trade-off between survival and reproductive success. In addition, the growth rate at sea affects both adult size (and therefore reproductive success) and survival<sup>30</sup>. There may also be complex relations between early and late life-history decisions, for example precocious male maturation (or parr maturation) leads to investment in gonad production over somatic growth and a postponed seaward migration<sup>19,31</sup>.

Interbreeding between domesticated and wild Atlantic salmon occurs in many parts of its natural range on both sides of the Atlantic<sup>32–36</sup>. Fish farms are common from Ireland and Scotland to the Russian coast of the Barents Sea and from Maine in the United States to Newfoundland in Canada. We investigated the effects of gene flow from domesticated salmon in 62 populations along the entire Norwegian coastline (Fig. 1a). Norway has both the world's largest Atlantic salmon farming industry and the largest remaining wild population<sup>37</sup>. The number of farmed escapees is estimated at approximately one million fish annually<sup>38</sup>. This is more than the total number of fish in the Norwegian salmon run<sup>37</sup>, and has led to extensive gene flow from domesticated to wild fish<sup>6,7</sup>.

## Results

**Eastern Atlantic phylogenetic group.** The Norwegian domesticated Atlantic salmon originate from populations along the west

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**Figure 1 | Effect of introgression (proportion of domesticated genome) on life history.** **a**, Map of the different salmon populations. See Supplementary Table 1 for population information. **b**, Effect of introgression on sea age at maturation (proportion of each sea-age category: 1, 2 and  $\geq 3$  years) for females and males in the Eastern Atlantic phylogenetic group. Lines represent model predictions and shaded areas represent one standard error (symmetrical on the logit scale). Statistical support is given by the difference in the Akaike information criterion ( $\Delta$ AIC) between a model excluding the effect of introgression and one including it. A  $\Delta$ AIC value more negative than  $-2$  is considered strong statistical support<sup>56</sup>. See Supplementary Table 2 for parameter estimates. **c**, Effect of introgression on the mass and length at maturation within each sea-age category in the Eastern Atlantic group; lines represent model predictions. The mass (kg) and length (cm) at no introgression and maximum observed introgression are given for each sea-age category. The slope of the regressions  $\pm$  one standard error gives the effect of introgression and its precision. See Supplementary Tables 3 and 4 for parameter estimates. **d, e**, Same as **b** and **c**, but for the Barents Sea phylogenetic group.

coast of Norway<sup>39</sup>, which represent the Eastern Atlantic phylogenetic group<sup>40</sup>. We estimated the effect of domesticated introgression in 48 populations of this phylogenetic group (Fig. 1a). Seven of these are among the ancestral populations to the breeding lines of domesticated salmon (Fig. 1a and Supplementary Table 1). These ancestral populations are all characterized by a high mean sea age at maturity, and are classified as large-salmon populations (Supplementary Table 1). Due to a shared ancestry, the phenotypic effects of introgression in the ancestral populations are expected to be less than in other populations<sup>41–43</sup>. Yet, we found a strong sex-dependent effect of domesticated introgression on sea age in these populations (Fig. 1b). There was no difference in the effect of introgression between the seven ancestral populations and the 15 non-ancestral large-salmon populations (Supplementary Fig. 1). Domesticated

introgression increased the number of females attaining maturity at a sea age of two years (proportion changed from 0.43 to 0.65 at full introgression) and the number of males attaining maturity at a sea age of one year (proportion changed from 0.36 to 0.57), while the other sea-age categories correspondingly declined (Fig. 1b).

Estimating the level of genetic introgression is difficult, and the discovery of these effects is remarkable considering that our measure of the introgression level in individual fish was inherently imprecise because of the close relatedness between domesticated and wild salmon<sup>44</sup>. This imprecision obscures and leads to underestimates of the effects of introgression, along with inflation of the observed range of introgression estimates (Supplementary Fig. 2). Hence, we only detected introgression effects when the biological signal was strong, and our results represent conservative estimates of the true effects.

Twenty-six of the Eastern Atlantic populations were qualitatively different from the ancestral populations in that they were dominated by smaller fish maturing at an early age, and thus classified as small-salmon populations (Fig. 1a and Supplementary Table 1). In these populations, we found little or no effect of introgression on sea age (Fig. 1b). There was, however, a strong effect of introgression on sea-age-independent size at maturity (Fig. 1c). The increase in mass from no introgression to complete introgression was estimated at 0.171 ln kg, which is equivalent to an increase of 18.6% in these populations. This effect was almost absent (3.4%) in the seven ancestral populations of the domesticated salmon breeding lines, and intermediate (9.5%) in the non-ancestral large-salmon populations (Fig. 1c). Hence, even though the domesticated salmon show strongly increased growth in the captive environment<sup>15,16</sup>, our results indicate that their genetically high growth potential does not lead to an increased sea-age-independent size at maturity in the wild, when compared with their ancestral lineages. This could be because either the ancestral populations have already maximized the growth potential possible in nature, or the fast-growing individuals, with high domestic introgression, die before attaining maturity.

**Barents Sea phylogenetic group.** We also investigated the effects of domesticated introgression in 14 populations of the Barents (and White) Sea phylogenetic group (Fig. 1a and Supplementary Table 1). These populations are more distantly related to the domesticated salmon than the populations of the Eastern Atlantic group<sup>40</sup>. Thus, the effects of introgression in these populations comprise both domestication and phylogenetic effects, and are therefore expected to be more pronounced than in the Eastern Atlantic populations. A relationship between population divergence and the effects of introgression has been shown experimentally in the Atlantic salmon<sup>45</sup>. In addition, the environmental differences between the Eastern Atlantic and Barents Sea populations, such as marine feeding grounds and a longer winter, may alter the effects of the domesticated introgression.

The effects of introgression in the Barents Sea populations were in several cases qualitatively different and to some degree stronger, compared with the Eastern Atlantic group (Fig. 1d,e). However, the results are not directly comparable for the two phylogenetic groups due to the difference in the uncertainty of the estimated introgression (Supplementary Fig. 2). In addition, the smaller sample size of the Barents Sea dataset makes the results more uncertain. In females, the effect of introgression on sea age was qualitatively similar to the corresponding Eastern Atlantic large- and small-salmon populations, but there was no statistical support for the observed changes (Fig. 1d). In males, there was a strong decline in one-sea-winter fish and a corresponding increase in two-sea-winter fish; these changes had strong statistical support in the small-salmon populations (Fig. 1d). Interestingly, the large-salmon populations of the Barents Sea group had a decreased sea-age-independent mass but an increased length at maturation (Fig. 1e). However, these effects were uncertain and not statistically significant. On the other hand, in the small-salmon populations there was a very strong effect on sea-age-independent size: an individual with half of its genome originating from domestication was on average 24% heavier and 5% longer at maturation than the wild type (Fig. 1e).

## Discussion

The present results are solely observational and no experimental manipulations have been performed. The advantage of this approach is that it provides estimates and can document effects arising from a naturally occurring introgression process in a large number of wild populations. The disadvantage is that factors correlated with the level of introgression may create a spurious relationship between the level of introgression and the investigated traits. For example, the level of introgression may change over time and therefore be

correlated with environmental changes affecting the phenotype of the salmon. Similarly, environmental differences between populations may affect both susceptibility to introgression and phenotypic characteristics. However, we control for both among population differences and among year differences. Our analysis, therefore, compares individuals in the same year and within the same population, but with different levels of introgression. Because there is limited scope for environmental factors to create a spurious correlation between the level of introgression and trait values within a population in a given year, we regard this problem as a minor one in our case.

The size and sea age at maturity increase with river size<sup>26</sup>, and there is also genomic evidence that these traits are selected to fit the natural environment of each population<sup>46</sup>. Introgression affecting these traits is therefore expected to lead to fitness reduction in the wild, which has been shown experimentally<sup>22,23</sup>. The life-history changes will also alter the demography of the populations, and may lead to their homogenization. The Eastern Atlantic populations become more similar to small-salmon populations when it comes to sea age, with high proportions of one- and two-sea-winter fish for males and females respectively, and more similar to large-salmon populations when it comes to growth, with high sea-age-independent size at maturation. Hence, the difference between these two classes of populations is less pronounced, which may have negative consequences for the temporal stability in total stock abundance, known as the portfolio effect<sup>47</sup>.

Fish aquaculture has seen a steady increase in production, reaching 73.8 million tonnes globally in 2014<sup>48</sup>. This involves more than 350 species of finfishes<sup>48</sup>, and in many instances escapees potentially interbreed with wild conspecifics<sup>49</sup>. Lab experiments have long suggested that there are potentially substantial functional genetic effects of interbreeding between wild and domesticated conspecifics. This study documents such an effect on a broad geographic scale for a culturally and economically important species. Taken together, our study and the extensive experimental literature on the subject provides solid evidence that domesticated introgression has a strong effect on important biological characteristics of wild Atlantic salmon, and we would expect gene flow from other genetically altered domesticated animals to have similar effects on their wild conspecifics.

## Methods

**Data.** The data comprise 4,101 Atlantic salmon captured from 62 rivers along the entire Norwegian coastline from 59 to 71°N (Fig. 1 and Supplementary Table 4). The large majority of the data was collected by anglers fishing the entire salmon-producing stretch during the recreational fishing season that covers most of the run time in Norway (mainly June to August; see Supplementary Fig. 3). We therefore regard our data as representative of the adult populations we were studying. There may still be biases in the data regarding size, age or level of introgression. Biases can arise from fishing regulations on fish size, bag limits, fishing gear or fishing season. These biases can affect population means and can potentially also weaken the observed phenotypic effect of introgression, but they are not expected to create a spurious increase in the effect of introgression on the phenotypic traits within populations and years.

The data are a subset of that used in a previous publication<sup>7</sup>, where the magnitude of introgression was reported for the different populations. We categorized the data depending on whether the population was dominated by small- or large-sized salmon, and also whether they were members of the Eastern Atlantic or Barents/White Sea phylogenetic groups (for comparison, see ref. <sup>40</sup>). The large-salmon populations (dominated by multi-sea-winter spawners) are qualitatively similar to the ancestral populations of the breeding lines of the domesticated salmon in that they attain maturity at an older sea age and at a larger age-independent size than the small-salmon populations (dominated by one- and two-sea-winter spawners). We categorized populations as large- or small-salmon populations along previously reported lines<sup>50</sup>: large-salmon populations had less than 60% of their catch below 3 kg, while small-salmon populations had more than 60% of their catch below 3 kg (based on the catch statistics from 1993 to 2012).

A subset of the Eastern Atlantic large-salmon populations dominated the domesticated salmon breeding lines after the initial generations of selection.

These rivers are (from south to north): Suldalslågen, Vosso, Årøyelva, Driva, Surna, Gaula and Namsen<sup>12,39</sup>.

**Measurement of introgression.** We used 48 single-nucleotide polymorphic loci previously identified as differentiating between wild and domesticated Atlantic salmon in Norway<sup>51</sup> to estimate the proportion of each individual's genome that was of domesticated origin, following a previously reported method<sup>44</sup>. In short, for each individual we estimated the proportional ancestry in the domesticated reference population relative to the wild reference population using the Structure software package<sup>52</sup> (v.2.3). Two *in silico* wild and domesticated reference populations were generated from the genotypes of a pool of samples from historical wild populations and the major breeding kernels in Norway (AquaGen, Salmobreed and Mowi), respectively, followed by random mating as implemented in HybridLab<sup>53</sup> (v.1.0). The historical wild samples represent Atlantic salmon of wild origin because they were conceived in the early- to mid-1980s, at an early stage of salmon farming. The domesticated reference samples from the breeding kernels were sampled between 1998 and 2008<sup>7,11</sup>. These breeding kernels have been kept isolated since they were founded from wild salmon in the 1970s<sup>12,39</sup>. We analysed single individuals together with the wild and the domesticated reference populations in Structure using the admixture model; 50,000 repetitions as burn in, and 100,000 repetitions after burn in, and no *a priori* information on sample designation. For each individual, we recorded the proportional ancestry in the domesticated reference population ( $P_{ind}$ ). The level of introgression, or proportion of domesticated genome relative to the domesticated and wild reference-population means, was calculated as  $(P_{ind} - P_W)/(P_D - P_W)$ , where  $P_W$  and  $P_D$  are the mean proportional ancestry in the domesticated reference population for the wild and domesticated reference samples, respectively. These values were estimated at  $P_W = 0.060$  and  $P_D = 0.903$  for the Eastern Atlantic phylogenetic group and  $P_W = 0.016$  and  $P_D = 0.992$  for the Barents/White Sea phylogenetic group.

**Phenotypic measurements.** On the capture of each fish, the angler measured the total length (mm; from the tip of the snout to the end of the caudal fin) and wet mass (g), recorded the sex and took a scale sample. A professional scale reader analysed the growth pattern of the scales, excluded escaped farmed salmon and recorded the time the wild fish had spent at sea before attaining maturity (sea age)<sup>54,55</sup>.

**Statistical analyses.** The effect of introgression on sea age was measured as the probability of maturing at different sea ages for an individual  $m$  (of sex  $j$ ) from population  $k$  (of population category  $i$ ) that was captured in year  $l$ . The effect was analysed using a multinomial (logit) mixed effect model:

$$\ln \frac{\Pr(y_{ijklm} = 1)}{\Pr(y_{ijklm} = 3+)} = a_{1ij} + b_{1ij}x_{ijklm} + d_{1ij}(x_{ijk**} - x_{ij***}) + r_{1ijk} + u_{1ijl}$$

$$\ln \frac{\Pr(y_{ijklm} = 2)}{\Pr(y_{ijklm} = 3+)} = a_{2ij} + b_{2ij}x_{ijklm} + d_{2ij}(x_{ijk**} - x_{ij***}) + r_{2ijk} + u_{2ijl}$$

where  $a$  is the intercept term,  $b$  is the within-population effect of the level of introgression ( $x$ ),  $d$  is the among-populations effect (in contrast to  $b$ ),  $r$  is the random effect of river,  $u$  is the random effect of year nested within category and sex, and the asterisks in the subscripts denote the average taken over the indicated data levels. The different values for  $y$  represent maturation at sea ages of 1 yr ( $y = 1$ ), 2 yr ( $y = 2$ ) and  $\geq 3$  yr ( $y = 3+$ ), respectively. The random effects were assumed independent and identically normally distributed, and a multinomial distribution was assumed for the response variable  $y$ . The population categories 'Ancestral' and 'Large' in the Eastern Atlantic phylogenetic group were pooled in this analysis, as there were no differences between these two categories for sea age or the effect of introgression (Supplementary Fig. 1). To evaluate the statistical support for an effect of the level of introgression on sea age for each sex within each population category, we compared the model above with one that excluded the effect of sea-age (that is, a model where parameters  $b_1$  and  $b_2$  were set to zero for the respective sex within each category). A decrease in the Akaike information criterion (AIC) of more than two when the effect of sea age was included was considered as strong statistical support<sup>56</sup>. This model was fitted using the statistical software package, TMB<sup>57</sup> (v.1.7.5), implemented in R<sup>58</sup> (v.3.3.1).

The length or mass at maturity of an individual  $m$  from population  $k$ , belonging to sea-age group  $j$  and population category  $i$ , that migrated out to sea at year  $l$  was log transformed and analysed in the linear mixed effect model:

$$\ln y_{ijklm} = a_{ij} + b_{ij}x_{ijklm} + d_{ij}(x_{ijk**} - x_{ij***}) + r_{ik} + u_{il} + e_{ijklm}$$

where  $a$ ,  $b$ ,  $d$ ,  $r$  and  $u$  have interpretations similar to those in the model for sea age, and  $e$  is the residual term. The effect of year ( $u$ ) was assumed to be the same for the population categories "Ancestral" and "Large". Both random effects and residuals were assumed independent and normally distributed. Sex was not included in the models because the two sexes had very similar estimates, and AIC did not support inclusion of sex difference in the model. The linear mixed models were implemented in the R package, lme4<sup>59</sup>. Diagnostic plots were used to assess the statistical assumptions of the models.

**Code availability.** R-code for the statistical models is available in Dryad Digital Repository with the identifier <http://dx.doi.org/10.5061/dryad.gk721>.

**Data availability.** The data supporting the findings of this study are available in the Dryad Digital Repository with the identifier <http://dx.doi.org/10.5061/dryad.gk721>.

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## Author contributions

G.H.B., K.H., O.H.D. and S.K. conceived the study. S.K. and O.H.D. generated and conducted bioinformatics on the molecular data. K.H., H.S., P.F., A.J.J., K.U., T.F.N., B.T.B., B.F.-L., H.L. and E.N. coordinated the collection of phenotypic data. G.H.B. analysed the data. G.H.B., K.H., G.R., B.J. and S.K. wrote the manuscript. All authors read and commented on the manuscript.

## Additional information

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## Competing interests

The authors declare no competing financial interests.