

Evolution and Selection of Quantitative Traits

II: Advanced Topics

B. Walsh and M. Lynch

Draft version 5 April 2013

CONTENTS	i
PREFACE	xiii
ROADMAP: DIFFERENT PATHS THROUGH THE BOOK	xiii
IX. ADVANCED UNIVARIATE TOPICS	xxx
30. SELECTION AND DEVELOPMENT OF PURE LINES	337
Pure Line Selection: Basic Issues	293
Multistage Selection: Finney's Rule	294
Controlling the Residual Variance	295
Replication	296
Field plot design	298
Accounting for $G \times E$	300
Choosing the Best Genotypes	303
Least significant difference (LSD) tests	303
Type I, II, and III Errors	303
Probability of choosing the best genotypes	305
Accuracy vs. intensity in selecting the best lines	306
Advancement of Generations	309
Pedigree selection	309
Bulk selection	314
Is early generation selection effective?	316
Single seed descent (SSD) selection	319
Doubled haploid (DH) selection	320
Comparison of the different methods	320
Sampling of Genotypes and Selection Limits	322
Choice of Parents	326
Using phenotypic information	327
Using information for crosses: Diallels and DHs	329
Using information for crosses: The Jinks-Pooni method	330
Number of crosses vs. number of lines per cross	332
Outcrossing hybrids before selfing	332
<i>Recurrent Selection</i>	332
31. SELECTION AND CROSSBREEDING I. BASIC CONCEPTS	1
Types of Crosses	2
Heterosis	3
Dominance and Heterosis	4

ii CONTENTS

Inbreeding vs. Panmictic Midparent heterosis	6
Dominance vs. overdominance and epistasis	7
Agricultural Exploitation of Heterosis	8
Hybrid Corn	9
Hybridization in Other Plants	11
Crossbreeding in Animal: General Concepts	11
Crossbreeding in Animals: <i>Bos indicus</i> – <i>Bos taurus</i> Crosses	13
Heterosis in Natural Populations	14
Variances Within and Between Crosses	14
Covariances for single crosses	14
Covariances for three- and four-way crosses	17
Selection among line crosses	19
Selection within line crosses	22
Estimating Heterotic and Crossbreeding Components	22
The Gardner-Eberhat decomposition of heterosis	22
Connection with GCA, SCA	23
Estimating the Amount of Heterosis in Maternal Effects	24
Using testors	27
Top crosses as predictors of double hybrid performance	28
General remarks on predicting the means of crosses	28
Three- and Four-way Crosses	29
Number of triple and double crosses	29
The problem	30
Predicting double and triple cross means: Jenkins' methods	31
The Cockerham and Eberhart Estimators	32
Single- vs. three- and four-way crosses	35
F ₁ vs. F ₂ performance	37
Rotational Crossbreeding	41
32. SELECTION AND CROSSBREEDING II. ADVANCED TOPICS	1
Prediction of value	229
BLUP prediction	229
Using molecular markers to predict heterotic groups	229
Reciprocal recurrent selection (RRS)	1
The Pure-Line-Crossbred Covariance	1
Selecting for both GCA and SCA – reciprocal recurrent selection	2
RRS Using Half-sibs Families	4
RRS Using Full-sibs Families	4
Diallele Selection Schemes	4
Synthetics	4
Wright's predictor and Powers-Kinman-Sprague Extension	6
Inbreeding in synthetics	8
Busbice's generalization of Wright's predictor	9
Synthetics Based on the Offspring of Selected Parents	11
Autotetraploids	13
Composites	15
Synthetic Values and Syntheizing Ability	18
Gallais' Test and Varietal Values	18
Detection of Lines Carrying New Elite Alleles	19
Triple Cross Estimators	20

Dudley's μG and $\ell \mu \bar{p}_\ell$ Estimators	21
Crossing Schemes for Optimal Introgression	24
Modification of Dudley's Original Estimators	25
The Upper Bound (UBND) and Net Improvement (NI) Estimators	28
Experimental Checks of the Various Estimators	32
33. SELECTION IN AGE-STRUCTURED POPULATIONS	304
Generation Intervals and Selection differentials	xxx
Response with Overlapping Generations	xxx
Asymptotic response	xxx
Non-asymptotic response	xxx
Nucleus populations and MOET schemes	xxx
Mimization of inbreeding under selection in an age-structured population	xxx
X. SELECTION ON MULTIPLE CHARACTERS: THEORY	3
34. MULTIVARIATE RESPONSE: CHANGES IN MEANS	1
The Multivariate Breeders Equation	1
Overview of key features and concepts	1
Derivation of the multivariate breeders equation	4
The multivariate secondary theorem of natural selection	7
Response when the parent-offspring regression is multivariate linear	8
Bivariate Selection	9
Correlated response to selection	10
Indirect selection may give a larger response than direct selection	12
Realized genetic correlations	13
General bivariate selection	15
Realized genetic correlations with bivariate selection	17
Asymmetric correlated responses are frequently seen	18
Comparison of Multivariate Responses	18
Standardization of response	19
Mean standarization and evolvability	21
Realized selection gradients	21
Evolutionary Constraints Imposed by Genetic Correlations	25
Dynamics of quantitative traits on an adaptive topography	26
What happens to mean fitness \bar{W} ?	27
Constraints are given by the eigenstructure of \mathbf{G}	27
Trade-offs, developmental constraints, genetic correlations, and the Lande equation	30
Multivariate measures of evolvability	32
Schluter's genetic line of least resistance, g_{\max}	33
Is there genetic variation in the direction of response?	36
Blow's matrix subspace projection	37
Conditional genetic variance and conditional evolvability	39
35. MULTIVARIATE RESPONSE: CHANGES IN COVARIANCES	1
Changes in \mathbf{G} Under the Infinitesimal Model	1
The dynamics of the disequilibrium matrix \mathbf{D}	2
The proportional change model for $\Delta\mathbf{P}$	3

Within-generation changes \mathbf{G} due to selection on variances and covariances	5
Asymmetric correlated responses occurs under the infinitesimal model	6
Response in \mathbf{G} under a multivariate Gaussian fitness function	8
Allele Frequency Changes and Instability of Genetic Covariances	11
Pleiotropic-based genetic correlations may become more negative over time	12
Genetic covariances are more fragile than genetic variances	12
It is difficult for antagonistic pleiotropy to maintain variation	13
Hidden Pleiotropy: A zero genetic covariance can still harbor many pleiotropic alleles	15
Experimental Studies of the Response to Selection to Change Covariances	16
Genetic Models of Covariances	19
Resource partitioning models: background	19
James' analysis of changes in covariances under resource partitioning models	19
Tradeoffs can lead to positive, as well as negative, covariances	21
Björklund's analysis	22
Optimization models, Functional Constraints, and \mathbf{G}	23
Long-Term Directional Selection	26
The infinitesimal model with drift	27
The infinitesimal model with drift and mutation	28
The balance between directional and stabilizing selection: infinitesimal model results	29
Long-term response is a function of the distribution of allelic effects	30
The balance between directional and stabilizing selection: Finite locus models	31
Long-term Quadartic Selection	32
Lande's multivariate model of pleiotropic mutation-selection balance	33
γ and \mathbf{G}	34
Model assumptions, genetic correlations, and hidden pleiotropy	35
Stability of \mathbf{G}	36
36. COMPARISONS OF \mathbf{G} AND ITS STABILITY	1
Changes in \mathbf{G} Under Drift	1
Under additivity, \mathbf{G} shows an expected proportional decrease	1
The experimental results of Phillips, Whitlock, and Fowler	2
Changes in \mathbf{G} when non-additive genetic variance is present	5
The eigenstructure of \mathbf{G} under drift and mutation	6
Comparing Covariance Matrices: Methodology	7
General issues of inference on \mathbf{G} using a population sample	8
Identity, proportionality, common orientation, common scaling	9
Element-by-element tests	11
Roff's jackknife MANOVA approach	12
Roff's T test	13
Mantel's test and other matrix correlation approaches	14
Regression methods: tests of proportionality	15
Likelihood-based tests assuming multivariate normality: variance components	16
Likelihood-based tests assuming multivariate normality: Bertlett's modified test	17
Random skewers: probing the geometry of \mathbf{G} with responses to selection response	18
Comparison of shared geometry: the Flury hierarchy	19
Comparison of shared geometry: Krzanowski subspace comparison	24
Still no ideal solution	25
Comparing Covariance Matrices: Data	25
Conclusions	28
Estimating the Dimension of a Covariance Matrix	28

Leading eigenvalues are overestimated, smaller eigenvalues underestimated	29
Problems with bootstrap-based confidence intervals for eigenvalues and rank	30
Canonical decomposition of the estimated covariance matrix	32
Amemiya’s rank test	33
Reduced Rank estimates of \mathbf{G}	34
Factor-analytic approaches for building reduced-rank estimates	35
Dimensionality of \mathbf{G} : data	37
Eigenvalue-based measures of effective dimensionality	38
37. THEORY OF INDEX SELECTION	400
General Theory Selection on a Linear Index	400
Genetic variance, heritability, and response of an index	400
Response in the individual components of the index	402
The retrospective index	403
The selection and response indices may contain different traits	404
Changes in the additive variance of I due to index selection	405
Changes in \mathbf{G} and \mathbf{P} under index selection	406
Optimizing the Expected Response of a Linear Index	408
The index of selection usually does not equal the index of response	408
Selection and response indices with non-overlapping traits	409
The Smith-Hazel index	411
Properties of the Smith-Hazel Index	412
Other useful results for the Smith-Hazel index	414
Estimated, base, and Elston indices	414
The Hayes-Hill transformation: detecting flaws in the estimated index	418
“Bending” and “rounding” corrections of the estimated index	419
Constraints on \mathbf{R} and \mathbf{S} given a specified selection intensity	420
Restricted and Desired-gains Indices	421
Restricted indices	421
Desired-gains indices	423
Summary of Linear Selection Indices	426
Nonlinear Selection Indices	427
Specific issues with nonlinear indices	427
Quadratic indices	428
Linear indices for nonlinear merit	431
Exact optimization of nonlinear indices	433
Optimal weights depend on the length of the experiment	433
Sequential Approaches: Tandem Selection and Independent Culling	434
Tandem selection	434
Independent culling	435
Selection of extremes	437
Relative Efficiencies of Index Selection, Independent Culling, and Tandem Selection	438
Theory	438
Data	440
Multistage Selection	441
Optimal values for multistage cullings	441
Cotterill and James’ approximately optimal two-stage selection	442
Multistage index selection	443
Xu and Muir’s method of transformed culling	

and orthogonal index selection	443
--------------------------------------	-----

XI. SELECTION ON MULTIPLE CHARACTERS: APPLICATIONS 3■

38. APPLICATIONS OF INDEX SELECTION 455

Improving the Response of a Single Character Using a Selection Index	455
General theory	456
More detailed analysis of two special cases	458
Repeated measures of a character	460
Using Information From Relatives	461
General Theory	461
Information from a single relative	462
Constructing selection indices when the individual itself is not measured	463
Within and Between Family Selection	465
Lush's index	466
Osborne's index	470
Selection on a Ratio	471
Approximate linear indices for ratio selection	472
Other linear-based indices for ratio selection	474
Which method is best?	474
Selection directly on a ratio: selection differentials and response	475
Selection and Sexual Dimorphic Traits	479
Components of the genotype \times sex interaction variance	480
Selection in sex-limited traits	480
Differential selection across the sexes	480
Sex-specific transmission differences	481
The joint response for a single dimorphic trait	481
Response with sex-linkage	485
Sexual dimorphism: a correlated or direct response?	486
Sexual dimorphism in size: Rensch's rule	487
Selection on a vector of sexually dimorphic traits	488
Selection of the Environmental Variance σ_E^2	490
The bivariate Mulder-Bijima-Hill Model: Estimation	490
The bivariate Mulder-Bijima-Hill Model: Response in σ_E^2	490
Extensions of the Mulder-Bijima-Hill Model: Accounting for skew	490
Extensions of the Mulder-Bijima-Hill Model: Family and Sire-selection	490
Changes in the genetic variances and covariance for A_m, A_v	490

39. BLUP SELECTION 483

Accounting for LD	
BLUP reduces effective population size	xxx
Maximizing response under fixed levels of inbreeding	xxx
Marker-Assisted Selection	xxx
Indirect selection on marker score: applications to sex-limited traits	xxx
Marker-assisted within- and between-family selection	xxx
Marker considerations	xxx
Optimal short-term versus long-term MAS	xxx
Genomic Selection	xxx

Genomic prediction	xxx
40. MARKER-ASSISTED AND GENOMIC SELECTION	483
41. MULTIPLE-TRAIT MODELS OF MATERNAL AND ASSOCIATIVE EFFECTS	xxx
Maternal Effects Models	xxx
Associative and indirect genetic effects (IGE) Models	xxx
Measuring Levels of selection	xxx
Social selection	xxx
42. PHENOTYPIC EVOLUTION MODELS	xx
Evolution of niche-width	xxx
Evolution of range size	xxx
Other ecological models	xxx
Coevolution among competing species	xxx
Estimating phenotypic selection from the fossil record	xxx
Peak shifts	xxx
Speciation models	xxx
Other models of macroevolution	xxx
XII. SELECTION AND G X E	xxx
43. SELECTION AND G X E: INTRODUCTION	455
Selection and G x E: Basic Ideas	456
G X E is both a challenge and an opportunity	456
Components of $\sigma_{G \times E}^2$: Variance heterogeneity and lack of correlations	457
G x E is context-specific	458
Response in Two Environments	458
Response in a target environment: Hammond’s conjecture	459
Improving an index of mean performance	461
Sensitivity and the Jinks-Connolly rule	463
Selecting in Two Environments	466
The cost to response from G x E	466
Selecting a group over several environments	466
Selection for mean performance versus sensitivity	468
Selecting in Multiple Environments	471
MET: Multiple-environment trials	471
Design trade-offs: years versus location	474
Design trade-offs: subdividing a target region	476
Participatory breeding and G x E	476
44. SELECTION AND G X E: ADVANCED TOPICS	483
Laying the Foundation: The Basic Model for G x E	484
Measuring and Selecting for Stability	485
Static vs. dynamic stability	485
Measuring stability: Finlay-Wilkinson regressions	486
Splitting the regression: The Varma-Chahal modification	488
Mean performance versus stability: insights from Finlay-Wilkinson regressions ..	489

Location-based modifications of the Finlay-Wilkinson regression	490
Finlay-Wilkinson regressions and Types 1 through 4 stability	490
Univariate measures of stability	492
Repeatability and breeding for stability	495
Joint selection for stability and performance	497
Probability criteria for selection: Risk aversion and safety-first	499
Seeking Structure in $G \times E$: AMMI, The SVD, and Biplots	500
The singular-value decomposition (SVD)	501
AMMI models	504
Modifications of the basic AMMI family of models	506
Using AMMI to predict cell means	506
Visualization of Interactions: Biplots	508
GGE/GGL Biplots	512
GGE vs. AMMI Biplots	515
Seeking Structure in $G \times E$: Incorporating Environmental Factors	516
Factorial regressions	517
Reduced rank factorial regressions	518
Mixed-Model Analysis of $G \times E$	520
BLUP estimates under compound symmetry assumptions	522
Structured covariance models: Introduction	526
Structured covariance models: Finlay-Wilkinson regressions	526
Structured covariance models: AMMI	528
Putting It All Together	529
Structured covariance matrices and stability measures	530
Structured covariance matrices and selection response	531

XII. QUANTITATIVE GENETICS OF CONTINUOUS FUNCTIONS

xxx

45. RANDOM REGRESSIONS AND INFINITE-DIMENSIONAL TRAITS	xx
Longitudinal and Functional Traits	xxx
Kirkpatrick's approach	xxx
The Covariance Function	xxx
Eigenfunction decomposition	xxx
Random Regressions	xxx
Gradient functions and matrices	xxx
Norms of Reaction and Phenotypic Plasticity	xxx