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

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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, which allowed for
43 estimating additive genetic variance (V_A) with narrow-sense heritability being $h^2 = V_A / V_P$ (Wray
44 and Visscher, 2008). In free-ranging populations this estimation has required the construction
45 of pedigrees that were then integrated into a mixed-effects model, known as the animal model
46 (Wilson *et al.*, 2010). The animal model disentangles V_P into its additive (V_A) and environmental
47 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 close to 50 million USD from deer farming (see https://www.nass.usda.gov/AgCensus/).
68 Antler and body size are positively correlated with male reproductive success (Newbolt *et al.*,
69 2017), and h^2 for these traits have been estimated in captively bred populations. For example,
70 h^2 was estimated using parent-offspring trios at 0.32 for the number of antler points and
71 for0.45 main beam length, though with high standard errors (Michel *et al.*, 2016). Similarly, h^2
72 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 95% ethanol 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 Scripts have 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 and 10,386 SNPs. The distribution of
121 relatedness values in the GRM showed primarily unrelated individuals, though there was
122 evidence of full-sibling or parent-offspring pairings (Figure 1). The filtered GRM distributions
123 differed with increased MAF and LM filters that skewed the relatedness coefficients (Table 2,

124 Figure 2). Variance between GRMs (i.e. abs(1-F-statistic)) and the difference in number of SNPs
125 used to build the GRMs were highly correlated (β = 1.63e-05, R^2 = 0.92, P < 0.001).
126 Dressed body mass and peroneus muscle mass for males and females together had
127 heritability estimates of 0.49 and 0.56 respectively; all other body metrics had relatively large
128 standard errors (SE; Table 3). Likewise, two male-only antler metrics had non-zero h^2 estimates
129 but high SE (Table 3). Smaller h^2 estimates were observed from GRMs built with fewer SNPs
130 (Table S2). Not surprisingly, age and sex had large effects on the body size metrics, with older
131 individuals and males being larger on average; antler metrics also increased with age (Table 3).
132 Estimates of h^2 were lower when age and sex were not included in the model (Table S2),
133 whereas removing year of harvest only had a minor effect (Tables S3; S4). We genotyped 74
134 males at the SRP54 locus (Dryad Accession XXXX); despite a positive effect size of this gene on
135 antler metrics, all estimates had high SE precluding any meaningful inference (Table S5; S6).

136 **Discussion**

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

152 populations, including farms, could see a response to selection, especially if V_A is higher (e.g.
153 Taft and Roff, 2012).

154 The heritability of traits can vary by sex, age, and across seasons (Réale *et al.*, 1999).
155 This is an important consideration with GRM approaches for phenotypically stratified
156 populations that despite circumventing the need for pedigrees, still require basic individual
157 metadata. In our study this meant aging individuals through cross-sections of incisors (Hamlin
158 et al. 2000), and not accounting for age and sex in the model resulted in downward biased h^2
159 estimates (Table S2). Likewise, accounting for parturition date and litter size increased h^2
160 estimates in captive white-tailed deer (Michel et al. 2016). Interestingly, including the year of
161 harvest that presumably reflect environmental variation, particularly during summer, had a
162 largely negligible effect on h^2 (Table S3; S4). The relatively high standard errors surrounding h^2,
163 even after accounting for age and sex, is not uncommon as seen in Michel et al.'s (2016)
164 analysis of captive deer, and more broadly ungulates (Thomas *et al.*, 2002; Coltman *et al.*,
165 2005). However, Sim and Coltman (2019) used GRMs and reported moderate h^2 estimates with
166 small SE of horn characteristics of thinhorn sheep (*Ovis dalli*): this difference is likely attributed
167 to antlers being shed and regrown annually, and horn length being a more easily quantifiable
168 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 and two other wild ungulate studies (Bérénos *et al.*, 2014; Gervais *et al.*, 2019) had
174 GRMs skewed towards distant relatives; this undoubtedly played a role in h^2 estimates, as
175 sampling the full spectrum of relatives is difficult in wild populations. The use of SNP data also
176 involves bioinformatics decisions. High MAF cutoffs should be avoided as this will shift the site-
177 frequency spectrum towards more common alleles, resulting in reduced h^2 estimates (Table S2;
178 Gervais et al. 2019) and appreciably different GRMs (Table 2; Figure 2). Introducing a stringent
179 loci missingness criteria in principle should improve estimates (Gervais et al. 2019), though we
180 saw minimal evidence of this, likely due to the reduced SNP number (Table 1). Collectively,

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

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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)	-