

Contents

Preface	xxiii
Introduction	xxv
1 Variability and its measurement	1
Chapter summary	1
Introduction	2
1.1. Classical and quantitative genetic studies of variability	3
1.1.i. Discrete variability	3
1.1.ii. Quantitative variability	4
1.1.ii.a. Describing quantitative variability	4
1.1.ii.b. Genotypes and phenotypes	7
1.1.ii.c. The genetic basis of quantitative variability	8
1.1.ii.d. Modeling quantitative trait inheritance	10
1.1.iii. Concealed variability and mutational variability	11
1.1.iii.a. Introduction	11
1.1.iii.b. The genetics of inbreeding depression	11
1.1.iv. Limitations of the classical and quantitative genetic approaches	13
1.2. Molecular variability	14
1.2.i. Gel electrophoresis of proteins	14
1.2.i.a. Introduction	14
1.2.i.b. The discovery of high molecular diversity	16
1.2.ii. Detecting variability by restriction mapping	20
1.2.iii. DNA sequencing	21
1.2.iii.a. Introduction	21
1.2.iii.b. DNA sequence polymorphisms; SNPs	22
1.2.iii.c. Other types of DNA sequence variants: repeat number polymorphisms and copy number polymorphisms	26
1.2.iv. Measuring DNA sequence variability	27
1.2.iv.a. Introduction	27
1.2.iv.b. Statistics for describing variability	27
1.2.v. Haplotypes	31
1.2.v.a. Definition and use in measuring variability	31
1.2.v.b. The effect of recombination on haplotype variability	32
1.3. The causes and maintenance of variability	33

1.3.i. Conservation of variability by the mechanism of inheritance	33
1.3.i.a. Hardy-Weinberg equilibrium	34
1.3.i.b. Gene conversion and mutation	35
1.3.ii. Nonrandom mating and identity by descent	35
1.3.ii.a. Identity by descent and coalescence of alleles in common ancestors	36
1.3.ii.b. Genotype frequencies with inbreeding and assortative mating	39
1.3.ii.c. Regular systems of mating	40
1.3.iii. Mutation: the source of new variants	42
1.3.iii.a. The nature of mutations	42
1.3.iii.b. Mutation rates	43
1.3.iii.c. Mutation and evolutionary change	43
Problems	45
 2 Basic selection theory and the maintenance of variation	47
Chapter summary	47
Introduction	48
2.1. Basic selection theory: constant fitnesses	49
2.1.i. Haploid populations	49
2.1.ii. Diploid populations	52
2.1.ii.a. Introduction	52
2.1.ii.b. Directional selection	54
2.1.ii.c. Heterozygote advantage and the maintenance of variation	56
2.1.ii.d. Biological implications of heterozygote advantage	59
2.1.ii.e. Mean fitness	61
2.1.ii.f. Heterozygote disadvantage	63
2.2. Variable fitnesses	64
2.2.i. Frequency-dependent selection	65
2.2.i.a. Theory	65
2.2.i.b. Examples of frequency dependence	65
2.2.ii. Fitnesses that vary in time	72
2.2.iii. Spatial variation in fitnesses, hard versus soft selection, and speciation	77
2.2.iv. The biochemical basis of fitness differences	81
Problems	83
 3 Directional selection and adaptation	85
Chapter summary	85

Introduction	86
3.1. Directional selection on a pair of allelic variants	88
3.1.i. Introduction	88
3.1.ii. Haploid populations	88
3.1.iii. Autosomal inheritance with random mating	90
3.1.iii.a. Introduction	90
3.1.iii.b. Results for weak selection	90
3.1.iii.c. Behavior at extreme frequencies	93
3.1.iii.d. Continuous time	93
3.1.iv. Biological applications	94
3.1.iv.a. Estimating the strength of selection	94
3.1.iv.b. Experimental evolution	95
3.1.iv.c. Haldane's sieve	96
3.1.iv.d. Developmental constraints on evolution	96
3.1.v. More complex selection models: relaxing some of the assumptions	97
3.1.v.a. Autosomal inheritance with sex differences in selection	97
3.1.v.b. Selection on an X-linked gene: Haldane's sieve and sexual antagonism	98
3.1.v.c. Selection in inbreeding populations	100
3.1.v.d. Kin selection	101
3.2. Survival and fixation probability of a favorable mutation	106
3.2.i. The problem	106
3.2.ii. The solution	107
3.2.iii. Biological implications	110
3.3. Selection on quantitative traits	114
3.3.i. Introduction	114
3.3.ii. Quantitative genetic parameters	114
3.3.ii.a. Introduction	114
3.3.ii.b. Components of genetic variance and covariances between relatives	115
3.3.iii. Response to selection	118
3.3.iii.a. Change over one generation	118
3.3.iii.b. Selection coefficients at individual sites	122
3.3.iii.c. Long-term responses to selection	124
3.3.iv. Multiple traits	126
3.4. The evolutionary genetics of adaptation of phenotypes and proteins	129
3.4.i. Introduction	129
3.4.ii. Fisher's geometric model of adaptation	130
3.4.iii. Adaptive evolution of sequences	133
3.4.iii.a. Introduction	133

3.4.iii.b. The distribution of the fitness effects of mutations fixed in an adaptive walk	133
3.4.iv. Testing the theory	135
3.4.iv.a. The theoretical predictions	135
3.4.iv.b. Genetics of interpopulation and interspecies crosses	136
3.4.iv.c. Experimental evolution	137
3.4.v. Multiple fitness peaks	138
Problems	141
4 Migration, mutation, and selection	143
Chapter summary	143
Introduction	144
4.1. Migration and selection	145
4.1.i. Migration and selection involving two populations	145
4.1.ii. Migration and selection in a continuous habitat	148
4.1.ii.a. Clines	148
4.1.ii.b. Modeling clines	150
4.1.ii.c. Using cline widths to measure selection	155
4.1.ii.d. Hybrid zones	157
4.1.ii.e. The wave of advance of a favorable mutation	158
4.2. Mutation and selection	159
4.2.i. Introduction	159
4.2.ii. Mutation-selection equilibrium	160
4.2.ii.a. Autosomes with random mating	160
4.2.ii.b. Other cases	161
4.2.ii.c. Mutation and selection at multiple sites	162
4.2.ii.d. Estimating mutation rates from equilibrium frequencies	163
4.3. Genetic load	164
4.3.i. Introduction	164
4.3.ii. Mutational load	164
4.3.ii.a. Autosomal inheritance with random mating	164
4.3.ii.b. Other cases	165
4.3.ii.c. Multiple sites	165
4.3.iii. Segregational load	168
4.3.iv. The cost of selection	169
4.4. Inbreeding depression	170
4.4.i. Introduction	170
4.4.ii. Mutation and inbreeding depression in a randomly mating population	171
4.4.ii.a. The effects of mutation and selection at a single site	171

4.4.ii.b. Multiple sites	171
4.4.ii.c. The inbreeding load	173
4.4.iii. Heterozygote advantage and inbreeding depression	174
4.4.iv. Testing alternative explanations of inbreeding depression	175
4.4.iv.a. Use of B/A ratios	175
4.4.iv.b. Alternative approaches	179
4.4.v. Does dominance evolve?	182
4.5. Genetic variation in fitness components and other quantitative traits	183
4.5.i. Mutational variation	183
4.5.i.a. Direct effects of mutations on fitness	183
4.5.i.b. Mutation and stabilizing selection	186
4.5.ii. Variability maintained by selection	191
Problems	192
5 The evolutionary effects of finite population size:	
basic theory	195
Chapter summary	195
Introduction	196
5.1. Modeling genetic drift	199
5.1.i. Drift without mutation	199
5.1.i.a. The Wright-Fisher model	199
5.1.i.b. Approach to genetic uniformity of a population	202
5.1.i.c. Increase in variance of allele frequencies	204
5.1.ii. Drift and mutation	205
5.1.ii.a. Identity in state of a pair of alleles and the infinite alleles model	205
5.1.ii.b. The infinite sites model	207
5.1.iii. The coalescent process	207
5.1.iii.a. Basic properties	207
5.1.iii.b. The genealogy of two alleles	207
5.1.iii.c. Gene genealogies in general	209
5.1.iii.d. Mutations, the coalescent process, and sequence diversity	209
5.1.iii.e. Simulating the coalescent process	211
5.1.iii.f. Microsatellite loci	215
5.2. Effective population size	216
5.2.i. Introduction	216
5.2.ii. Effective population size and the coalescent process	217
5.2.ii.a. Defining effective population size	217
5.2.ii.b. Calculating N_e with constant population size	218

5.2.iii. Effective population sizes for some biologically interesting cases	221
5.2.iii.a. Different modes of inheritance (constant population size)	222
5.2.iii.b. Comparisons of different modes of inheritance	223
5.2.iii.c. Varying population size	225
5.2.iii.d. Age- and stage-structured populations and the Moran model	226
5.2.iii.e. Estimating effective population sizes	227
5.3. Probability distributions of allele frequencies	228
5.3.i. Introduction	228
5.3.ii. The Wright-Fisher model with mutation and selection	229
5.3.ii.a. The transition from one generation to the next	229
5.3.ii.b. The probability distribution of variant frequencies	230
5.3.ii.c. Diffusion equations	231
5.3.iii. Allele frequency distributions: beyond the Wright-Fisher model	231
5.3.iii.a. Variance effective population size	231
5.3.iii.b. Solving the forward diffusion equation	232
5.3.iii.c. The equilibrium distribution with mutation between neutral variants	233
5.3.iii.d. The equilibrium distribution with mutation and selection	239
5.3.iii.e. Biological implications	240
Appendix to Chapter 5: Diffusion equations	241
5A.1. General formulation	241
5A.2. Determining the equilibrium distribution of allele frequencies	242
Problems	243
6 Molecular evolution and variation	245
Chapter summary	245
Introduction	246
6.1. Measuring rates of DNA sequence evolution	247
6.1.i. Comparing a pair of sequences	247
6.1.ii. Estimating rates of divergence	248
6.1.ii.a. Basic principles	248
6.1.ii.b. Correcting for multiple changes	250
6.1.ii.c. Stochasticity of the substitution process	251
6.1.ii.d. Correcting for reverse and multiple changes	252

6.1.ii.e. Nonsynonymous and synonymous changes	254
6.1.ii.f. Approximate rate constancy of molecular sequence evolution	256
6.2. The causes of DNA sequence evolution	257
6.2.i. Introduction	257
6.2.ii. Neutral sequence evolution	257
6.2.ii.a. Expectations for sequence divergence under neutrality	257
6.2.ii.b. Fixation of neutral mutations and divergence of sequences from closely related species	258
6.2.ii.c. Testing the neutrality of sequence evolution	260
6.2.iii. Selection in finite populations	261
6.2.iii.a. Rates of substitution for unique mutations	261
6.2.iii.b. Rates of substitution for recurring mutations	264
6.2.iv. Implications for molecular evolution and for studying selection	264
6.2.v. Detecting positive selection when purifying selection also acts: codon-based models	266
6.3. The distribution of variant frequencies under mutation, selection, and drift	268
6.3.i. Introduction	268
6.3.ii. Statistical equilibrium under mutation, selection, and drift	270
6.3.ii.a. The general model	270
6.3.ii.b. The equilibrium frequency distribution under neutrality	272
6.3.ii.c. Properties of the statistical equilibrium with selection: rates of evolution	275
6.3.ii.d. Properties of the statistical equilibrium with selection: variability	277
6.4. Testing for selection from polymorphism and divergence data	279
6.4.i. Introduction	279
6.4.ii. The McDonald-Kreitman (MK) test	280
6.4.ii.a. Introduction	280
6.4.ii.b. Principle of the MK test	281
6.4.ii.c. Potential difficulties with the MK test	284
6.4.ii.d. Estimating the fraction of amino acid fixations caused by positive selection	285
6.4.iii. Tests based on variant frequencies	287
6.4.iii.a. Introduction	287
6.4.iii.b. Tajima's <i>D</i>	288
6.4.iii.c. Fu's and Li's test statistics	289
6.4.iii.d. Other test statistics	290

6.4.iii.e. Problems of interpretation of tests using variant frequencies	290
6.4.iv. Estimating selection intensities	291
6.4.iv.a. Introduction	291
6.4.iv.b. Fitting the distribution of variants to a one-way mutation model	292
6.4.iv.c. Other methods and implications of the results ...	294
6.4.iv.d. Using polymorphism and divergence statistics ...	296
Appendix to Chapter 6: More diffusion equation results	297
6A.1. Fixation probabilities	297
6A.2. The equilibrium distribution of variant frequencies with one-way mutations	299
Problems	301
7 Genetic effects of spatial structure	303
Chapter summary	303
Introduction	304
7.1. Describing population differentiation	305
7.1.i. Use of genetic markers to describe differences among populations	305
7.1.i.a. Variances in allele frequencies and F_{ST}	305
7.1.i.b. Gene diversities for allelic variants	308
7.1.i.c. Nucleotide site diversity	309
7.1.i.d. Other methods	309
7.1.ii. Empirical patterns	310
7.2. The theory of neutral variation with spatial structure	310
7.2.i. General principles	313
7.2.i.a. Introduction	313
7.2.i.b. Fast time scales and migration models	313
7.2.ii. Mean coalescence times for migration models	315
7.2.ii.a. Introduction	315
7.2.ii.b. The island model	317
7.2.ii.c. Stepping-stone models	320
7.2.ii.d. Mean coalescence times for general migration models	322
7.2.ii.e. The strong migration limit	328
7.2.iii. Continuous populations	329
7.2.iii.a. General considerations	329
7.2.iii.b. Genetic differentiation in continuous populations	332
7.2.iv. Colonization and extinction models	333
7.2.iv.a. Introduction	333
7.2.iv.b. The exchangeable deme model	334

7.2.v. Sampling of alleles from spatially structured populations	338
7.2.v.a. Introduction	338
7.2.v.b. The large deme number approximation	340
7.2.v.c. Scattering and collecting phases	341
7.2.v.d. Within-population coalescence times	347
7.2.vi. The effects of population history	348
7.2.vi.a. Introduction	348
7.2.vi.b. Distinguishing historical changes from stable structure	348
7.3. The theory of selection with spatial structure	350
7.3.i. Introduction	350
7.3.ii. Fixation probabilities in structured populations	350
7.3.iii. Variant frequency distributions with selection and spatial structure	353
7.3.iii.a. The infinite-deme island model	353
7.3.iii.b. Quantitative traits and Q_{ST} values	359
7.3.iii.c. The sampling properties of alleles under the large deme number approximation	360
7.3.iv. Effects of population structure on mean fitness and selection among demes	361
7.3.iv.a. The effects of drift on population mean fitness	361
7.3.iv.b. Inter-deme selection	362
Problems	364
8 Multiple sites and loci	366
Chapter summary	366
Introduction	368
8.1. Describing the state of a population	368
8.1.i. Haplotype frequencies	368
8.1.ii. Measures of linkage disequilibrium	370
8.1.ii.a. Pairs of sites	370
8.1.ii.b. Multiple sites	373
8.1.iii. Empirical results on linkage disequilibrium	374
8.1.iii.a. Observations based on classical genetics	374
8.1.iii.b. Results from electrophoretic surveys	376
8.1.iii.c. Results from surveys of DNA sequence variability	376
8.1.iii.d. Mapping disease genes and quantitative trait loci	378
8.2. Causes of linkage disequilibrium: neutral sites	378
8.2.i. Introduction	378
8.2.ii. Neutral sites at two loci in an infinite population	379

8.2.ii.a. Random mating	379
8.2.ii.b. Inbreeding populations	382
8.2.iii. The effects of finite population size on linkage disequilibrium	383
8.2.iii.a. Linkage disequilibrium and drift in a panmictic population	383
8.2.iii.b. Linkage disequilibrium and the coalescent process	384
8.2.iii.c. Estimating recombination rates	386
8.2.iii.d. The effects of spatial structure	387
8.2.iii.e. Other factors affecting linkage disequilibrium	389
8.3. Neutral and nearly neutral variants linked to selected sites	390
8.3.i. Introduction	390
8.3.ii. The effects of balancing selection	393
8.3.ii.a. The effects of balancing selection on neutral variability	393
8.3.ii.b. Associative overdominance caused by heterozygote advantage	396
8.3.ii.c. Testing for the signature of balancing selection: the HKA test	397
8.3.ii.d. Testing for balancing selection: D_T , D_F , and haplotype tests	398
8.3.iii. Background selection	398
8.3.iii.a. Reduced neutral variability caused by linked deleterious mutations	398
8.3.iii.b. Associative overdominance due to linkage disequilibrium with deleterious mutations	403
8.3.iii.c. Associative overdominance due to identity disequilibrium	404
8.3.iv. The joint effects of spatial and genetic structure	406
8.3.v. Hitchhiking by favorable mutations (selective sweeps)	407
8.3.v.a. Effects on levels of neutral variability at linked sites	407
8.3.v.b. Effects on variant frequency spectra	413
8.3.v.c. Selective sweeps with recombination	415
8.3.v.d. Partial sweeps	416
8.4. Selection at multiple sites in the genome	418
8.4.i. Introduction	418
8.4.ii. Two-site systems	418
8.4.ii.a. General description	418
8.4.ii.b. Two-site fitness matrices	421
8.4.ii.c. Properties of stable equilibria	423
8.4.ii.d. Weak selection and loose linkage	425

8.4.iii. Multisite systems	429
8.4.iii.a. Properties of equilibria	429
8.4.iii.b. Dynamics under QLE	430
8.4.iv. The evolutionary dynamics of quantitative traits	430
8.4.iv.a. The infinitesimal model	430
8.4.iv.b. Extending the infinitesimal model	434
8.4.v. Wright's shifting balance model of evolution	434
8.4.v.a. Epistasis and multiple peaks of mean fitness	434
8.4.v.b. The fixation of chromosomal rearrangements	436
8.4.vi. The evolution of hybrid fitness loss	437
Appendix to Chapter 8: Linkage disequilibrium at neutral sites in finite populations	439
8A.1. The general method	439
8A.2. Application to linkage disequilibrium	440
Problems	442
9 The evolution of breeding systems, sex ratios, and life histories	444
Chapter summary	444
Introduction	445
9.1. Sexual versus asexual reproduction; inbreeding versus outcrossing	447
9.1.i. Introduction	447
9.1.ii. Asexual versus sexual reproduction	447
9.1.ii.a. Introduction	447
9.1.ii.b. The cost of sex	447
9.1.ii.c. The maintenance of sexual reproduction	449
9.1.iii. Sexual systems and mating systems	450
9.1.iii.a. Sexual systems	450
9.1.iii.b. Mating systems	450
9.1.iii.c. Self-incompatibility	452
9.1.iii.d. Detecting outcrossing and estimating outcrossing rates in natural populations	453
9.2. The evolution of inbreeding and outbreeding	455
9.2.i. Introduction	455
9.2.ii. The evolution of selfing rates	456
9.2.ii.a. Introduction	456
9.2.ii.b. The transmission advantage of selfing (the cost of outcrossing)	458
9.2.ii.c. Why do many organisms outcross? Inbreeding depression and the evolution of selfing rates	458
9.2.ii.d. More realistic models of inbreeding depression; purging of deleterious mutations	464

9.2.ii.e. Origins and evolution of self-incompatibility systems	465
9.2.iii. The breakdown of self-incompatibility systems	466
9.2.iii.a. The breakdown of heterostyly	466
9.2.iii.b. The breakdown of homomorphic SI	467
9.3. The evolution of separate sexes	467
9.3.i. Introduction	467
9.3.ii. The evolutionary stability of cosexuality	468
9.3.iii. Pathways to dioecy from cosexuality	468
9.3.iv. When will unisexuals invade cosexual populations?	471
9.3.iv.a. The establishment of cytoplasmic male sterility factors in populations	471
9.3.iv.b. The establishment of nuclear male sterility factors	472
9.3.iv.c. Testing the theory	474
9.3.iv.d. Androdioecy	476
9.3.v. The transition from gynodioecy to dioecy	478
9.3.v.a. The effect of the presence of females	478
9.3.v.b. The importance of linkage	480
9.4. Evolutionarily stable strategies, sex ratios, and sex allocation	483
9.4.i. Introduction	483
9.4.ii. Evolutionarily Stable Strategies	484
9.4.iii. The ESS sex ratio in a panmictic population	486
9.4.iii.a. Equal costs of male and female offspring	486
9.4.iii.b. Unequal costs of sons and daughters	486
9.4.iv. Extraordinary sex ratios	488
9.4.iv.a. Local mate competition	488
9.4.iv.b. Haplodiploid eusocial insects	490
9.4.v. Sex allocation in cosexuals	492
9.4.v.a. Theoretical models	492
9.4.v.b. Empirical tests	493
9.5. Age-structured populations and the evolution of life histories	494
9.5.i. Introduction	494
9.5.ii. Demographic models	494
9.5.ii.a. Basic concepts and notation	494
9.5.ii.b. Predicting population growth	496
9.5.ii.c. Population genetics for age-structured populations	502
9.5.iii. Selection equations	502
9.5.iii.a. The general recursion relations with no sex differences	502

9.5.iii.b. Equilibrium conditions	504
9.5.iii.c. Stability and invasion conditions	505
9.5.iii.d. Weak selection approximations	506
9.5.iii.e. Relationships between different fitness measures	507
9.5.iii.f. More general situations	508
9.5.iv. Implications for population genetic studies	508
9.5.v. Principles of life history evolution	510
9.5.v.a. The sensitivity of fitness to changes in demographic parameters	510
9.5.v.b. Trade-off models	512
9.5.v.c. Other life history models	514
9.5.v.d. The evolution of aging	515
Problems	519
10 Some topics in genome evolution	521
Chapter summary	521
Introduction	522
10.1. Evolution of noncoding sequences and codon usage	523
10.1.i. Introduction	523
10.1.i.a. Base composition	523
10.1.i.b. Codon usage bias	524
10.1.ii. Evolutionary forces affecting base composition	525
10.1.ii.a. Introduction	525
10.1.ii.b. Mutation and genetic drift	526
10.1.ii.c. Lower effectiveness of selection with reduced recombination	527
10.1.ii.d. Biased gene conversion	527
10.1.ii.e. Departures from equilibrium base composition	529
10.1.iii. Evolutionary forces affecting codon usage	530
10.1.iii.a. Measuring codon usage bias	530
10.1.iii.b. Causes of selection for codon usage bias	533
10.1.iv. Estimating the intensity of selection or biased gene conversion	535
10.1.iv.a. The intensity of selection and BGC on noncoding sites	536
10.1.iv.b. The intensity of selection on codon usage	537
10.2. The evolutionary causes and consequences of genetic recombination	539
10.2.i. Introduction	539
10.2.ii. The cost of recombination	540

10.2.iii. The evolution of close linkage	543
10.2.iii.a. Inversion polymorphisms	543
10.2.iii.b. Supergenes	543
10.2.iii.c. Centromeric and telomeric suppression of crossing over	544
10.2.iii.d. Congealing of the genome versus selection for recombination	545
10.2.iv. Possible advantages of sex and recombination: deterministic mechanisms	546
10.2.iv.a. Introduction	546
10.2.iv.b. Fluctuating epistasis	548
10.2.iv.c. Moving optima	548
10.2.iv.d. Mutation and selection	549
10.2.v. Stochastic processes	550
10.2.v.a. General considerations	550
10.2.v.b. Selective sweeps	551
10.2.v.c. Background selection	552
10.2.v.d. Muller's ratchet	552
10.2.v.e. Reverse mutation and Hill-Robertson interference	556
10.2.vi. Empirical evidence concerning the consequences of recombination	556
10.2.vi.a. Reduced levels of adaptation in regions with low recombination	556
10.2.vi.b. Discriminating between the different possible advantages of recombination	559
10.3. Selfish DNA	561
10.3.i. Introduction	561
10.3.ii. Gametic selection and segregation distortion	561
10.3.ii.a. Gametic selection	561
10.3.iii. Meiotic drive and segregation distortion	562
10.3.iii.a. Introduction	562
10.3.iii.b. Segregation distortion	563
10.3.iii.c. Examples of segregation distorter systems	565
10.3.iii.d. The evolution of segregation distorter systems	568
10.3.iv. Transposable elements	571
10.3.iv.a. Introduction	571
10.3.iv.b. The evolution of TEs in genomes	573
10.3.iv.c. TE behavior in genomes and populations	574
10.3.iv.d. Population dynamics of TEs	576

10.3.iv.e. Discriminating among possible regulators of element abundance	580
10.3.iv.f. Genomes and genomic regions with high TE contents	584
Problems	585
Appendix	587
A1. Basic mathematics	587
A1.i. Differentiation	587
A1.ii. Representing functions by series	588
A1.ii.a. Taylor's series	588
A1.ii.b. Approximate numerical solutions of equations ..	589
A1.ii.c. Some useful series	589
A1.iii. Integration	590
A1.iv. Vectors and matrices	591
A1.iv.a. Some definitions	591
A1.iv.b. The inverse of a matrix and the solution of linear equations	593
A1.iv.c. Eigenvalues and eigenvectors	594
A1.iv.d. The spectral expansion of a matrix	596
A2. Basic probability and statistics	597
A2.i. Introduction	597
A2.ii. The rules of probability	597
A2.iii. The moments of a distribution	598
A2.iv. Pairs of variables	599
A2.v. Some important probability distributions	601
A2.v.a. The binomial distribution	601
A2.v.b. The multinomial distribution	602
A2.v.c. The geometric and exponential distributions	602
A2.v.d. The Poisson distribution	603
A2.v.e. The normal distribution	603
A2.v.f. Other distributions	605
A2.vi. Statistical estimation	605
A2.vi.a. Introduction	605
A2.vi.b. Maximum likelihood	606
A2.vi.c. Bayesian methods	608
Answers to problems	609
Chapter 1	609
Chapter 2	611
Chapter 3	614
Chapter 4	618

Chapter 5	621
Chapter 6	624
Chapter 7	629
Chapter 8	633
Chapter 9	637
Chapter 10	640
References	642
Author Index	715
Subject Index	723