Quantitative Genetics

ARMANDO CABALLERO

University of Vigo, Galicia, Spain



Contents

Preface	<i>page</i> xiii
Preface to the Spanish Version	xv
Continuous Variation	1
1.1 Quantitative Traits	1
1.2 Basic Concepts and Definitions	3
1.3 Historical Perspective	4
1.3.1 Beginnings of Quantitative Genetics: Heritable Variation	
and Evolution	4
1.3.2 The Development of the Central Body of Quantitative	
and Population Genetics	7
1.4 The Infinitesimal Model	10
Problems	13
Self-Assessment Questions	14
Forces of Change in the Allele Frequencies	15
2.1 Allele, Gamete and Genotype Frequencies	15
2.2 Hardy–Weinberg Equilibrium	16
2.3 Gametic or Linkage Disequilibrium	19
2.4 Forces of Change in the Allele Frequencies	23
2.5 Genetic Drift: The Ideal Population of Wright-Fisher	23
2.6 Change in Allele Frequencies by Mutation	26
2.7 Change in Allele Frequencies Due to Migration	27
2.8 Change in Allele Frequencies by Natural Selection	28
2.8.1 General Model of Fitness for a Locus	28
2.8.2 Change of Frequency of a Lethal Recessive Allele	30
2.8.3 Change in the Allele Frequency of a Favourable Allele	32
2.8.4 Overdominance and Underdominance	33
2.8.5 Natural Selection and Hardy–Weinberg Disequilibrium	37
2.8.6 Recreation of the Evolutionary Change in the Laboratory	38
Problems	39
Self-Assessment Questions	40
Components of Phenotypic Values and Variances	42
3.1 Decomposition of the Genotypic Value for a Locus	42
3.2 Decomposition of the Genotypic Variance for a Locus	46
3.3 Decomposition of Genotypic Values and Variances for More	
than One Locus	48
3.3.1 Gametic Disequilibrium Variance	48

3

2

1

entro a alta

viii

5

2017.00000000000		
	3 3 2 Epistatic Variance	51
	3.4 Concepts of Heritability and Genetic Correlation	54
	3.4.1 Degree of Genetic Determination	54
	3 4 2. Heritability	55
	3 4 3 Genetic Correlation between Traits	57
	3.5 The Environmental Deviation and Its Contribution	
	to Phenotypic Variance	59
	3.5.1 Phenotypic Plasticity	59
	3.5.2 Genotype–Environment Interaction	61
	3.5.3 Genotype–Environment Correlation	63
	3.5.4 Decomposition of the Environmental Variance:	
	Repeatability	63
	Problems	65
	Self-Assessment Questions	66
4	Inbreeding and Coancestry	67
	4.1 The Coefficients of Inbreeding and Coancestry	67
	4.1.1 Calculation of F and f from Genealogies	69
	4.1.2 Molecular Coancestry and Inbreeding Coefficients	71
	4.1.3 The Expected Inbreeding in the Ideal Population	76
	4.2 Populations with Regular Inbreeding	78
	4.2.1 Highly Inbred Lines	78
	4.2.2 Inbreeding in Large Populations	80
	4.3 Modulation of Inbreeding by the Effect of Mutation and Selection	81
	4.3.1 Mutation–Drift Equilibrium	82
	4.3.2 The Purged Inbreeding Coefficient	82
	4.4 Inbreeding in Subdivided Populations	83
	4.4.1 Wright's F Statistics	83
	4.4.2 Change of Base Population in the Estimation of Inbreeding	87
	4.4.3 Migration–Drift Equilibrium	88
	4.4.4 Estimation of F_{ST} with Genetic Markers	90
	Problems	93
	Self-Assessment Questions	93
_	Effective Deputation Circ	05
5	Effective Population Size	95
	5.1 Demnition and Methods for the Frediction of the Effective	05
	Population Size	93
	5.2 Prediction of N_e in Onselected Populations	97
	5.2.1 Absence of Self-Fertilization	97
	5.2.2 Different Number of Males and Females	90
	5.2.5 Variable Population Size across Generations	98 00
	5.2.4 Non-Kandoln Controlation of Patents to Offspring	99 101
	5.2.5 Partial Mating among Kelalives	101
	5.2.0 Overlapping Generations 5.2.7 Different Models of Inheritance and Depreduction	102
	5.2.7 Different would of infernance and Reproduction	103

NAME OF CONTRACTOR OF CONT

ix

and the second second

5.3	Prediction of N_e in Selected Populations	104
	5.3.1 Cumulative Effect of Selection	104
	5.3.2 The Impact of Linkage	106
5.4	Prediction of N_e in Subdivided Populations	107
	5.4.1 Prediction with Different Models of Population Structure	107
	5.4.2 General Model	107
5.5	Applications of the Theory of Effective Population Size	
	to Conservation	109
	5.5.1 Contributions with Minimal Variance	109
	5.5.2 Mating Systems	111
5.6	Estimation of Effective Population Size Using Demographic	
	Methods	113
5.7	Estimation of Effective Population Size Using the Allelism of	
	Lethals Method	114
5.8	Estimation of Effective Population Size with Molecular Markers	116
	5.8.1 Heterozygosity Excess Method	116
	5.8.2 Linkage Disequilibrium Method	116
	5.8.3 Temporal Method	117
	5.8.4 Coancestry and Sib Frequency Methods	118
	5.8.5 Methods with Multiple Information Sources	118
5.9	Estimates of N_e/N in Natural Populations	119
Pro	blems	119
Sel	f-Assessment Questions	120
Est	imation of Genetic Values, Variances and Covariances	122
6.1	Estimation of Heritability with Simple Experimental Designs	122
•••-	6.1.1 Estimation Based on the Degree of Resemblance	
	between Parents and Offspring	123
	6.1.2 Estimation Based on the Degree of Resemblance	
	between Sibs	125
	6.1.3 Effect of Assortative Mating	129
	6.1.4 Estimation Based on the Degree of Similarity between Twins	129
	6.1.5 Coefficients of Additive and Dominance Relationships	131
6.2	Estimation of Genetic Correlation	132
6.3	Estimation of Variance Components and Prediction of Additive	
0.0	Values with Complex Structure of the Data	133
	6.3.1 Estimation of Mean and Variance by Maximum Likelihood	134
	6.3.2 REML Estimation with the Animal Model	136
	6.3.3 Prediction of Additive Values by BLUP	138
	6.3.4 Example of BLUP Prediction and BLUE Estimation	140
	6.3.5 Use of Molecular Coancestries with Genetic Markers	142
	6.3.6 Comparison between Estimates of Heritability with	.
	Genealogical and Molecular Data	144
Pro	blems	145
Sel	f-Assessment Questions	146
~~~	Xueenono	1.0

NU. NAVARIN (D. 1. NOVING MARK

- -----

Chronophonethological and an

7	Mutation	148
•	7.1 Estimation and Analysis of Mutation in Quantitative Traits	148
	7.1.1 Probability of Fixation of a Mutation	150
	7.1.2 Estimation of the Rate of Mutation and Mutational Effects	152
	7.1.3 Estimation of the Dominance Coefficient	157
	7.1.4 Beneficial Mutations and Summary of Mutational	
	Parameters for Fitness	160
	7.1.5 Combined Effect of Mutations and Environmental Factors	161
	7.1.6 Estimation of Mutational Parameters for Neutral or	
	Quasi-Neutral Traits	163
	7.2 Implications of Deleterious Mutations in Populations of Large Size	165
	7.2.1 Equilibrium between Deleterious Mutation and Selection	165
	7.2.2 Mutation Load	166
	7.2.3 Estimation of the Average Dominance Coefficient in the	
	Mutation-Selection Equilibrium	168
	7.2.4 Estimation of Mutational Parameters in the Mutation-	
	Selection Equilibrium from Data of Panmictic and Inbred	
	Populations	169
	7.3 Mutation and Recombination	170
	7.3.1 Evolutionary Advantage of Recombination	170
	7.3.2 The Hill-Robertson Effect	172
	Problems	173
	Self-Assessment Questions	174
8	Consequences of Inbreeding	175
	8.1 Effects of Inbreeding on the Mean and Variance of Quantitative	
	Traits	176
	8.1.1 Decomposition of the Genotypic Value and Variance in a	
	Non-Panmictic Population	176
	8.1.2 Estimation of Inbreeding Depression and Inbreeding Load	179
	8.2 Inbreeding in Panmictic Populations of Reduced Census Size	185
	8.2.1 Redistribution of Within- and Between-Line Genetic Variance	185
	8.2.2 Genetic Differentiation in Quantitative Traits	188
	8.2.3 Mutational Meltdown and Purging of the Inbreeding Load	191
	8.3 Evolution of Inbreeding in Natural Populations	193
	8.4 Crossbreeding and Heterosis	196
	8.4.1 General and Specific Combining Abilities	197
	8.5 Applications in Conservation	201
	8.5.1 The Minimum Effective Size of a Viable Population	202
	8.5.2 Consequences of Conservation Methods	203
	8.5.3 Molecular Variation as a Complement to Quantitative	
	Genetic Variation	204
	Problems	205
	Self-Assessment Questions	206

Х

xi

Artif	icial Selection	207
9.1	Principles of Artificial Selection and Its Applications	207
	9.1.1 Response to Selection and Its Prediction	208
	9.1.2 Correlated Response	211
	9.1.3 Measure of the Response	212
	9.1.4 Asymmetry of the Response	214
	9.1.5 Change of Allele Frequency Due to Selection	216
9.2	Effect of Selection on Genetic Variance	218
	9.2.1 The Bulmer Effect	218
	9.2.2 The Effective Population Size with Artificial Selection	219
	9.2.3 Combined Effect of Genetic Drift and Selection on Genetic	
	Variance	220
9.3	Long-Term Response	221
	9.3.1 Prediction of the Long-Term Selection Response	221
	9.3.2 Comparison with Empirical Data	224
9.4	Family, Within-Family and BLUP Selection	228
9.5	Use of Molecular Markers	231
Prob	blems	232
Self	-Assessment Questions	233
Natu	Iral Selection	234
10.1	Quantitative Traits and Fitness	234
10.2	The Response to Natural Selection	235
10.3	Directional, Stabilizing and Diversifying Selection	238
	10.3.1 The Intensity of Real and Apparent Stabilizing	
	Selection	240
	10.3.2 Selection in Heterogeneous Environments	242
	10.3.3 Genetic Variance and Natural Selection	245
10.4	Genomic Footprint of Natural Selection	247
Prob	blems	247
Self	-Assessment Questions	248
Geno	omic Analysis of Quantitative Traits	250
11.1	Mapping of Quantitative Trait Loci	250
11.2	Genome-Wide Association Studies	253
11.3	Detection of the Footprint of Selection	258
	11.3.1 Principles of Methods Based on Polymorphism	
	and Divergence	258
	11.3.2 Linkage Disequilibrium Methods	259
	11.3.3 Detection of Diversifying and Convergent Selection	261
11.4	Genomic Selection	263
Prob	plems	268
Self	-Assessment Questions	268

11

9

NA LANASIM NA 111 MANDA 2 MARINA 2

Solutions to Problems and Self-Assessment Questions	269
Glossary	286
References	299
Index	318

Sector and the sector of the s