

# Contents

<b>1 Fundamentals</b>	1
1.1 A brief history of life histories	1
1.1.1 Breadth	1
1.1.2 'Life history' in the nineteenth century	2
1.1.3 The turning point: 1930	3
1.1.4 Fifty years on (1930–1980)	4
1.1.5 Life-history 'classics'	7
1.2 A primer of population growth	8
1.2.1 Intrinsic rate of natural increase	8
1.2.2 Density-independent population growth	10
1.2.3 Density-dependent population growth	11
1.3 Life-history traits	13
1.4 A conceptual life-history framework	14
1.5 Summing up and a look ahead	16
<b>2 Life-History Variation</b>	17
2.1 Why are there so many kinds of life histories?	17
2.2 Life-history variability among species	18
2.2.1 Differences across phylogenetically diverse organisms	18
2.2.2 Body size	19
2.2.3 Age at maturity	21
2.2.4 Offspring number	22
2.2.5 Offspring size	23
2.2.6 Lifespan	25
2.2.7 Life-history differences within species can be considerable	26
2.2.8 Growth rate	28
2.3 Life-history constraints and invariants	30
2.3.1 Constraints	30
2.3.2 Life-history invariants	31
2.4 Patterns of trait covariation	35
2.4.1 Trait covariation in plants	35
2.4.2 Trait covariation in animals: early thinking	36
2.4.3 <i>r</i> - and <i>K</i> -selection	37
2.4.4 <i>r</i> - <i>K</i> -ic?	38
2.4.5 The ubiquity of <i>r</i> -selection	39
2.4.6 Fast-slow continuum	39
2.4.7 Pace-of-life syndrome	40
2.5 Summing up and a look ahead	41



<b>3 Genetic Variation and Phenotypic Plasticity</b>	<b>43</b>
3.1 Genetic underpinnings	43
3.1.1 Distinguishing phenotype from genotype	43
3.1.2 Genes and phenotypes	44
3.1.3 Quantitative genetics and partitioning genetic variance	45
3.2 Measuring evolutionary change in response to selection	47
3.2.1 Heritability and additive genetic variance	47
3.2.2 Response to selection	47
3.2.3 Genetic trade-offs	49
3.2.4 Genetic architecture	50
3.3 Phenotypic plasticity	52
3.4 Norms of reaction	54
3.5 Summing up and a look ahead	58
<b>4 Reproductive Effort and Costs</b>	<b>59</b>
4.1 Trading off one set of fitness benefits for another	59
4.2 The nature of trade-offs	61
4.3 Reproductive effort	62
4.4 Costs of reproduction	64
4.5 Energetic, ecological, and genetic basis for reproductive costs	66
4.5.1 What constrains reproduction?	66
4.5.2 Energetic constraints	67
4.5.3 Ecological and behavioural constraints	69
4.5.4 Senescence	70
4.5.5 Measuring effort and costs: challenges and caveats	71
4.6 Summing up and a look ahead	73
<b>5 Vital Rates</b>	<b>75</b>
5.1 Schedules of mortality and reproduction	75
5.2 Life tables	76
5.2.1 Age-specific survival and fecundity	76
5.2.2 An example of a life table	77
5.3 Fitness	78
5.3.1 Rates of increase	78
5.3.2 Net reproductive rate, $R_0$	79
5.3.3 Intrinsic rate of increase, $r$	79
5.3.4 Reproductive value, $RV$	81
5.3.5 Caveats	82
5.4 Estimating fitness from a life table	83
5.5 Life-table approach to exploring optimal age at maturity	85
5.5.1 Incorporating a fecundity cost of reproduction	85
5.5.2 Incorporating a survival cost of reproduction	87
5.5.3 Incorporating new sources of extrinsic mortality	89
5.5.4 The ratio of juvenile to adult survival	91
5.6 Summing up and a look ahead	96



<b>6 Life-History Evolution in a Changing Environment</b>	99
6.1 Shifts in the mean and variance of environmental conditions	99
6.2 Evolution of age and reproductive effort at maturity	100
6.2.1 Semelparity versus iteroparity	100
6.2.2 Life-history responses to changes in survival	101
6.2.3 Life-history responses to changes in the variance in survival	103
6.3 Life-history evolution in a variable environment	104
6.3.1 Hedging evolutionary bets	104
6.3.2 Reducing the variance in fitness	105
6.3.3 Bet-hedging life histories	107
6.3.4 Deterministic versus stochastic $r$	111
6.4 Summing up and a look ahead	113
<b>7 Number and Size of Offspring</b>	115
7.1 Extreme variability in the production of propagules	115
7.2 Offspring number and size: not all options are possible	116
7.3 Evolution of offspring number	118
7.3.1 Early thinking: clutch size in birds	118
7.3.2 The Lack clutch size	119
7.3.3 Observed clutch sizes often differ from the Lack clutch size	120
7.4 Evolution of offspring size	121
7.4.1 Early thinking: a trade-off between size and number of offspring	121
7.4.2 Investment per offspring	123
7.4.3 Smith-Fretwell model of optimal size and number of offspring	123
7.4.4 Selection for increased fecundity	126
7.5 Summing up and a look ahead	127
<b>8 Alternative Life Histories</b>	129
8.1 Alternative reproductive phenotypes	129
8.2 Dichotomies in sex, size, and status	130
8.3 Thresholds and conditional tactics	135
8.4 Genetic polymorphisms	137
8.5 Genotype-by-environment thresholds for alternative strategies	142
8.5.1 Threshold reaction norms	142
8.5.2 Thresholds for alternative strategies under selection	144
8.6 Frequency-dependent selection	148
8.7 Clarity in terminology	149
8.8 Summing up and a look ahead	151
<b>9 Applications: Conservation Biology</b>	153
9.1 Three paradigms	153
9.2 A stimulus for incorporating life history to assess species vulnerability	154
9.3 Life-history correlates of $r_{\max}$	156



9.4	Species vulnerability assessments	159
9.4.1	Extinction	159
9.4.2	Exploitation	161
9.4.3	Climate change	163
9.5	A comparison of vulnerability assessments	165
9.6	Species and population recovery	167
9.6.1	Generalized approaches are uncommon	167
9.6.2	Life-history correlates of recovery potential	168
9.6.3	The portfolio effect	170
9.7	Summing up and a look ahead	171
<b>10</b>	<b>Applications: Sustainable Exploitation of Evolving Resources</b>	<b>173</b>
10.1	Sustainability	173
10.2	The collapse of Canadian cod	174
10.3	Maximum sustainable yield	175
10.3.1	The basic concept	175
10.3.2	MSY depends on population size	177
10.3.3	Estimating MSY	178
10.3.4	MSY for data-poor species	180
10.3.5	Understanding mortality: the key to sustainability	182
10.4	Reference points to guide sustainability initiatives	184
10.4.1	Limits, targets, and MSY	184
10.4.2	Reference points and life history	186
10.5	Harvest-induced evolution	188
10.5.1	Fisheries-induced changes in life history	188
10.5.2	Fisheries-induced evolution	190
10.5.3	Hunting-induced evolution	192
10.6	Summing up	195
	<b>References</b>	<b>197</b>
	<b>Subject Index</b>	<b>217</b>
	<b>Taxonomic Index</b>	<b>223</b>