Heritability estimates of antler and body traits in white-tailed deer (*Odocoileus virginianus*) from genomic-relatedness matrices

Aidan Jamieson[1], Spencer J Anderson[2], Jérémie Fuller[3], Steeve D Côté[3], Joseph M Northrup[2,4], Aaron BA Shafer[2,5.]

1. Biology Department, Trent University, K9J 7B8. Peterborough, Canada.

2. Environmental and Life Sciences Graduate Program, Trent University, K9J 7B8. Peterborough, Canada.

3. Département de biologie, Centre d'études nordiques & NSERC Industrial Research Chair in integrated resource management of Anticosti Island, Université Laval, G1V 0A6. Québec, QC, Canada

4. Wildlife Research and Monitoring Section, Ontario Ministry of Natural Resources and Forestry, Trent University, K9J 7B8. Peterborough, Canada.

5. Forensics Program Trent University, K9J 7B8 Peterborough, Canada.

Correspondence: aaronshafer@trentu.ca AND https://orcid.org/0000-0001-7652-225X

Keywords

Animal model, pedigree-free, antlers, natural population, game farm, harvest

Abstract

Estimating heritability (h^2) is required to predict the response to selection and is useful in species that are managed or farmed using trait information. Estimating h^2 in free-ranging populations is challenging due to the need for pedigrees; genomic-relatedness matrices (GRMs) circumvent this need and can be implemented in nearly any system where phenotypic and SNP data are available. We estimated the heritability of five body and three antler traits in a free-ranging population of white-tailed deer (*Odocoileus virginianus*) on Anticosti Island, Quebec, Canada. We generated GRMs from >10,000 SNPs: dressed body mass and peroneus muscle mass had moderate h^2 values of 0.49 and 0.56, respectively. Heritability in male-only antler features ranged from 0.00 to 0.51 and had high standard errors. We explored the influence of minor allele frequency and data completion filters on h^2: GRMs derived from fewer SNPs had reduced h^2 estimates and the relatedness coefficients significantly deviated from those generated with more SNPs. As a corollary, we discussed limitations to the application of GRMs in the wild, notably how skewed GRMs increase variance around h^2 estimates. This is the first study to estimate h^2 on a free-ranging population of white-tailed deer and should be informative for breeding designs and management.

38 How individuals respond to selection is dependent, in part, on the heritability (h^2) of the focal
39 traits (Wright, 1920; Falconer and Mackay, 1996; Gillespie, 2004). Quantifying h^2 is essential to
40 predicting adaptive responses (e.g. Dziedzic *et al.*, 2019), opening the potential for gene
41 targeted management and conservation (Kardos and Shafer, 2018). Classically, h^2 was
42 estimated by comparing the phenotypic variance (V_P) of known relatives that allowed for
43 estimating additive genetic variance (V_A), with narrow-sense heritability being $h^2 = V_A / V_P$
44 (Wray and Visscher, 2008). In free-ranging populations this estimation has required the
45 construction of pedigrees that were then integrated into a mixed-effects model, known as the
46 animal model (Wilson *et al.*, 2010). The animal model disentangles V_P into its additive (V_A) and
47 environmental components, enabling h^2 to be estimated.

48 The tracking of individuals and construction of pedigrees in free-ranging populations is
49 time-consuming and costly (Clutton Brock and Sheldon, 2010). As a result, alternative pedigree-
50 free approaches have emerged in which molecular genealogies can be structured into
51 relatedness matrices that replace the pedigree in an animal model (Frentiu *et al.*, 2008). These
52 genealogies have relied on microsatellites, which can be problematic due to biased estimates in
53 small sample sizes (Wang, 2017) and the recommended number of loci exceeding that used in
54 most studies (Kopps *et al.*, 2015). This changed with the advent of high-throughput sequencing
55 that made the generation of thousands of single nucleotide polymorphisms (SNPs) feasible for
56 most organisms (Andrews *et al.*, 2016). Genomic-relatedness matrices (GRM) can be generated
57 and used to estimate the total amount of V_P captured by the panel of SNPs (Yang *et al.*, 2011;
58 Stanton-Geddes *et al.*, 2013). Here, V_A is estimated across SNPs (see Ritland, 1996) and has
59 produced h^2 estimates similar to those of sibling studies (Yang *et al.*, 2010). Though few, recent
60 applications to wild populations have paid special attention to the impact of model choice and
61 influence of missing data and minor allele frequencies (MAF) on number of retained SNPs and
62 h^2 estimates (e.g. Perrier *et al.*, 2018; Gervais *et al.*, 2019).

63 Quantifying h^2 of specific traits in wild species that are farmed or harvested can be
64 valuable for breeding design (Guo *et al.*, 2018) and management decisions (Coltman, 2008).
65 White-tailed deer (*Odocoileus virginianus*) are a big game species with economic and cultural
66 values across North America. Annual revenue from hunting is in the billions (Cambronne, 2013)

67 and from farming close to 50 million USD (see https://www.nass.usda.gov/AgCensus/). Antler
68 and body size are positively correlated with male reproductive success (Newbolt *et al.*, 2017),
69 and h^2 for these traits have been estimated in captively bred populations. For example, h^2 was
70 estimated using parent-offspring trios at 0.32 and 0.45 for the number of antler points and
71 main beam length respectively, though with high standard errors (Michel *et al.*, 2016). Similarly,
72 h^2 was estimated between 0.58 and 0.64 for body mass (Williams *et al.*, 1994). Recent work
73 suggests a highly polygenic nature of these traits (Anderson *et al.*, 2019), but h^2 has yet to be
74 quantified in a free-ranging population of white-tailed deer. Theoretical and empirical evidence
75 suggests that bottlenecked populations, such as those we might expect to see in captivity, have
76 increased V_A (Goodnight, 1988; Whitlock *et al.*, 1993; van Heerwaarden *et al.*, 2008; Jarvis *et al.*,
77 2011; Taft and Roff, 2012), thus it is unclear how h^2 values transfer from captivity to the wild.
78 Here, we take advantage of an extensive phenotypic database and DNA archive to estimate h^2
79 in antler and body traits of free-ranging white-tailed deer using GRMs.

80 Materials and Methods

81 Individual Sampling and phenotypes

82 Ear or muscle tissue was obtained and preserved in ethanol 95% between 2003 and 2014 from
83 harvested white-tailed deer on Anticosti Island, Quebec, Canada (Figure S1). This population
84 originated from ~220 individuals introduced in the late 1800s and shows no evidence of a
85 founder effect (Fuller *et al.*, 2020). All individuals had an extensive set of phenotypic metrics
86 taken (Table S1), were sexed, and aged using cementum layers in incisor teeth (Hamlin *et al.*,
87 2000) with only animals >1.5 years analyzed. Phenotypes were assessed for correlation and
88 only one was retained if Spearman's *r* was > 0.70. DNA was isolated from the tissue using
89 Qiagen DNeasy Blood & Tissue Kit and stored at -80 °C.

90 Genome relatedness matrix and genotyping

91 We used the SNP data generated in Fuller *et al.*, (2020) that applied a rigorous filtering
92 approach to generate 13,420 SNPs. We took this VCF file and further filtered it to include only
93 scaffolds that had >1 SNP present, and made a separate data file that only included males. To
94 quantify the impact of loci missingness (LM) and MAF filters on downstream inferences (e.g.
95 Shafer *et al.*, 2017) we generated subsets of data with 70, 80, 90 and 100% completion as well

96 1, 5 and 10% MAF requirements. The SNP genotypes were converted into a binary fileset using
97 PLINK v.19 (Purcell *et al.*, 2007) that was used to generate a GRM in GCTA v1.92.4 (Yang *et al.*,
98 2011). The GRMs were input to a mixed-effects linear model that included year of harvest, age,
99 and sex with a restricted maximum-likelihood (REML) approach to estimate h^2 (Meyer, 1989).
100 An F test of equality of variances was conducted in R v. 3.6.3. to test whether the GRM
101 distributions differed among the filtered datasets, and we tested whether deviations from a 1:1
102 ratio, calculated as abs(1-F statistic), correlated to differences in the number of SNPs used to
103 build the GRMs.
104 For a subset of male samples we genotyped the SRP54 locus that was previously found
105 to be associated with antler morphology (Anderson *et al.*, 2019). We custom designed a rhAmp
106 SNP assay and genotyped individuals via qPCR with a QuantStudio 3 Real-Time PCR System
107 (Thermo Fisher Scientific, Waltham, MA, USA). The thermocycling condition was 60 °C for 30
108 seconds followed by 95 °C for 10 minutes, then 40 cycles of 95 °C for 10 seconds, 60 °C for 30
109 seconds, and 68 °C for 20 seconds, followed by a final 30 seconds at 60 °C. The qPCR had a 5 µL
110 reaction volume in each 0.1 mL well of a sealed 96-well optical plate. As above the GRMs were
111 fitted to include year of harvest, age, and the SRP54 locus in an additive framework (0, 1, or 2
112 alleles).
113
114 All scripts been uploaded to a GIT repository: https://gitlab.com/WiDGeT_TrentU
115

116 **Results**

117 We obtained samples from 219 male and 218 female deer. The number of SNPs retained for
118 body size and antler estimates are provided in Table 1. Increased loci completeness
119 requirements and higher MAF values reduced the number of SNPs used to build the GRM, with
120 the final SNP datasets containing between 1,041 to 10,386 SNPs. The distribution of relatedness
121 values in the GRM showed primarily unrelated individuals, though there was evidence of full-
122 sibling or parent-offspring pairings (Figure 1). The filtered GRM distributions differed with
123 increased MAF and LM filters that skewed the relatedness coefficients (Table 2, Figure 2).

Variance between GRMs (i.e. abs(1-F-statistic) and the difference in number of SNPs used to build the GRMs were highly correlated (β = 1.63e-05, R^2 = 0.92, P < 0.001).

Dressed body mass and peroneus muscle mass for male and female together had heritability estimates of 0.49 and 0.56 respectively; all other body metrics had relatively large standard errors (SE; Table 3). Likewise, two antler metrics had non-zero h^2 estimates but high SE (Table 3). Smaller h^2 estimates were observed from GRMs built with fewer SNPs (Table S2). Not surprisingly, age and sex had large effects on the body size metrics, with older individuals and males being larger on average; antler metrics also increased with age (Table 3). h^2 decreased when age and sex were not included in the model (Table S2), whereas removing year of harvest only had a minor effect (Tables S3; S4). We genotyped 74 males at the SRP54 locus (Dryad Accession XXXX); despite a positive effect size of this gene on antler metrics, all estimates had high SE precluding any meaningful inference (Table S5; S6).

Discussion

White-tailed deer are an important big-game species that are hunted and farmed across North America. If larger antlered or bodied animals are preferentially harvested or bred, there is the potential for artificial selection provided such traits are heritable. Our data suggest that body and muscle mass are heritable (Table 2), which is consistent with most vertebrates (Mousseau and Roff, 1987) including deer (Williams *et al.*, 1994). For antler metrics, despite h^2 values similar to previous estimates (i.e. Lukefahr and Jacobson, 1998; Michel *et al.*, 2016), our estimates had large standard errors; this is likely a reflection of the smaller male-only data set and a GRM skewed towards unrelated individuals (Figure 1) as captive studies suggest moderate levels of heritability. Whether harvest could induce artificial selection in white-tailed deer is an open question: data has shown harvested antlers being larger than those naturally shed (Schoenebeck and Peterson, 2014; but see Ditchkoff *et al.*, 2000). Still, non-genetic factors are large contributors to body size and antlers (Table 2) and in our view it is unlikely that harvest is a strong enough selective pressure to reduce antler size in most managed regions, given the generally large population size of deer, varied regulations, and often opportunistic nature of the hunt. Small and isolated populations, including farms, could see a response to selection, especially if V_A is higher (e.g. Taft and Roff, 2012).

153 The heritability of traits can vary by sex, age, and across seasons (Réale *et al.*, 1999).
154 This is an important consideration with GRM approaches for phenotypically stratified
155 populations that despite circumventing the need for pedigrees, still require basic individual
156 metadata. In deer, this meant aging individuals through cross-sections of incisors (Hamlin et al.
157 2000); not accounting for age and sex resulted in downward biased h^2 estimates (Table S2).
158 Likewise, accounting for parturition date and litter size increased h^2 estimates in captive white-
159 tailed deer (Michel et al. 2016). Interestingly, including the year of harvest that presumably
160 reflect environmental variation, particularly during summer, had a largely negligible effect on h^2
161 (Table S3; S4). Possibly between year climate variation on Anticosti island was not sufficient
162 enough to drive large phenotypic change in the years we obtained samples. The relatively high
163 standard errors surrounding h^2, even after accounting for age and sex is not uncommon as seen
164 in Michel et al.'s (2016) analysis of captive deer, and more broadly ungulates (Thomas *et al.*,
165 2002; Coltman *et al.*, 2005). However, Sim and Coltman (2019) used GRMs and reported
166 moderate h^2 estimates with small SE of horn characteristics of thinhorn sheep (*Ovis dalli*): this
167 difference is likely attributed to antlers being shed and regrown annually, and horn length being
168 a more easily quantifiable metric.
169 Sample size, SNP number, and filtering criteria all must be considered when estimating
170 h^2 with GRMs (Visscher and Goddard, 2015; Gervais *et al.*, 2019). Small sample size increases
171 sampling variance, typically biasing V_A downwards (Villemereuil *et al.*, 2013). With SNP data,
172 the GRM variance is inversely proportional to that of h^2 (Visscher and Goddard, 2015). Both our
173 analysis (i.e. Figures 2) and two other wild ungulate studies (Bérénos *et al.*, 2014; Gervais *et al.*,
174 2019) had GRMs skewed towards distant relatives; this undoubtedly played a role in h^2
175 estimates, as sampling the full spectrum of relatives is difficult in wild populations. The use of
176 SNP data also involves bioinformatics decisions. High MAF cutoffs should be avoided as this will
177 shift the site-frequency spectrum towards more common alleles, resulting in reduced h^2
178 estimates (Table S2; Gervais et al. 2019) and appreciably different GRMs (Table 2; Figure 2).
179 Introducing a stringent loci missingness criteria in principle should improves estimates (Gervais
180 et al. 2019), though we saw minimal evidence of this, likely due to the reduced SNP number
181 (Table 1). Collectively, these filtering parameters all impact the quality and number of SNPs

182 used to build the GRM, with wild vertebrate studies using a few thousand (Gervais *et al.*, 2019;
183 Sim and Coltman, 2019) to tens of thousands SNPs (Bérénos *et al.*, 2014; Perrier *et al.*, 2018).
184 While the optimal sample size and SNP number will depend on demographic history and life
185 history strategies, the generation of GRMs and estimates of h^2 in the wild opens up numerous
186 basic and applied research opportunities, notably quantifying and predicting the response to
187 selection under harvest and climate change scenarios. In the case of white-tailed deer, we have
188 shown that body size and likely antlers are moderately heritable and could respond to
189 selection, which would be most likely in small and isolated populations.
190

191 **Acknowledgements**

192 This work was supported by the Natural Sciences and Engineering Research Council of Canada
193 Discovery Grants (ABAS and SDC); ComputeCanada Resources for Research Groups (ABAS);
194 Canadian Foundation for Innovation: John R. Evans Leaders Fund (ABAS); and Industrial Chairs
195 and Collaborative Research and Development Grants from the Natural Sciences and
196 Engineering Research Council of Canada (SDC). We thank the outfitters of Anticosti Island and
197 the Ministère des Forêts, de la Faune et des Parcs du Québec for logistical help associated with
198 fieldwork, and all of the field assistants and technicians who collected samples and made
199 phenotypic measurements. Special thanks to Louis Bernatchez for supporting the lab work.

200 **References**

201 Anderson SJ, Côté SD, Richard JH, Shafer AB (2019). Genomic architecture of artificially and
202 sexually selected traits in a wild cervid. *bioRxiv*: 841528.

203 Andrews KR, Good JM, Miller MR, Luikart G, Hohenlohe PA (2016). Harnessing the power of
204 RADseq for ecological and evolutionary genomics. *Nat Rev Genet* **17**: 81–92.

205 Bérénos C, Ellis PA, Pilkington JG, Pemberton JM (2014). Estimating quantitative genetic
206 parameters in wild populations: a comparison of pedigree and genomic approaches.
207 *Molecular Ecology* **23**: 3434–3451.

208 Cambronne A (2013). *Deerland: America's hunt for ecological balance and the essence of*
209 *wildness*. Rowman & Littlefield.

210 Clutton Brock T, Sheldon BC (2010). Individuals and populations: the role of long-term,
211 individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol Evol*
212 **25**: 562–573.

213 Coltman DW (2008). Molecular ecological approaches to studying the evolutionary impact of
214 selective harvesting in wildlife. *Molecular Ecology* **17**: 221–235.

215 Coltman DW, O'Donoghue P, Hogg JT, Festa-Bianchet M (2005). Selection and genetic
216 (co)variance in Bighorn sheep. *Evolution* **59**: 1372–1382.

217 Ditchkoff SS, Jr ERW, Lochmiller RL (2000). Using cast antler characteristics to profile quality of
218 white-tailed deer Odocoileus virginianus populations. *wbio* **6**: 53–58.

219 Dziedzic KE, Elder H, Tavalire H, Meyer E (2019). Heritable variation in bleaching responses and
220 its functional genomic basis in reef-building corals (Orbicella faveolata). *Molecular*
221 *Ecology* **28**: 2238–2253.

222 Falconer D, Mackay T (1996). Introduction to quantitative genetics. Essex. *UK: Longman Group*.

223 Frentiu FD, Clegg SM, Chittock J, Burke T, Blows MW, Owens IPF (2008). Pedigree-free animal
224 models: the relatedness matrix reloaded. *Proc Roy Soc B* **275**: 639–647.

225 Fuller J, Ferchaud A-L, Laporte M, Luyer JL, Davis TB, Côté SD, *et al.* (2020). Absence of founder
226 effect and evidence for adaptive divergence in a recently introduced insular population
227 of white-tailed deer (Odocoileus virginianus). *Molecular Ecology* **29**: 86–104.

228 Gervais L, Perrier C, Bernard M, Merlet J, Pemberton JM, Pujol B, *et al.* (2019). RAD-sequencing
229 for estimating genomic relatedness matrix-based heritability in the wild: A case study in
230 roe deer. *Molecular Ecology Resources* **19**: 1205–1217.

231 Gillespie JH (2004). *Population genetics: a concise guide*. JHU Press.

232 Goodnight CJ (1988). Epistasis and the effect of founder events on the additive genetic
233 variance. *Evolution* **42**: 441–454.

234 Guo H, Zeng Q, Li Y, Wang Y, Chen Z, Lin P, *et al.* (2018). Estimating realized heritability for
235 growth in Zhikong scallop (Chlamys farreri) using genome-wide complex trait analysis.
236 *Aquaculture* **497**: 103–108.

237 Hamlin KL, Pac DF, Sime CA, DeSimone RM, Dusek GL (2000). Evaluating the accuracy of ages
238 obtained by two methods for Montana ungulates. *The Journal of Wildlife Management*
239 **64**: 441–449.

240 van Heerwaarden B, Willi Y, Kristensen TN, Hoffmann AA (2008). Population bottlenecks
241 increase additive genetic variance but do not break a selection limit in rain rorest
242 drosophila. *Genetics* **179**: 2135–2146.

Jarvis JP, Cropp SN, Vaughn TT, Pletscher LS, King-Ellison K, Adams-Hunt E, *et al.* (2011). The effect of a population bottleneck on the evolution of genetic variance/covariance structure. *Journal of Evolutionary Biology* **24**: 2139–2152.

Kardos M, Shafer AB (2018). The peril of gene-targeted conservation. *Trends in ecology & evolution* **33**: 827–839.

Kopps AM, Kang J, Sherwin WB, Palsbøll PJ (2015). How well do molecular and pedigree relatedness correspond, in populations with diverse mating systems, and various types and quantities of molecular and demographic data? *G3: Genes, Genomes, Genetics* **5**: 1815–1826.

Lukefahr SD, Jacobson HA (1998). Variance component analysis and heritability of antler traits in white-tailed deer. *The Journal of Wildlife Management* **62**: 262–268.

Meyer K (1989). Restricted maximum likelihood to estimate variance components for animal models with several random effects using a derivative-free algorithm. *Genetics Selection Evolution* **21**: 317.

Michel ES, Demarais S, Strickland BK, Smith T, Dacus CM (2016). Antler characteristics are highly heritable but influenced by maternal factors. *Jour Wild Mgmt* **80**: 1420–1426.

Mousseau TA, Roff DA (1987). Natural selection and the heritability of fitness components. *Heredity* **59**: 181–197.

Newbolt CH, Acker PK, Neuman TJ, Hoffman SI, Ditchkoff SS, Steury TD (2017). Factors influencing reproductive success in male white-tailed deer. *The Journal of Wildlife Management* **81**: 206–217.

Perrier C, Delahaie B, Charmantier A (2018). Heritability estimates from genomewide relatedness matrices in wild populations: Application to a passerine, using a small sample size. *Molecular Ecology Resources* **18**: 838–853.

Purcell S, Neale B, Todd-Brown K, Thomas L, Ferreira MAR, Bender D, *et al.* (2007). PLINK: A tool set for whole-genome association and population-based linkage analyses. *The American Journal of Human Genetics* **81**: 559–575.

Réale D, Festa-Bianchet M, Jorgenson JT (1999). Heritability of body mass varies with age and season in wild bighorn sheep. *Heredity* **83**: 526–532.

Ritland K (1996). A marker-based method for inferences about quantitative inheritance in natural populations. *Evolution* **50**: 1062.

Schoenebeck CW, Peterson BC (2014). Evaluation of hunter antler-size selection through an age-specific comparison of harvested and naturally cast antler metrics. *Journal of Fish and Wildlife Management* **5**: 167–173.

Shafer ABA, Peart CR, Tusso S, Maayan I, Brelsford A, Wheat CW, *et al.* (2017). Bioinformatic processing of RAD-seq data dramatically impacts downstream population genetic inference. *Methods Ecol Evol* **8**: 907–917.

Sim Z, Coltman DW (2019). Heritability of horn size in Thinhorn sheep. *Front Genet* **10**.

Stanton-Geddes J, Yoder JB, Briskine R, Young ND, Tiffin P (2013). Estimating heritability using genomic data. *Methods in Ecology and Evolution* **4**: 1151–1158.

Taft HR, Roff DA (2012). Do bottlenecks increase additive genetic variance? *Conservation Genetics* **13**: 333–342.

Thomas SC, Coltman DW, Pemberton JM (2002). The use of marker-based relationship information to estimate the heritability of body weight in a natural population: a cautionary tale. *Journal of Evolutionary Biology* **15**: 92–99.

Villemereuil P de, Gimenez O, Doligez B (2013). Comparing parent–offspring regression with frequentist and Bayesian animal models to estimate heritability in wild populations: a simulation study for Gaussian and binary traits. *Methods in Ecology and Evolution* **4**: 260–275.

Visscher PM, Goddard ME (2015). A General Unified Framework to Assess the Sampling Variance of Heritability Estimates Using Pedigree or Marker-Based Relationships. *Genetics* **199**: 223–232.

Wang J (2017). Estimating pairwise relatedness in a small sample of individuals. *Heredity* **119**: 302–313.

Whitlock MC, Phillips PC, Wade MJ (1993). Gene interaction affects the additive genetic variance in subdivided populations with migration and extinction. *Evolution* **47**: 1758–1769.

Williams JD, Krueger W, Harmel DH (1994). Heritabilities for antler characteristics and body weight in yearling white-tailed deer. *Heredity* **73**: 78–83.

Wilson AJ, Réale D, Clements MN, Morrissey MM, Postma E, Walling CA, *et al.* (2010). An ecologist's guide to the animal model. *J Anim Ecol* **79**: 13–26.

Wray N, Visscher P (2008). Estimating trait heritability. *Nature education* **1**: 29.

Wright S (1920). The relative importance of heredity and environment in determining the piebald pattern of guinea-pigs. *Proceedings of the National Academy of Sciences of the United States of America* **6**: 320.

Yang J, Benyamin B, McEvoy BP, Gordon S, Henders AK, Nyholt DR, *et al.* (2010). Common SNPs explain a large proportion of the heritability for human height. *Nature genetics* **42**: 565.

310 Yang J, Lee SH, Goddard ME, Visscher PM (2011). GCTA: a tool for genome-wide complex trait
311 analysis. *The American Journal of Human Genetics* **88**: 76–82.

312

313

314 **Figure Captions**

315 **Figure 1.** Genomic-relatedness matrices (GRMs) for white-tailed deer (*Odocoileus virginianus*)
316 on Anticosti Island, Quebec, Canada. GRMs are divided into the entire dataset (male and
317 female) and male only.

318

319 **Figure 2.** Genomic-relatedness matrices (GRMs) for the sampled white-tailed deer (*Odocoileus*
320 *virginianus*). GRMs are from the entire dataset (male and female) and were generated with
321 varying minor allele frequency (MAF) and loci missing (LM) filters.

322

323

Table 1. Number of SNPs and individuals retained in each genomic-relatedness matrix (GRM) after standard filtering. Additional filtering was only applied to full male & female datasets using different minor allele frequency (MAF) required loci completion (LM) criteria.

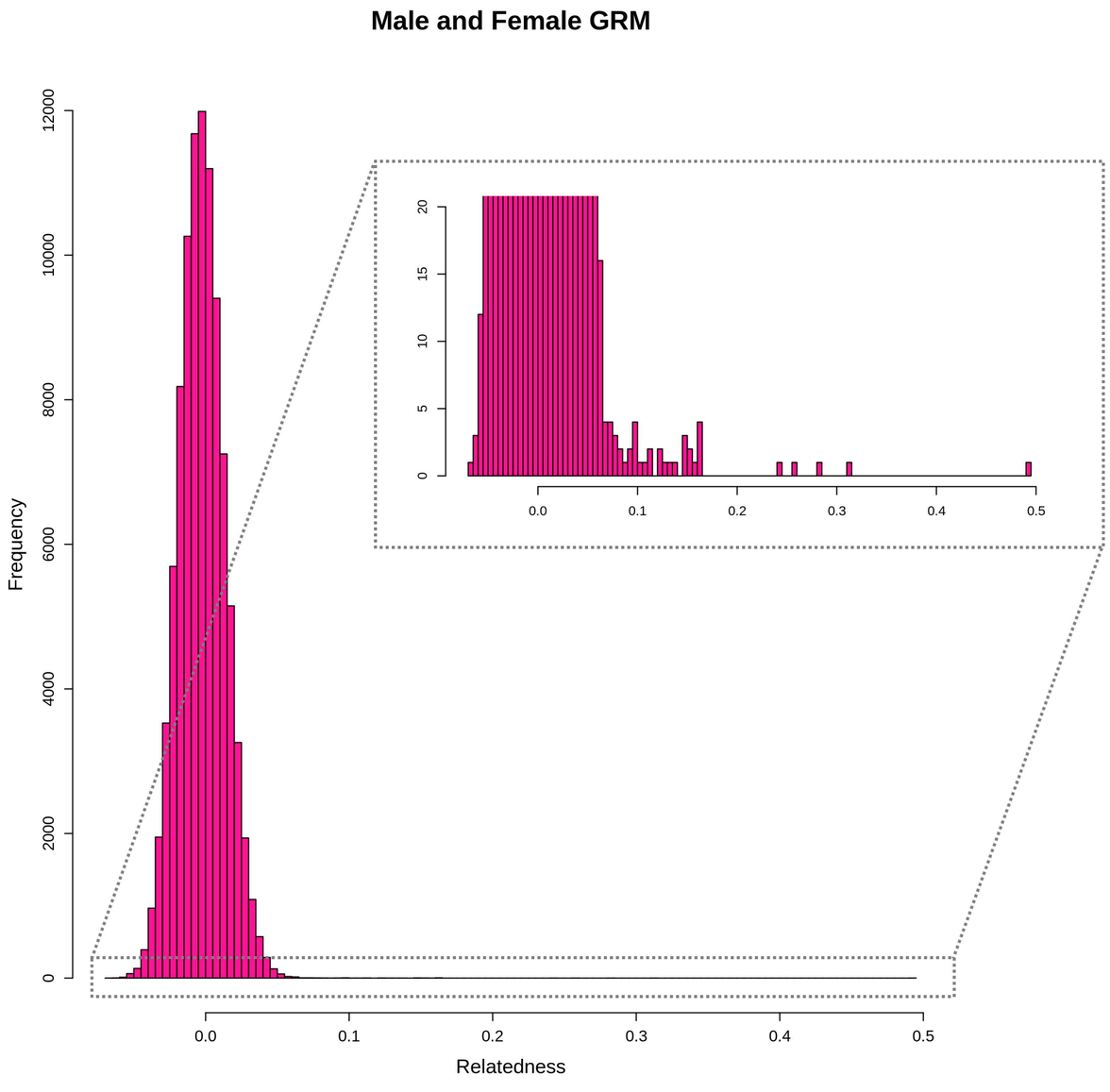
GRM	No. of SNPs	No. of Individuals
Male & female		
MAF 1%, LM 70%	10386	437
MAF 5%, LM 70%	9723	437
MAF 10%, LM 70%	2344	437
MAF 1%, LM 80%	10380	437
MAF 1%, LM 90%	10148	437
MAF 1%, LM 100%	1041	437
MAF 5%, LM 80%	9719	437
Male only		
MAF 1%, LM 70%	10386	219

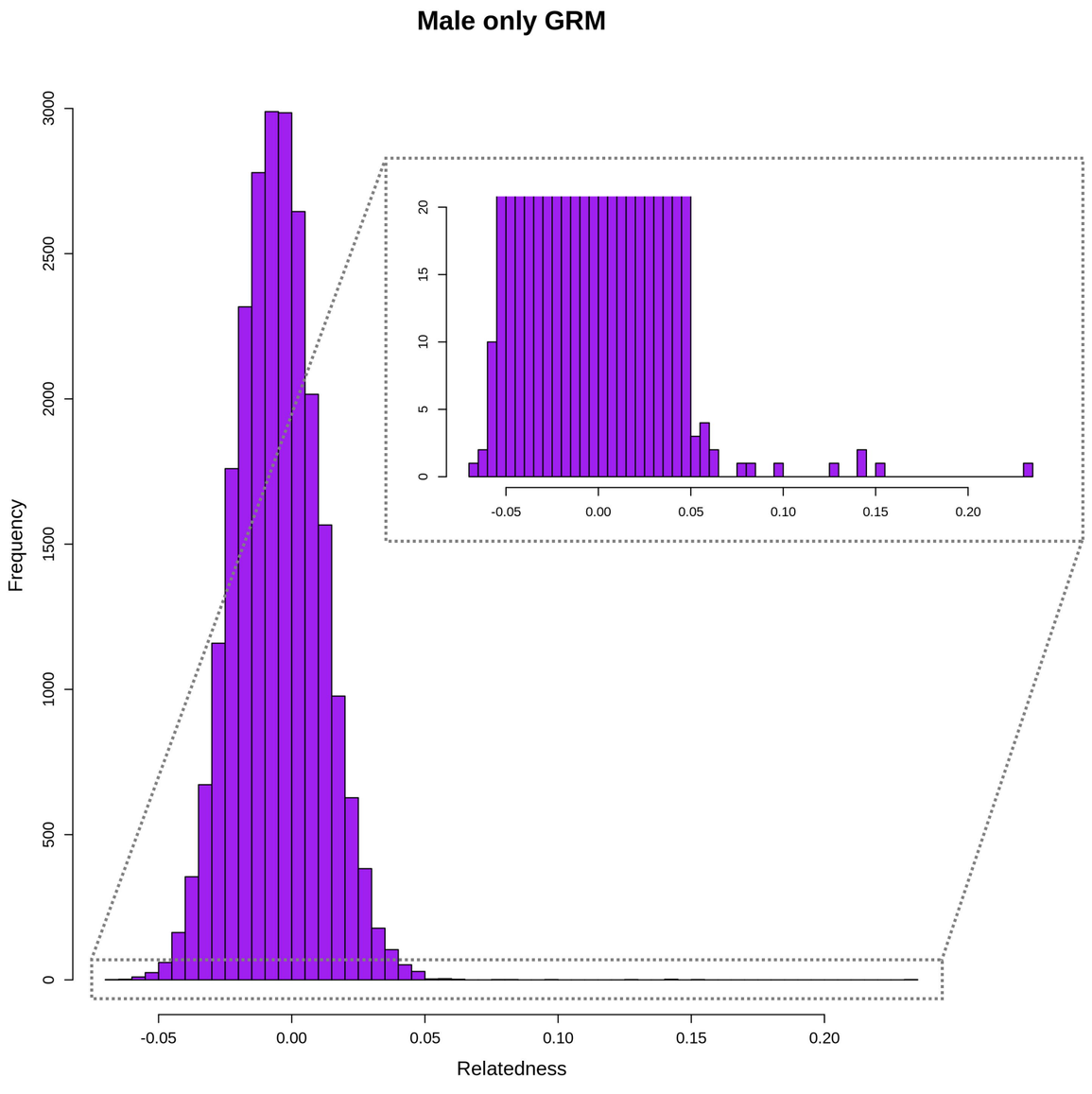
Table 2. Pairwise F tests of variances of the filtered genomic-relatedness matrices (GRM) in white-tailed deer (*Odocoileus virginanus*). We used different minor allele frequency (MAF) required loci completion (LM) criteria to generate GRMs. The F statistics and P values are presented, and *n* is 436. ΔSNPs refers to the difference in no. SNPs used to build the GRMs.

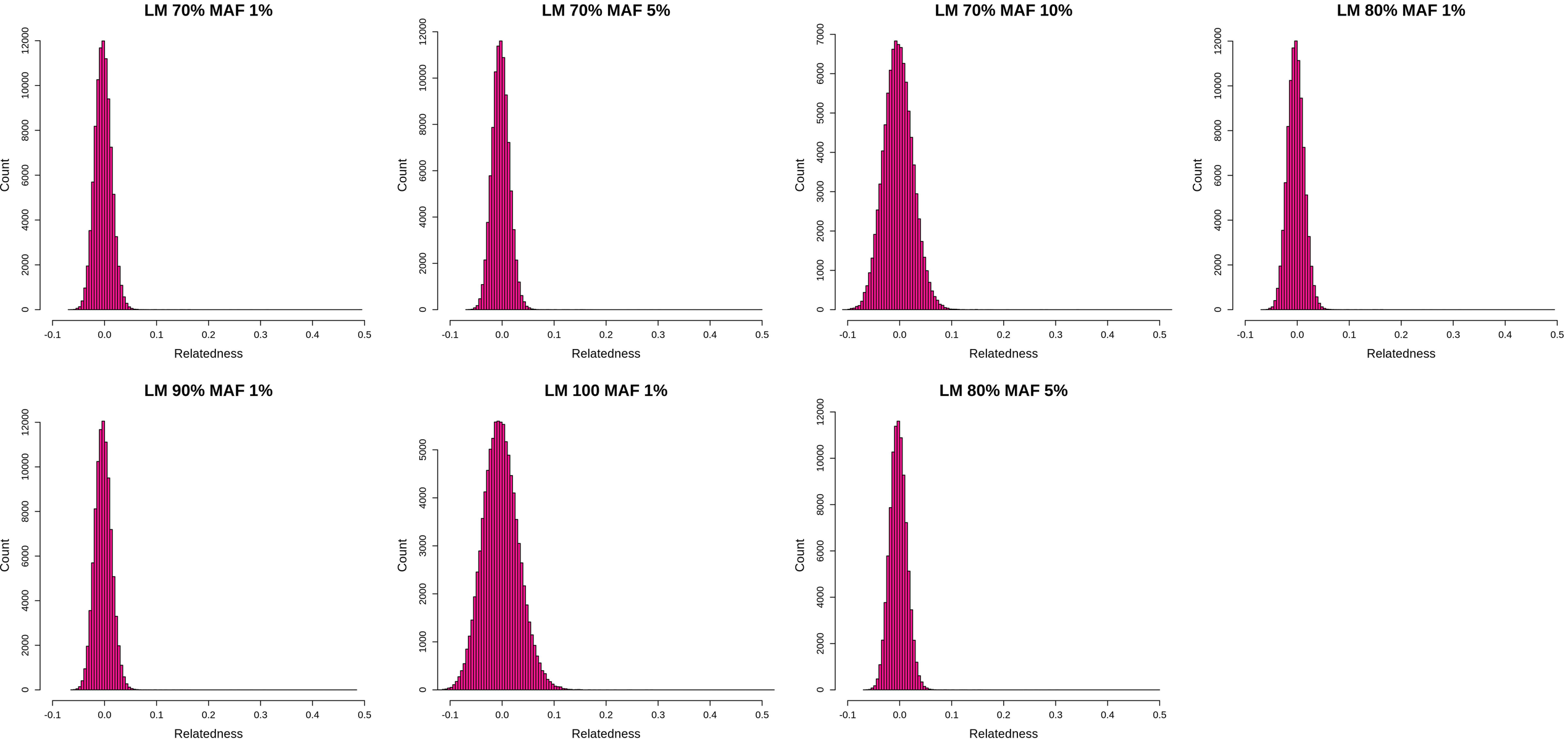
GRM 1	GRM 2	ΔSNPs	F statistic	P value
MAF 1%, LM 70%	MAF 5%, LM 70%	663	0.99	0.38
MAF 1%, LM 70%	MAF 10%, LM 70%	8042	0.86	<0.001
MAF 1%, LM 70%	MAF 1%, LM 80%	6	1.00	0.93
MAF 1%, LM 70%	MAF 1%, LM 90%	238	1.01	0.002
MAF 1%, LM 70%	MAF 1%, LM 100%	9345	0.88	<0.001
MAF 1%, LM 70%	MAF 5%, LM 80%	667	1.00	0.41
MAF 5%, LM 70%	MAF 10%, LM 70%	7379	0.86	<0.001
MAF 5%, LM 70%	MAF 1%, LM 80%	657	1.00	0.33
MAF 5%, LM 70%	MAF 1%, LM 90%	425	1.02	<0.001
MAF 5%, LM 70%	MAF 1%, LM 100%	8682	0.88	<0.001
MAF 5%, LM 70%	MAF 5%, LM 80%	4	1.00	0.95
MAF 10%, LM 70%	MAF 1%, LM 80%	8036	1.16	<0.001
MAF 10%, LM 70%	MAF 1%, LM 90%	7804	1.17	<0.001
MAF 10%, LM 70%	MAF 1%, LM 100%	1303	1.01	0.006
MAF 10%, LM 70%	MAF 5%, LM 80%	7375	1.15	<0.001
MAF 1%, LM 80%	MAF 1%, LM 90%	232	1.01	0.004
MAF 1%, LM 80%	MAF 1%, LM 100%	9339	0.88	<0.001
MAF 1%, LM 80%	MAF 5%, LM 80%	661	1.00	0.36
MAF 1%, LM 90%	MAF 1%, LM 100%	9107	0.86	<0.001
MAF 1%, LM 90%	MAF 5%, LM 80%	429	0.98	<0.001
MAF 1%, LM 100%	MAF 5%, LM 80%	8678	1.14	<0.001

Table 3. Estimation of heritability (h^2) for body and antler traits in white-tailed deer (*Odocoileus virginianus*) on Anticosti Island, Quebec, Canada. The genomic-relatedness matrix (GRM) was generated using a minor allele frequency of 1% and required loci completion of 70%. Mean trait values and effect sizes of age and sex are provided but the effect of year is not shown. Standard errors for all metrics are included in parentheses. *N* refers to the number individuals retained after filtering for phenotype completeness.

GRM	*N*	h^2	Mean	Age	Sex
Male & female GRM					
Dressed body mass (kg)	399	0.49 (0.24)	32 (1.2)	1.3 (0.1)	13 (0.8)
Total length (cm)	399	0.00 (0.22)	160 (1.7)	1.6 (0.2)	12 (1.1)
Hind food length (cm)	399	0.39 (0.26)	45 (0.3)	0.26 (0.04)	3.1 (0.2)
Chest circumference (cm)	399	0.24 (0.23)	84 (1.0)	1.0 (0.1)	8.7 (0.7)
Peroneus muscle mass (g)	399	0.56 (0.25)	86 (2.5)	2.3 (0.3)	27 (1.7)
Male only GRM					
Antler spread (cm)	171	0.00 (0.53)	17 (1.8)	3.1 (0.3)	-
No. of points	182	0.51 (0.51)	2.1 (0.4)	0.63 (0.05)	-
Main antler beam (cm)	175	0.23 (0.50)	1.5 (0.1)	0.17 (0.01)	-


Male and Female GRM
Frequency
Relatedness
0
2000
4000
6000
8000
10000
12000
0.0
0.1
0.2
0.3
0.4
0.5
0
5
10
15
20


Male only GRM
Frequency
Relatedness
0
500
1000
1500
2000
2500
3000
-0.05
0.00
0.05
0.10
0.15
0.20
0
5
10
15
20


LM 70% MAF 1%
LM 70% MAF 5%
LM 70% MAF 10%
LM 80% MAF 1%
LM 90% MAF 1%
LM 100 MAF 1%
LM 80% MAF 5%
Count
Relatedness
-0.1
0.0
0.1
0.2
0.3
0.4
0.5