

Matrix Population Models

CONSTRUCTION, ANALYSIS, AND INTERPRETATION

Second Edition

HAL CASWELL
Biology Department
Woods Hole Oceanographic Institution



Sinauer Associates, Inc. Publishers
Sunderland, Massachusetts

Contents

Preface	xvii
Preface to the First Edition	xxi
1 Introduction	1
1.1 The life cycle: Linking the individual and the population	1
1.2 Demography	2
1.3 Overview of the book	3
1.3.1 Examples	4
1.3.2 MATLAB programs	5
1.4 Construction, analysis, and interpretation	5
1.5 Mathematical prerequisites	5
1.6 Notation	6
2 Age-Classified Matrix Models	8
2.1 The Leslie matrix	8
2.2 Projection: the simplest form of analysis	11
2.2.1 A set of questions	18
2.3 The Leslie matrix and the life table	20
2.3.1 Survival	21
2.3.2 Reproduction	22
2.4 Constructing age-classified matrices	22
2.4.1 Birth-flow populations	23
2.4.2 Birth-pulse populations	25
2.5 Assumptions: Projection vs. forecasting	29
2.6 History	31
3 Stage-Classified Life Cycles	35
3.1 State variables	35
3.1.1 Zadeh's theory of state	36
3.1.2 State variables in population models	37

3.2	Age as a state variable: When does it fail?	38
3.2.1	Size-dependent vital rates and plastic growth	39
3.2.2	Multiple modes of reproduction	40
3.2.3	Population subdivision and multistate demography	41
3.3	Statistical evaluation of state variables	41
3.3.1	Continuous response, continuous or discrete state	41
3.3.2	Discrete state, discrete response	43
3.3.3	Continuous state, discrete response	54
3.4	Overview	55
4	Stage-Classified Matrix Models	56
4.1	The life cycle graph	56
4.2	The matrix model	59
4.3	Metapopulation and multistate models	62
4.3.1	Modelling dispersal	65
4.3.2	Integrodifference equation models	71
4.3.3	Other examples	72
4.4	Solution of the projection equation	72
4.4.1	Derivation 1	74
4.4.2	Derivation 2	75
4.4.3	Effects of the eigenvalues	76
4.5	Ergodicity	79
4.5.1	The Perron-Frobenius theorem	79
4.5.2	Population growth rate: The strong ergodic theorem	84
4.5.3	Imprimitive matrices	87
4.5.4	Reducible matrices	88
4.6	Reproductive value	92
4.7	Transient dynamics and convergence	94
4.7.1	The damping ratio and convergence	95
4.7.2	The period of oscillation	100
4.7.3	Measuring the distance to the stable stage distribution	101
4.7.4	Population momentum	104
4.8	Computation of eigenvalues and eigenvectors	106
4.8.1	Eigenvalues and eigenvectors in MATLAB	107
4.8.2	The power method	108
4.9	Assumptions revisited	109
5	Events in the Life Cycle	110
5.1	$\mathbf{A} = \mathbf{T} + \mathbf{F}$	110
5.1.1	The life cycle as a Markov chain	111
5.1.2	The analysis of absorbing chains	112
5.2	Lifetime event probabilities	115
5.3	Age-specific traits	116

5.3.1	Age-specific survival	118
5.3.2	Age-specific fertility	120
5.3.3	Age at first reproduction	124
5.3.4	Net reproductive rate	126
5.3.5	Generation time	128
5.3.6	Age-within-stage distributions	130
6	Parameter Estimation	133
6.1	Identified individuals	134
6.1.1	Observed transition frequencies	134
6.1.2	Mark-recapture methods	136
6.2	Inverse methods for time series	142
6.2.1	Regression methods	142
6.2.2	Wood's quadratic programming method	144
6.2.3	A maximum likelihood approach	152
6.2.4	Stage-frequency methods	154
6.3	Stable stage-distribution methods	154
6.3.1	Age-classified models	154
6.3.2	Size-classified models	157
6.3.3	Death assemblages	157
6.4	Stage-duration distributions	159
6.4.1	The geometric distribution	160
6.4.2	Fixed stage durations	160
6.4.3	Variable stage durations	162
6.4.4	Iterative calculation	164
6.4.5	Negative binomial stage durations	164
6.4.6	Duration distributions compared	165
6.5	Multiregional or age-size models	166
6.6	The Vandermeer-Moloney algorithms	169
6.7	Fertilities in stage-classified models	171
6.7.1	Birth-flow populations	171
6.7.2	Birth-pulse populations	172
6.7.3	Anonymous reproduction	173
6.8	Overview	174
7	Analysis of the Life Cycle Graph	176
7.1	The z -transform	177
7.1.1	z -transform solution of difference equations	177
7.1.2	The z -transformed life cycle graph	178
7.2	Reduction of the life cycle graph	178
7.2.1	Multistep transitions	181
7.3	The characteristic equation	181
7.3.1	Derivation	184

7.4	The stable stage distribution	185
7.4.1	Derivation	187
7.5	Reproductive value	187
7.5.1	A second interpretation of reproductive value	189
7.5.2	A note on eigenvectors of reducible matrices	190
7.6	Partial life cycle analysis	190
7.7	Annual organisms	192
8	Structured Population Models	194
8.1	Partial differential equation models	194
8.1.1	Lotka's renewal equation	196
8.1.2	Discretizing Lotka's equation: Don't bother	197
8.1.3	Diffusion models	198
8.1.4	PDE models and matrix models	198
8.1.5	The escalator boxcar train	199
8.2	Delay-differential equation models	201
8.3	Integrodifference equation models	202
8.4	i -state configuration models	202
8.5	Choosing a model	204
9	Sensitivity Analysis	206
9.1	Eigenvalue sensitivity	208
9.1.1	Perturbations of matrix elements	208
9.1.2	Sensitivity and age	211
9.1.3	Sensitivities in stage- and size-classified models	213
9.1.4	What about those zeros?	215
9.1.5	Sensitivity to multistep transitions	217
9.1.6	Total derivatives and multiple perturbations	218
9.1.7	Sensitivity to changes in development rate	220
9.1.8	Predictions from sensitivities	224
9.1.9	An overall eigenvalue sensitivity index	224
9.1.10	A third interpretation of reproductive value	225
9.2	Elasticity analysis	226
9.2.1	Elasticity and age	227
9.2.2	Elasticities as contributions to λ	229
9.2.3	Elasticities of λ to lower-level parameters	232
9.2.4	Comparative analysis of elasticity patterns	233
9.2.5	Predictions from elasticities	240
9.2.6	Sensitivity or elasticity?	243
9.3	Sensitivity analysis of transient dynamics	244
9.3.1	Sensitivity of the damping ratio	244
9.3.2	Sensitivity of the period	247
9.4	Sensitivities of eigenvectors	247

9.4.1	Sensitivities of scaled eigenvectors	250
9.5	Generalized inverses in sensitivity analysis	251
9.6	Sensitivity analysis of Markov chains	251
9.7	Second Derivatives of Eigenvalues	254
9.7.1	Perturbation analysis of elasticities	256
10	Life Table Response Experiments	258
10.1	Fixed designs	260
10.1.1	One-way designs	260
10.1.2	Factorial designs	263
10.2	Random designs and variance decomposition	269
10.3	Regression designs	273
10.4	Extensions	274
10.4.1	Higher-order terms	274
10.4.2	Other demographic statistics	275
10.4.3	Other demographic models	275
10.4.4	More mechanisms	276
10.4.5	Statistics	277
10.5	Prospective and retrospective analyses	277
11	Evolutionary Demography	279
11.1	Fitness	280
11.1.1	Population genetics	281
11.1.2	Quantitative genetics	282
11.1.3	Invasion and ESS analysis	291
11.2	Sensitivity, elasticity, and selection	295
11.3	Lifetime reproductive success and individual fitness	295
11.4	Fitness and reproductive value	297
12	Statistical Inference	299
12.1	Confidence intervals and uncertainty	300
12.1.1	Series approximations	300
12.1.2	Bootstrap standard errors	304
12.1.3	Bootstrap confidence intervals	306
12.1.4	Complex data structures	309
12.1.5	More on the bootstrap	315
12.1.6	Monte Carlo uncertainty analysis	319
12.1.7	The precision of estimates of λ	322
12.2	Loglinear analysis of transition matrices	326
12.2.1	One factor	327
12.2.2	Two factors	330
12.2.3	Model selection and <i>AIC</i>	332

12.2.4	Presentation of loglinear analyses	334
12.3	Randomization tests	335
12.3.1	The randomization test procedure	337
12.3.2	Types of data	338
12.3.3	Examples of randomization tests	338
12.3.4	Advantages of randomization tests	343
12.3.5	Implementation	345
13	Periodic Environments	346
13.1	Periodic matrix products	347
13.1.1	Notation	348
13.1.2	Eigenvalues and eigenvectors	349
13.1.3	Matrices don't commute, and why that matters	354
13.1.4	Sensitivity analysis of periodic matrix models	356
13.2	Annual organisms	361
13.2.1	Periodic matrix models for annuals	362
13.3	Other approaches to periodic environments	368
13.3.1	Classification by season of birth	368
13.3.2	Discrete Fourier analysis	368
13.4	Deterministic, aperiodic environments	369
13.4.1	Weak ergodicity	369
14	Environmental Stochasticity	377
14.1	Formulation of stochastic models	377
14.1.1	Models for the environment	378
14.1.2	Linking the environment and the vital rates	381
14.1.3	Projecting the population	382
14.2	Stochastic ergodic theorems	382
14.2.1	Stage distributions	382
14.2.2	Stochastic reproductive value	384
14.2.3	Sufficient conditions for stochastic ergodicity	384
14.2.4	An overview of ergodic results	386
14.3	Stochastic population growth	387
14.3.1	The Lewontin-Cohen model	387
14.3.2	Beyond iid processes	392
14.3.3	Ergodic properties of random matrix products	393
14.3.4	Growth of the mean	394
14.3.5	Which growth rate is relevant?	395
14.3.6	Calculating the stochastic growth rate	396
14.3.7	Calculation of the variance σ^2	399
14.3.8	Scalar and matrix models compared	400
14.4	Sensitivity and elasticity analyses	401
14.4.1	From numerical simulations	402

14.4.2	From Tuljapurkar's approximation	407
14.4.3	Sensitivity of $\log \lambda_s$ to variability	408
14.5	Examples of stochastic models	409
14.5.1	Striped bass: Variability in recruitment	409
14.5.2	Clams: Parametric distributions of recruitment	410
14.5.3	Stochastic models from sequence of matrices	415
14.5.4	Markov chain models for the environment	419
14.5.5	Random selection of matrix elements	430
14.5.6	Applications of Tuljapurkar's approximation	435
14.5.7	Some suggestions	435
14.6	Evolution in stochastic environments	436
14.6.1	Fitness and ESS in stochastic environments	436
14.6.2	An example: Delayed reproduction	437
14.6.3	Life history studies	440
14.7	Stochastic and deterministic sensitivity	443
14.8	Extinction in stochastic environments	443
14.8.1	A model for quasi-extinction	444
14.8.2	Sensitivity analysis	447
14.9	Short-term stochastic forecasts	449
15	Demographic Stochasticity	452
15.1	Stochastic simulations	453
15.1.1	Assumptions, essential and otherwise	456
15.1.2	Simulating individuals	456
15.1.3	A computationally efficient alternative	458
15.1.4	Bad luck, or something worse?	462
15.1.5	Time-varying and density-dependent models	464
15.2	The Galton-Watson branching process	464
15.2.1	Probability generating functions	466
15.2.2	Population projection	467
15.2.3	Projection of moments	470
15.2.4	Limit theorems and asymptotic dynamics	471
15.2.5	Extinction	472
15.2.6	Quasi-stationary distributions	475
15.2.7	Extinction, effective population size, and elasticity	475
15.3	Multitype branching processes	478
15.3.1	From matrix models to branching processes	479
15.3.2	Mean and covariance of offspring production	483
15.4	Analysis of multitype branching processes	486
15.4.1	Population projection	486
15.4.2	Projection of moments	486
15.4.3	Limit theorems and asymptotic dynamics	491
15.4.4	Extinction probability	493

15.4.5	Extinction probability and reproductive value	497
15.4.6	Elasticities of extinction probability and of λ	497
15.4.7	Subcritical multitype branching processes	499
15.5	Branching processes in random environments	501
15.6	Assumptions revisited	502
16	Density-Dependent Models	504
16.1	Model construction	505
16.1.1	Types of density dependence	505
16.1.2	Examples	508
16.2	Asymptotic dynamics and invariant sets	513
16.2.1	Finding equilibria	518
16.3	Stability and instability	519
16.4	Local stability of equilibria	519
16.4.1	The Jury criteria	522
16.5	Bifurcation diagrams	525
16.6	Bifurcations of equilibria: A field guide	526
16.6.1	+1 bifurcations	528
16.6.2	-1 bifurcations: The flip bifurcation	533
16.6.3	Complex conjugate pairs: The Hopf bifurcation	533
16.6.4	Supercritical and subcritical bifurcations	537
16.7	Chaos	538
16.7.1	Lyapunov exponents and quantitative unpredictability	542
16.7.2	Routes to chaos	543
16.7.3	Chaotic power spectra	546
16.8	Transient dynamics	548
16.8.1	Reactivity and resilience of stable equilibria	548
16.8.2	Unstable equilibria	550
16.8.3	Strange repellers and chaotic transients	551
16.8.4	Effects of random perturbations	551
16.9	Multiple attractors and qualitative unpredictability	552
16.10	<i>Tribolium</i> : Models and experiments	553
16.11	Perturbation analysis and evolution	557
16.11.1	Sensitivity analysis of equilibria	559
16.11.2	Invasion and evolution	560
16.12	Stochasticity and density dependence	565
17	Two-Sex Models	568
17.1	Sexual dimorphism in the vital rates	568
17.2	Dominance, sex ratio, and the marriage squeeze	570

17.3	Two-sex models	571
17.3.1	A simple two-sex model	572
17.3.2	The birth and fertility functions	574
17.3.3	Frequency and density dependence	576
17.3.4	The equilibrium population structure	576
17.3.5	Stability of population structure	578
17.3.6	Nussbaum’s global stability theorem	581
17.4	Competition for mates	581
17.4.1	Numerical results: Competition and instability	583
17.5	The birth matrix-mating rule model	585
17.6	More detailed models of mating	587
17.7	Frequency and density dependence combined	588
17.8	Extinction and the sex ratio	589
18	Conservation and Management	591
18.1	Conservation	592
18.1.1	Assessment	592
18.1.2	Diagnosis	601
18.1.3	Prescription	604
18.1.4	Prognosis	619
18.1.5	Conservation conclusions	629
18.2	Pest control	629
18.2.1	Reducing population size	630
18.2.2	Extermination	631
18.2.3	Halting invasion	632
18.2.4	Some examples of pest control	634
18.3	Harvesting	640
18.3.1	Optimal harvesting	642
18.4	Overview	644
19	Concluding Remarks	646
19.1	The most important task	646
19.2	Testing models	648
19.3	A complete demographic analysis	649
19.4	Directions for research	651
A	The Basics of Matrix Algebra	653
A.1	Motivation	653
A.2	Definitions	654
A.3	Operations	655
A.3.1	Addition	655
A.3.2	Scalar multiplication	655
A.3.3	The transpose and the adjoint	655

A.3.4	The trace	656
A.3.5	Scalar product	656
A.3.6	Matrix multiplication	656
A.3.7	The Kronecker and Hadamard products	658
A.4	Matrix inversion	659
A.4.1	The identity matrix	659
A.4.2	Inversion and the solution of algebraic equations	659
A.4.3	A useful fact about homogeneous systems	660
A.5	Determinants	660
A.5.1	Properties of determinants	662
A.6	Eigenvalues and eigenvectors	662
A.6.1	Eigenvectors	662
A.6.2	Left eigenvectors	663
A.6.3	The characteristic equation	663
A.6.4	Finding the eigenvectors	664
A.6.5	Complications	665
A.6.6	Linear independence of eigenvectors	665
A.6.7	Left and right eigenvectors	666
A.6.8	Computation of eigenvalues and eigenvectors	666
A.7	Similarity	666
A.7.1	Properties of similar matrices	667
A.8	Norms of vectors and matrices	667
A.9	Suggested reading	668
	Bibliography	669
	Copyright Permissions	711
	Index	713