Longitudinal population demography of the allied rock-wallaby, *Petrogale assimilis*.

Thesis submitted by

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Statement of the contribution of others

In completing this thesis I received stipend support from the School of Tropical Environment Studies and Geography, James Cook University during the period 1997-1999. My supervisors were Professor Helene Marsh, Dean of Graduate Research Studies, James Cook University, and Dr. Glenn De'ath, Senior Research Fellow, Australian Institute of Marine Science. Statistical advice was provided by Dr. De'ath, however I carried out all statistical analyses presented in this thesis.

My research was supported by a Merit Research Grant (1998) from James Cook University, and a Small Mammal Research Grant (1997) from the Queensland Department of Environment and Heritage. Additional funding during the early years of the research program (prior to my involvement) was provided by James Cook University (Merit Research Grants) and the Australian Research Council (ARC Large and ARC Small to Professor Helene Marsh and Dr. Peter Spencer).

The long-term capture-recapture study of the biology of *Petrogale assimilis* at Black Rock began in 1986, and the research was coordinated by the principal investigator Professor Helene Marsh. These research studies investigated the life history and reproductive ecology, the behavioural ecology, and the population genetics of the population. My research used capture-recapture data from *P. assimilis* at Black Rock collected by Dr. Robyn Delaney between 1986 and 1988 (Delaney 1993), Dr. Alan Horsup between 1986 and 1988 (Horsup 1996), and Dr. Peter Spencer between 1989 and 1993 (Spencer 1996).

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Abstract

The allied rock-wallaby, *Petrogale assimilis*, is a medium-sized, monomorphic, continuously-breeding macropodid marsupial that lives in rocky habitats in the climatically unpredictable wet-dry tropics of north-eastern Australia. Long-term capture-recapture records of individually marked *P. assimilis* from an isolated population inhabiting Black Rock, a sandstone escarpment in western Queensland, were used to investigate the population demography of the species over 12 years.

In natural populations, both extrinsic environmental variation and intrinsic density-dependence contribute to variability in demographic fitness components. Changes in these fitness components, and trade-offs between them, determine the dynamics of populations. Almost no information is available on the temporal variability of the demographic fitness components and their relationship with rates of population change for kangaroos and wallabies. This research provides the first long-term study of a macropod species that is based on individually-marked animals, which are required to estimate such fitness components and their temporal variation. A major aim of this research was to determine the impact of variability in the fitness components on the population dynamics of this macropod species, and to compare these results with those available for other long-lived herbivores. The demographic components of the life history of *P. assimilis* at Black Rock were investigated, along with the interrelationships between long-term temporal variability in these components and intrinsic and extrinsic factors, and individual fitness. The long-term fitness of the population and the influence of temporal covariation between the demographic components on variability in population fitness were also examined.

The growth relationship between the size and age of *P. assimilis* at Black Rock was determined using various nonlinear models within a mixed-effects framework. The age and individual variation in growth of animals of unknown age were estimated from measurements of body size. Parametric nonlinear models did not fit the growth pattern, but semi-parametric spline models adequately described the growth pattern and accounted for individual variation. Differences in growth between the sexes were small, suggesting no strong sexual size dimorphism in *P. assimilis*. Growth rates were highest during pouch development, were lower during the weaning period, and decreased dramatically after weaning. The age structure of the population of *P. assimilis* at Black Rock varied substantially over the study period.

The log-transformed relationships between body mass and various body size measures were nonlinear and the head length was the best predictor of body mass of *P. assimilis* at Black Rock. Indices of body condition were calculated from the residuals of mixed-effects models that estimated the form of the size-mass relationship using splines. Substantial variation in body

condition was explained by annual and seasonal variability and lagged rainfall, as well as variation between individual animals. Variation in body condition was not associated with sex or age-class, and did not depend on the lactation status of females. The estimated index of body condition appeared to represent the nutritional status of individual *P. assimilis* at Black Rock and was used as a predictor of variation in demographic rates associated with individual fitness.

Directional goodness-of-fit tests for Cormack-Jolly-Seber capture-recapture models showed that individual *P. assimilis* at Black Rock had a trap happy response to capture. The likelihood of recapture varied over time and depended on whether animals were captured on the previous sampling occasion. Recapture probability was generally very high, and was lower for adult females not marked as young than for other females marked as young and for all males, regardless of age at marking. Similar effects on recapture probability were identified using generalised linear mixed models, though the time-dependent effect could be simplified to a year by season interaction plus the effect of trapping effort. There was strong agreement between estimates of population size based on different methods. Population size fluctuated substantially over the study with periods of consistent increase and decline, and showed evidence of rapid population recovery from relatively low numbers under positive environmental conditions.

Support for the Trivers-Willard hypothesis (TWH), which states that if the costs of reproduction differ between the sexes then the offspring sex ratio will vary depending on the parent's ability to allocate resources, was evaluated. The sex ratio at birth was equal and not correlated with mother's age, body mass or body condition. Sex ratio varied seasonally; being female-biased in the mid- to late-dry season and male-biased in the late dry and early wet seasons. Survival from birth to pouch emergence was correlated with environmental conditions, depending on sex, in the direction consistent with TWH; male survival was higher than female survival under good conditions and lower under poor conditions. Also, survival was higher for pouch young of heavier mothers or mothers in good condition. Survival to pouch emergence was also density-dependent. In support of TWH, the sex ratio at pouch emergence was male-biased under good environmental conditions and was male-biased for mothers in good condition or heavier mothers. Mothers in good condition produced offspring in good condition, satisfying an assumption of TWH, and higher mass at pouch emergence resulted in improved survivorship to weaning.

Survival from pouch emergence to weaning was higher for females than males, and was positively correlated with environmental conditions. Females had higher survival to weaning than males in the hotter seasons, but there was no sex difference in survival in the cooler seasons. Survival was also higher for females than for males born to lighter mothers, but there was no difference between the sexes born to heavier mothers. Male-biased sex ratios at weaning were observed under good environmental conditions and for mothers with higher body mass, providing support for TWH at this life history stage. The body mass of offspring at weaning was correlated with maternal body mass, satisfying an assumption of TWH, and offspring mass was also higher under high rainfall conditions. Patterns of variability in the sex ratio and pre-weaning survival of *P. assimilis* at Black Rock were influenced by a combination of: (1) adaptive allocation of resources between the sexes depending on maternal condition; and (2) non-adaptive extrinsic modification associated with environmental stochasticity, allowing mothers to respond quickly in a variable environment to maximise their current reproduction and future survival.

Male *P. assimilis* matured later and were heavier at maturity than females. Early maturity was favoured for females but not for males under high rainfall conditions, independent of size at maturity. Age at maturity was density-dependent for males only, with delayed maturity at lower population sizes. Maturation was delayed for both sexes when body mass at weaning was low relative to individuals with high weaning mass.

Subadult male survival was lower than for females, and survival of both sexes increased under high rainfall conditions. Adult survival was higher than subadult survival, independent of sex, and survival of older adults was lower than that of prime-aged adults, indicating senescence. Survival increased under positive climatic conditions and was density-dependent, with lower survival at high population sizes. Males had lower survival to sexual maturity than females, and increased body mass improved survival for both sexes. Population growth rate was most sensitive to changes in prime-aged adult survival, as is typical for longer-lived vertebrates. The temporal variance in the juvenile survival stages was much higher than in adult survival. Therefore, consistent with other longer-lived, iteroparous vertebrates, the impact of relative changes to adult survival on population growth were much greater than changes of the same magnitude to either survival in the juvenile stages, or to the fecundity rate.

There was a negative relationship between temporal variation in the demographic rates and their sensitivities, indicating that the more variable vital rates had low effects on long-term population growth. The most variable demographic rates covaried suggesting that common factors contributed to temporal variability. Covariation in survival between the juvenile and pre-maturity life history stages accounted for most of the variability in the population growth rate, indicating survivorship in the juvenile stages was more important than adult survival in determining changes in the population growth rate of *P. assimilis* at Black Rock. The survival patterns of different life history stages were variable for *P. assimilis* at Black Rock, and responded differently to environmental variability and population density. Density-dependent and density-independent limiting factors primarily acted on the juvenile survival components of the life history, and covariation among these fitness components influenced the dynamics of the population. Survival of prime-aged adult *P. assimilis* at Black Rock was much less sensitive to these limiting factors, showed the highest elasticity, and appeared to be buffered against temporal variability. These results add to growing evidence from natural populations that natural selection may favour traits that are highly buffered against environmental variability.

Abbreviations

Abbreviation	*Explanation*
AIC	Akaike's Information Criterion
AIC_c	Akaike's Information Criterion corrected for small sample size
BIC	Bayesian Information Criterion
BIC_R	BIC from restricted maximum likelihood
CI	Confidence interval (95^{th} percentile, unless otherwise stated)
CJS	Cormack-Jolly-Seber capture-recapture model
CV	Coefficient of variation
df	Degrees of freedom
EMH	Extrinsic modification hypothesis
ENSO	El Niño Southern Oscillation phenomenon
JS	Jolly-Seber capture-recapture model
LRT	Likelihood-ratio test
ML	Maximum likelihood
REML	Restricted (or Residual) maximum likelihood
SD	Standard deviation
SE	Standard error
SN	Season (i.e. early dry, late dry, and wet seasons)
SOI	Southern Oscillation Index
TWH	Trivers-Willard hypothesis

Table of contents

Chapter 1. General Introduction 1
1.1 Long-term studies in population ecology 1
1.2 Mammalian population demography...2
1.2.1 Survival and reproduction as components of population demography 3
1.2.2 Environmental stochasticity and density-dependence 4
1.2.3 Sex ratio variation 6
1.3 Macropod population dynamics 7
1.4 Distribution and ecology of rock-wallabies...8
1.5 *Petrogale assimilis* at Black Rock 10
1.6 Aims of this thesis 14
1.7 Structure of this thesis...16
Chapter 2. Methods 18
2.1 Long-term capture-recapture study site at Black Rock...18
2.1.1 Study site 18
2.1.2 Vegetation...18
2.1.3 Climate..20
2.1.3.1 Coding environmental covariates for analyses 26
2.2 Sampling methods 27
2.2.1 Marking methods 28
2.2.2 Measurements 29
2.2.2.1 Females...29
2.2.2.2 Males...32
2.2.3 Age-specific life history stages 32
2.3 Statistical methods 32
2.3.1 Model selection 33
2.3.1.1 Likelihood-ratio tests 33
2.3.1.2 Akaike's Information Criterion 34
2.3.1.3 Bayesian Information Criterion...35
2.3.1.4 Model uncertainty...36
2.3.2 Mixed-effects models...36
2.3.2.1 Random-effects models 37
2.3.2.2 Restricted maximum likelihood estimation for mixed-effects models 38
2.3.3 Smoothers for estimating nonlinear relationships 39
2.3.3.1 Regression splines...39
2.3.3.2 Smoothers in linear mixed-effects models 40
2.3.4 Statistical software 40
Chapter 3. Mixed-model growth curve analysis and age estimation.........................41
3.1 Summary 41
3.2 Introduction...41
3.3 Methods..44
3.3.1 Field data 44
3.3.2 Captive colony data 44
3.3.3 Statistical analyses 45
3.4 Results 46
3.4.1 Estimating age and between-individual variation 46
3.4.2 Estimating the age of captive animals 46
3.4.3 Modelling variation in growth between individual animals.................................49
3.4.4 Population age structure...51
3.5 Discussion 52
Chapter 4. Estimating body condition: nonlinearity and the effects of environmental variation. 55
4.1 Summary 55
4.2 Introduction...55

4.3 Methods....59
  4.3.1 Field data....59
  4.3.2 Statistical analyses....60
    4.3.2.1 The size-mass relationship....60
    4.3.2.2 Mixed-effects models of the size-mass relationship....60
    4.3.2.3 Estimating temporal, environmental and sex differences....61
    4.3.2.4 Determining the best measure to represent size....61
    4.3.2.5 Prediction of body condition index....62
4.4 Results....62
  4.4.1 Selection of the best measure to represent body size....62
  4.4.2 The size-mass relationship using linear mixed-effects models....64
  4.4.3 Variation in body condition with temporal, environmental, and sex effects....65
  4.4.4 Prediction of body condition index....69
  4.4.5 Effect of reproductive status on female body condition....71
4.5 Discussion....71
Chapter 5. Modelling recapture probability and estimating population size....76
5.1 Summary....76
5.2 Introduction....77
5.3 Methods....79
  5.3.1 Field data....79
  5.3.2 Capture-recapture analysis....80
    5.3.2.1 Jolly-Seber model....80
    5.3.2.2 Cormack-Jolly-Seber model....80
    5.3.2.3 Cormack-Jolly-Seber model assumptions....81
  5.3.3 Goodness-of-fit tests of Cormack-Jolly-Seber models....82
  5.3.4 Estimation of recapture probability with Cormack-Jolly-Seber models....84
  5.3.5 Closed population models....85
  5.3.6 Estimation of recapture probability with generalised linear mixed-models....86
  5.3.7 Estimates of population size using the Horvitz-Thompson method....86
5.4 Results....87
  5.4.1 Assumption of constant probability of survival and recapture of individuals marked on different sampling occasions....88
  5.4.2 Assumption of constant probability of recapture between newly and previously captured individuals....88
  5.4.3 Cormack-Jolly-Seber modelling of variation in recapture probabilities....90
  5.4.4 Generalised linear mixed modelling of variation in recapture probabilities....92
    5.4.4.1 Temporal and group effects....93
    5.4.4.2 Random effects....93
  5.4.5 Temporal variation in population size....95
    5.4.5.1 Horvitz-Thompson (HT) estimates and the minimum number known alive95
    5.4.5.2 Closed capture model estimates....97
5.5 Discussion....97
  5.5.1 Independence of fates and identity of rates assumptions of the CJS model....97
  5.5.2 Variation in recapture rates from CJS models....99
  5.5.3 Variation in recapture rates from GLMM models....100
  5.5.4 Estimates of population size....101
  5.5.5 Conclusion....102
Chapter 6. Sex ratio variation and pre-weaning survival....104
6.1 Summary....104
6.2 Introduction....105
  6.2.1 Sex ratio variation in marsupials....109
6.3 Methods....113
  6.3.1 Data collection....113
    6.3.1.1 Temporal, environmental and maternal covariates....114
  6.3.2 Statistical methods....115
    6.3.2.1 Generalised linear mixed-model analysis....115
    6.3.2.2 Survival analysis....116
      6.3.2.2.1 Cox proportional hazards model....116
      6.3.2.2.2 Time-dependent survival model....118
6.4 Results....118

6.4.1 Sex ratio variation at birth 118
6.4.1.1 Temporal variation in sex ratio at birth 119
6.4.1.2 Differences between pouch young from ‘continuous’ and ‘non-continuous’ births 119
6.4.1.3 Environmental and maternal variation in sex ratio at birth 122
6.4.1.4 Dependence of birth sex ratio on the sex and survival of the previous offspring 122
6.4.2 Survival from birth to pouch emergence 123
6.4.2.1 Temporal variation in survival from birth 125
6.4.2.2 Proportional hazards assumption for survival from birth to pouch emergence 125
6.4.2.3 Time-dependent changes in probability of survival to pouch emergence 127
6.4.2.3.1 Environmental variation in survival to pouch emergence 127
6.4.2.3.2 Maternal variation in survival to pouch emergence 127
6.4.3 Sex ratio at pouch emergence 129
6.4.3.1 Temporal variation in sex ratio at pouch emergence 129
6.4.3.2 Environmental variation in sex ratio at pouch emergence 129
6.4.3.3 Maternal variation in sex ratio at pouch emergence 130
6.4.4 Body mass and condition at pouch emergence 131
6.4.5 Survival from pouch emergence to weaning 131
6.4.5.1 Temporal variation in survival to weaning 132
6.4.5.2 Environmental variation in survival to weaning 133
6.4.5.3 Maternal variation in survival to weaning 134
6.4.6 Sex ratio at weaning 136
6.4.6.1 Temporal variation in sex ratio at weaning 136
6.4.6.2 Environmental variation in sex ratio at weaning 136
6.4.6.3 Maternal variation in sex ratio at weaning 136
6.4.7 Age at weaning 137
6.4.8 Body mass at weaning 139
6.5 Discussion 140
6.5.1 Birth sex ratio variation 140
6.5.2 Survival and sex ratio variation at pouch emergence 144
6.5.3 Survival and sex ratio variation at weaning 149
6.5.4 Accordance with the assumptions of TWH 152
6.5.5 Conclusions 153
Chapter 7. Age at maturity, post-weaning survival, and demographic perturbation analysis 157
7.1 Summary 157
7.2 Introduction 158
7.2.1 Post-weaning survival 160
7.2.2 Age at maturity 160
7.2.3 Demographic patterns 161
7.3 Methods 164
7.3.1 Field data 164
7.3.1.1 Environmental variables and population size 164
7.3.1.2 Individually-varying covariates and maternal factors 165
7.3.2 Age at maturity 165
7.3.2.1 Determination of sexual maturity 165
7.3.2.2 Factors affecting age at maturity 166
7.3.3 Estimation of fecundity rates 166
7.3.4 Multi-state capture-recapture models 166
7.3.5 Time-dependent modelling of age-specific survival 169
7.3.6 Demographic perturbation analysis 169
7.3.6.1 Life cycle graph and population projection matrix 169
7.3.6.2 Sensitivity and elasticity analyses 172
7.3.6.3 Life table response experiment 173
7.4 Results 174
7.4.1 Age at maturity 174
7.4.2 Annual fecundity 176
7.4.3 Multi-state capture-recapture survival analysis 177

7.4.3.1 Multi-state capture-recapture analysis with two stage-classes 177
7.4.3.2 Senescence in adult survival 178
7.4.4 Time-dependent Cox modelling of age-specific survival probabilities 180
7.4.4.1 Age-specific survival probabilities 181
7.4.4.2 Density, environmental, and individual correlates of survival 182
7.4.5 Demographic perturbation analysis 184
7.4.5.1 Sensitivity and elasticity analysis 184
7.4.5.1.1 Sensitivity and elasticity analysis of lower-level vital rates 186
7.4.5.2 Temporal variation and covariation in lower-level vital rates 187
7.4.5.3 Life table response experiment 188
7.4.5.3.1 Variance decomposition among elements of the population projection matrix 189
7.4.5.3.2 Variance decomposition among lower-level vital rates 191
7.5 Discussion 193
7.5.1 Factors affecting age at maturity 194
7.5.2 Factors affecting post-weaning survival rates 196
7.5.3 Temporal variation in survival and reproductive rates 202
7.5.4 Demographic patterns 204
7.5.4.1 Trade-off between temporal variation and elasticity of vital rates 206
7.5.4.2 Life table response experiment 208
7.5.5 Conclusions 210
Chapter 8. Discussion 214
8.1 The demographic components of the life histories of *P. assimilis* 214
8.1.1 Age estimation 215
8.1.2 Fluctuations in population size 215
8.1.3 Variability in physiological condition 216
8.1.3.1 Relationships between offspring and maternal condition 217
8.1.3.2 Body mass, but not condition, correlated with subadult and adult survival219
8.1.3.3 Future research 220
8.1.4 Sex ratio variation 220
8.1.4.1 Birth sex ratio variation 221
8.1.4.2 Survival and sex ratio variation at pouch emergence 222
8.1.4.3 Survival and sex ratio variation at weaning 223
8.1.4.4 Conclusions 225
8.1.4.5 Future research 225
8.1.5 Age and size at maturity 226
8.1.5.1 Future research 227
8.1.6 Age-specific post-weaning survival 228
8.1.6.1 Variability in the demographic rates 231
8.1.6.2 Future research 232
8.2 Long-term population fitness 232
8.2.1 Trade-off between temporal variation and elasticity of vital rates 234
8.2.2 Covariation between demographic traits and variability of population fitness 236
8.2.3 Future research 237
8.3 Patterns of variability in *P. assimilis* life histories 238
References 241
Appendix A – Field data sheets 269
Appendix B – Chapter 5 Goodness-of-fit tests of CJS models 272
Goodness-of-fit tests of CJS models 272
Program RELEASE 272
Program U-CARE 273
Results of goodness-of-fit tests of CJS models 274
Assumption of constant probability of survival and recapture of individuals marked on different sampling occasions 274
Assumption of constant probability of recapture between newly and previously captured individuals 274
Appendix C – Chapter 6 Model selection summary tables 276
Sex ratio variation at birth 276
Temporal variation in sex ratio at birth 276
Environmental variation in sex ratio at birth 277

        Maternal variation in sex ratio at birth 278
    Survival from birth to pouch emergence 279
        Temporal variation in survival from birth 279
        Environmental variation in survival from birth 280
        Maternal variation in survival from birth...281
    Time-dependent changes in probability of survival to pouch emergence.........................282
        Temporal variation in survival to pouch emergence...282
        Environmental variation in time-dependent survival to pouch emergence 283
        Maternal variation in time-dependent survival to pouch emergence.........................284
    Sex ratio at pouch emergence 285
        Temporal variation in sex ratio at pouch emergence 285
        Environmental variation in sex ratio at pouch emergence 286
        Maternal variation in sex ratio at pouch emergence 287
    Survival from pouch emergence to weaning..288
        Temporal variation in survival to weaning 288
        Environmental variation in survival to weaning 289
        Maternal variation in survival to weaning 290
    Sex ratio at weaning...291
        Temporal variation in sex ratio at weaning..291
        Environmental variation in sex ratio at weaning..292
        Maternal variation in sex ratio at weaning...293
    Age at weaning...294
        Temporal factors affecting the age at weaning 294
        Environmental factors affecting the age at weaning 295
        Maternal factors affecting the age at weaning 296
    Body mass at weaning 297
        Environmental factors affecting body mass at weaning..297
        Maternal and environmental factors affecting body mass at weaning 298
Appendix D – Chapter 7 Model selection summary tables 299
    Age at maturity 299
        Temporal variation in age at maturity..299
        Environmental variation in age at maturity 300
        Weaning mass variation in age at maturity 302
    Time-dependent post-weaning survival analysis 303
        Sex differences in survival...303
        Temporal variation in survival..304
        Environmental variation in survival..305
        Mass and condition variation in survival..307
Appendix E – Chapter 7 Population projection analysis code 308
    R (http://www.r-project.org/) code for population projection analysis 308

List of figures

Figure 1.1. Distribution of *Petrogale* taxa in Australia. The taxa in bold are resolved as full species (*P. purpureicollis* is also now recognised as a full species). The exceptions are the sub-species and races of *P. lateralis* (*P. l. pearsoni, P. l. hacketti,* the West Kimberley race, and the MacDonnell Ranges race), and the Queensland sub-species of *P. xanthopus* (*P. x. celeris*). (Reproduced from Horsup (1996); originally modified from Eldridge and Close (1993))....................9

Figure 1.2. Male allied rock-wallaby, *Petrogale assimilis*, at Black Rock (Photo: A. Horsup).....11

Figure 1.3. Diagram representing the conceptual framework of my thesis. The central components are the demographic fitness components of the life history of *Petrogale assimilis*. The mean and variation in the demographic rates are directly and indirectly affected by intrinsic and extrinsic factors, fitness differences between individuals, and maternal factors. Temporal variation in demographic rates causes fluctuations in population density. Selection pressures operating on the demographic traits are reflected in the interaction between population fitness and temporal variation in demography, and the outcome of such interactions identify patterns of variability in the life histories of *P. assimilis*....................15

Figure 2.1. Location of Black Rock, 265km WNW of Townsville on Lyndhurst Station in the wet-dry tropics region of North Queensland, Australia (inset)....................19

Figure 2.2. Aerial view of the Black Rock escarpment on Lyndhurst Station. North is to the right. The rock piles along the eastern face are in the darkened area of the figure. The gullies evident at the southern end are also present to the north....................19

Figure 2.3. Aerial view looking down onto the rock piles along the eastern face. The eastern edge of the escarpment is approximately 25m above the surrounding mixed woodland habitat....................20

Figure 2.4. Vegetation zones at Black Rock. The rock-wallaby feeding area was determined from radio-tracking (Horsup 1996). (Reproduced from Horsup and Marsh (1992)).......20

Figure 2.5. (a) Total monthly rainfall at Lyndhurst Station, 30km from Black Rock, between 1986 and 1997. Dashed line represents 100 year mean monthly rainfall; (b) Difference of monthly total rainfall from mean (100 year) monthly total rainfall at Lyndhurst Station between 1986 and 1997; and (c) Difference in monthly rainfall to mean (100 year) monthly rainfall as a proportion of mean monthly rainfall at Lyndhurst Station between 1986 and 1997....................22

Figure 2.6. (a) Number of days on which rain was recorded in each month at Lyndhurst Station, 30km from Black Rock, between 1986 and 1997; (b) mean monthly maximum and minimum temperatures at Lyndhurst Station between 1986 and 1997, dashed lines represent 100 year mean monthly maximum and minimum temperatures; and (c) the Southern Oscillation Index for north Queensland between 1986 and 1997. 24

Figure 2.7. New born *P. assimilis* pouch young attached to a teat. (Photo: A. Horsup). 31

Figure 2.8. Adult female *P. assimilis* with large pouch young in the pouch. (Photo: A. Horsup).31

Figure 2.9. Adult female *P. assimilis* interacting with her young-at-foot. (Photo: A. Horsup)......31

Figure 3.1. Diagram representing the elements of the conceptual framework of the thesis investigated in this chapter (bolded). Accurate estimates of the age of individuals, and sex-specific differences in growth, allowed the age structure of the population to be determined. Age-specific variation in the demographic fitness components of the life history of *Petrogale assimilis* could be determined based on the estimated ages of individuals....43

Figure 3.2. Raw individual profiles of growth from ‘time since first capture’ (in days) against head length (mm) for 44 individual *P. assimilis* at Black Rock. 46

Figure 3.3. Standardised residual plots against estimated head length (mm) of *P. assimilis* at Black Rock from the: (a) Chapman-Richards; (b) quartic polynomial; and (c) beta-spline (df = 6) mixed-effects models. Solid lines represent fitted cubic smoothing splines (df = 4); dashed lines are 95% confidence intervals showing: (a) and (b) lack-of-fit to the growth pattern for the Chapman-Richards and polynomial models; and (c) adequate fit to the beta-spline (df = 6) model....47

Figure 3.4. Individual growth profiles of head length for: (a) 17 known-age *P. persephone*; and (b) a random sample of measurements from each of the same 17 *P. persephone* that simulate the ‘time since first capture’ data recorded from wild-caught animals such as *P. assimilis*. 48

Figure 3.5. Linear relationship between the bias in age estimation (days) and the head length (mm) at the simulated first capture for 17 captive-bred *P. persephone* from: (a) Chapman-Richards; (b) beta-spline (df = 3); and (c) beta-spline (df = 3) weighted on the inverse of head length mixed-effects models. Dashed lines represent 95% confidence intervals for the linear trend. 49

Figure 3.6. Estimated individual growth profiles of head length for *P. assimilis* at Black Rock from the average beta-spline model (df = 6) with individual variation represented as linear deviations from the mean profile. Dashed line indicates the age at permanent emergence from the pouch (PEP); dotted lines indicate the age range where sexual maturity was reached....50

Figure 3.7. Mean difference in estimated head length between males and females from 500 bootstrap samples of the mean growth profiles for each sex for *P. assimilis* at Black Rock. Solid line represents the mean difference; dashed lines are 95% confidence intervals. 50

Figure 3.8. The relative population age structure for *P. assimilis* at Black Rock in each year of the study determined from the first capture of individuals in each year. There were substantial fluctuations in the proportions in each age-class through time. The age-classes represent the: immature (unfilled); prime-aged adult (dashed); and old adult (solid) life history stages. The immature age-class included young-at-foot (YAF) and subadult (SA) animals; old adults were greater than 9 years of age; numbers above bars are mean estimated annual population size. 51

Figure 4.1. Diagram representing the elements of the conceptual framework of the thesis investigated in this chapter (bolded). Variation in body condition was expected to have important fitness consequences and therefore an index of body condition was needed to assess the influence of individual fitness on temporal variability in the demographic traits that affect the dynamics of the population of *P. assimilis* at Black Rock. 59

Figure 4.2. Line plots of: (a) head; (b) pes; (c) leg; and (d) arm length (*ln* mm) against body mass (*ln* g) for 56 individual *P. assimilis* at Black Rock that ranged in age from 0.25 to 5.0 years....63

Figure 4.3. (a) Scatterplot; and (b) line plot of head length (*ln* mm) against body mass (*ln* g) for 130 *P. assimilis* at Black Rock that ranged in age from 0.25 to 5.0 years. Solid line in (a) represents the estimated mean profile using a natural spline (df = 6); lines in (b) represent individual profiles. 65

Figure 4.4. Partial effects plot of the mean body condition index for *P. assimilis* at Black Rock in each year of the study. Error bars represent 95% confidence intervals. The partial effects were estimated at the mean 210 day cumulative rainfall lag (i.e. 237 mm). 68

Figure 4.5. Difference in BIC from the minimum BIC model (Δ BIC) for candidate models with the cumulative rainfall covariate lagged over one to 12 months (in increments of 10 days). Models with Δ BIC < 6 have some support. Solid line represents a cubic smoothing spline (df = 6); dashed lines represent approximate 95% confidence intervals; dotted line shows Δ BIC = 6 (i.e. all lag months below the dotted line had some support). 69

Figure 4.6. The estimated change in body condition for *P. assimilis* at Black Rock associated with proportional changes in cumulative rainfall for lags between one and 12 months (in increments of 10 days). Error bars represent 95% confidence intervals. Shaded area represents the mean change in body condition estimated from the set of supported models. 69

Figure 4.7. Estimated body condition index (expressed as a percentage) versus the head length (*ln* mm) for 261 individual *P. assimilis* at Black Rock. There was no systematic bias in the predicted body condition index dependent on head length. Solid line represents a cubic smoothing spline (df = 5); dashed lines represent approximate 95% confidence intervals. 70

Figure 4.8. Partial effects plot of the mean predicted body condition index for *P. assimilis* at Black Rock in each year of the study. The partial effects were estimated at the mean 210 day cumulative rainfall lag (i.e. 237 mm). Error bars represent 95% confidence intervals. 71

Figure 5.1. Diagram representing the elements of the conceptual framework of the thesis investigated in this chapter. Identification of an appropriate model for the probability of recapturing individual *P. assimilis* was necessary for the analysis of survival rates and to estimate the size of the colony at Black Rock. Population size estimates were critical to answering questions about density-dependence in the demographic rates and to understand fluctuations in the population. 78

Figure 5.2. Overall tests for the three global reference models of goodness-of-fit. The framework allows selection of an appropriate starting model. Pooled tests associated with each arrow examine the goodness-of-fit of the data to the indicated model. Symbol ϕ represents survival probability; ρ represents recapture probability. Terms in parentheses indicate covariates for each parameter: *t*, sampling occasion; *a2*, two age-classes; *m*, marked on previous sampling occasion. Reproduced from Choquet *et al*. (2003). 83

Figure 5.3. Hierarchy of tests of the goodness-of-fit of the capture-recapture data for *P. assimilis* at Black Rock for three global reference models. Pooled tests associated with each arrow test the goodness-of-fit of the data to the indicated model. The best model was the trap-dependence model $\phi(t)\ \rho(m+t)$, and all other tests showed significant departure from the fitted models. ϕ, survival probability; ρ, recapture probability. Terms in parentheses indicate covariates for each parameter: *t*, sampling occasion; *a2*, two age-classes; *m*, marked on previous sampling occasion. 89

Figure 5.4. Estimated probability of recapture of *P. assimilis* for both sexes on each primary sampling occasion at Black Rock from 1986 to 1997. Error bars represent 95% confidence intervals. 92

Figure 5.5 Partial effects plots for: (a) seasons in years; (b) age for each sex; (c) minimum number known alive population size; and (d) trap effort ($\log_2$ number of trap nights) on the log odds of recapture. Solid points or lines represent estimated effect; error bars or dashed lines are approximate 95% confidence intervals. ED, early dry season; LD, late dry season; W, wet season. 95

Figure 5.6 (a) Horvitz-Thompson population size estimates (solid points) at each sampling occasion. Error bars are bootstrap 95% confidence intervals; solid line is minimum number known alive. (b) Coefficient of variation of population size estimates over time. Solid line represents fitted smooth trend (df = 4); dashed lines represent 95% confidence intervals. (c) Population size estimates from January 1994 to July 1997. Horvitz-Thompson estimates (solid line) with bootstrap 95% confidence intervals (dotted lines); Minimum Number Alive method (dashed line); and closed population method (filled circles) with 95% confidence intervals (error bars). 96

Figure 6.1. Diagrammatic representation of the reproductive pattern of *P. assimilis* at Black Rock. Births are followed by a post-partum oestrus and the resulting embryo remains quiescent until the lactation-controlled embryonic diapause ends with the mortality or completed development of the pouch young. A 30 day gestation period follows the natural death of a pouch young, or begins when a surviving pouch young reaches approximately 170 days of age. Young permanently exit the pouch (pouch emergence) at about 200 days and continue to suckle as young-at-foot (YAF) until the end of weaning (~330 days). Births either occur immediately after pouch emergence, or after a 30 day gestation following mortality of the previous pouch young. 110

Figure 6.2. Diagram representing the elements of the conceptual framework of the thesis investigated in this chapter. Variation in the demographic sex ratio, juvenile survival, and age/size at weaning components of the life history of *P. assimilis* affected by intrinsic and extrinsic factors, fitness differences between individuals, and maternal factors were examined. The overall aim was to examine whether sex ratio variation could be explained by the Trivers-Willard hypothesis (TWH). 112

Figure 6.3. Estimated probability of a male pouch young at birth for *P. assimilis* at Black Rock over days of the year from a periodic-spline (df = 4) model. Dashed lines represent 95% confidence intervals; horizontal dotted line represents an even sex ratio; vertical dotted lines are positioned at quarterly intervals to aid interpretation; and average season durations are shown. 119

Figure 6.4. Histogram of the number of days between pouch young transitions that occurred either 30 or more days after pouch emergence of the previous young or 60 or more days after mortality of the previous young for *P. assimilis* at Black Rock, indicating the number of possible gestation periods between offspring resulting from “non-continuous” reproductive cycles. 120

Figure 6.5. Estimated probability of a male pouch young from: (a) “continuous” births; and (b) “non-continuous” births for *P. assimilis* at Black Rock over days of the year from a periodic-spline (df = 4) model. Dashed lines represent 95% confidence intervals; horizontal line represents an even sex ratio; vertical lines are positioned at quarterly intervals to aid interpretation; and average season durations are shown. 121

Figure 6.6. Distribution of the maximum ages (days) of known-sex, pre-pouch emergence juvenile *P. assimilis* at Black Rock. The peak around the median age of 199 days shows the mean length of pouch life and the observations skewed to the left shows the relatively uniform distribution of the ages of pouch young mortality 124

Figure 6.7. Baseline probability of survival with age (days) for: (a) females (dashed line), males (thick black line), and unknown individuals (thin black line); and (b) for all known-sex *P. assimilis* at Black Rock. Solid lines represents mean survival; dashed lines represent 95% confidence intervals. Confidence intervals were not displayed in (a) for clarity. ..125

Figure 6.8. (a) Estimated mean probability of survival from birth to 200 days (circles); and (b) total number of births in each month over the study period for *P. assimilis* at Black Rock between 1986 and 1997. Error bars represent 95% confidence intervals; black bars represent females and grey bars represent males. 126

Figure 6.9. Rescaled Schoenfeld residuals plotted against the age (days) of *P. assimilis* pouch young at Black Rock for the: (a) Southern Oscillation Index*age; and (b) maternal mass*age interactions, representing departure from the assumption of proportional hazards for the Southern Oscillation Index and maternal mass covariates. Solid lines represent fitted smoothing splines (df = 4); dashed lines represent 95% confidence intervals. 126

Figure 6.10. Estimated mean probability of survival to 200 days for *P. assimilis* at Black Rock with: (a) population size; (b) six month mean Southern Oscillation Index for females (solid line) and males (bold solid line); (c) the interaction between cumulative rainfall ($\log_2$) and mean Southern Oscillation Index; (d) six month cumulative rainfall for females (solid line) and males (bold solid line); (e) maternal mass (kg); and (f) maternal age at maturity (years) (i.e. estimated from data where maternal age at maturity was known). Dashed lines represent 95% confidence intervals...128

Figure 6.11. Estimated probability of a male pouch young at pouch emergence for *P. assimilis* at Black Rock with: (a) within-year periodic-spline (df = 3) model; (b) the mean Southern Oscillation Index over the preceding six months; (c) maternal condition index; and (d) maternal body mass (kg). Dashed lines represent 95% confidence intervals; horizontal dotted line represents an equal sex ratio; vertical dotted lines in (a) are positioned quarterly for interpretation; and average season durations are shown.........................130

Figure 6.12. (a) Baseline probability of survival from pouch emergence to weaning for female (thin line) and male (thick line) *P. assimilis* at Black Rock. Dashed lines represent 95% confidence intervals; and (b) partial effects plot of differences in probability of survival from pouch emergence to average weaning age (330 days) between years. Error bars represent 95% confidence intervals. 132

Figure 6.13. Observations on individual *P. assimilis* in the Black Rock population over years by age. Each line represents an individual animal. The age structure was skewed toward older individuals in the early years of the study. Periods of low or no recruitment were evident from 'gaps' between the groups of diagonal profiles. The age range from the mean age at sexual maturity for females (lower limit) to males (upper limit) is represented by the grey bar; the age at transition from prime-aged (PA) to old-aged (OA) adults is shown by the dashed line..133

Figure 6.14. Partial effects plots of probability of survival from pouch emergence to weaning (330 days) for *P. assimilis* at Black Rock with: (a) mean Southern Oscillation Index over preceding six months; (b) cumulative rainfall over preceding six months ($\log_2$(mm)); (c) mean temperature over preceding six months for each sex; (d) interaction between Southern Oscillation Index and temperature; (e) interaction between temperature and rainfall; and (f) maternal mass (kg) for each sex. Dashed lines represent 95% confidence intervals. 135

Figure 6.15. Estimated probability of a male pouch young at weaning for *P. assimilis* at Black Rock with: (a) three month mean Southern Oscillation Index; and (b) maternal body mass (kg). Dashed lines represent 95% confidence intervals; horizontal dotted line represents an equal sex ratio. 137

Figure 6.16. Partial effects plots of the age at weaning of *P. assimilis* at Black Rock with: (a) three month mean Southern Oscillation Index; (b) three month mean temperature (°C); (c) three month cumulative rainfall ($\log_2$(mm)) for each sex; and (d) population size for each sex. Partial effects were estimated at the mean of the other covariates in the model. Dashed lines represent 95% confidence intervals. 138

Figure 6.17. Partial effects plot of age (days) on young-at-foot body mass at weaning for *P. assimilis* at Black Rock. Solid lines represent estimated body mass for each sex; dashed lines represent 95% confidence intervals. Solid circles represent females; open circles represent males. 139

Figure 7.1. Diagram representing the elements of the conceptual framework of the thesis investigated in this chapter. Variation in the demographic survival, fecundity, and age/size at maturity components of the life history of *P. assimilis* affected by intrinsic and extrinsic factors and fitness differences between individuals were examined. The elasticity and sensitivity of population growth to, and temporal variation in, these demographic rates were estimated to investigate patterns of variability in the life histories trajectories of *P. assimilis*. 163

Figure 7.2. The life cycle of female *P. assimilis*: EPY, early pouch young (0-100 days); LPY, late pouch young (100-200d); YAF, young-at-foot (200-330d); SA, subadult (330-580d); PA, prime-aged adult (1.6-9 years); OA, old adult (>9y). *G* represents the probability of surviving and growing to the next stage at the next time interval; *P* represents the probability of surviving and remaining in the stage at the next time interval; and *F* represents the fertility of the stage. Arrows indicate all possible transitions. 170

Figure 7.3. The partial effects of: (a) body mass at maturity; and (b) cumulative rainfall over the preceding six months (on a $\log_2$ scale) on age at sexual maturity for *P. assimilis* at Black Rock. Solid lines represent estimated age at maturity; dashed lines are 95% confidence intervals. Solid circles in (a) represent females; open circles in (a) represent males...175

Figure 7.4. The partial effects of: (a) population size; and (b) mean temperature (°C) over the preceding six months on age at sexual maturity for *P. assimilis* at Black Rock. Solid lines represent estimated age at maturity; dashed lines are 95% confidence intervals.176

Figure 7.5. The partial effects of the residual body mass at weaning after accounting for age at weaning on age at sexual maturity for *P. assimilis* (pooled across the sexes) at Black Rock. Solid lines represent estimated age at maturity; dashed lines are 95% confidence intervals. 176

Figure 7.6. Estimates of the probability of survival in each year for: (a) subadults; (b) prime-aged adults; (c) old adults; and the probability of transition between (d) subadult and prime-aged adult stages; and (e) prime-aged adult and old adult stages for *P. assimilis* at Black Rock. Filled circles represent females and squares represent males, except in (b) and (e) where filled circles represent the average across the sexes. Error bars represent 95% confidence intervals. Estimates without error bars were fixed at zero or one in the analysis because the parameters were inestimable because of sparse data. 179

Figure 7.7. Baseline probability of survival: (a) after independence for females (black line) and males (blue line) (solid lines represents mean survival, dashed lines represent 95% confidence intervals); (b) mean probability of surviving another year at each age for females (solid line) and males (dashed line) estimated from time-dependent survival analysis; and (c) mean annual survival probability for each stage-class for *P. assimilis* at Black Rock. Filled circles represent females and squares represent males. EPY, early pouch young; LPY, late pouch young; YAF, young-at-foot; SA, subadult; PA, prime-aged adult; OA, old adult survival. 182

Figure 7.8. Variation in the relative hazard rate ($\log_e$) with: (a) population size; (b) nine month cumulative rainfall ($\log_2$ mm) for subadults, prime-aged adults and old adults (solid lines); (c) nine month average Southern Oscillation Index for males and females (solid lines); and (d) body mass (kg) for *P. assimilis* at Black Rock. Dashed lines represent 95% confidence intervals. 183

Figure 7.9. The annual intrinsic rate of increase ($r = ln\ \hat{\lambda}$) estimated from annual projection matrices for *P. assimilis* at Black Rock. r = 0 in 1988 and 1989. 188

Figure 7.10. (a) The among year covariances of the elements (a_{ij}) of the population projection matrix *A*; and (b) the contributions of the covariances to $V(\hat{\lambda})$ for female *P. assimilis* at Black Rock. The matrix elements are arbitrarily numbered column-wise. The largest (co)variances were: (1) late pouch young survival; (2) between late pouch young and young-at-foot to subadult survival/transition; (3) young-at-foot to subadult survival/transition; (4) between young-at-foot to subadult survival/transition and subadult survival; (5) subadult survival and subadult to prime-aged adult survival/transition (two peaks); (6) between and young-at-foot to subadult survival/transition and old adult survival; (7) between subadult and old adult survival; (8) between old adult survival and fertility; and (9) old adult survival. The largest contributions to $V(\hat{\lambda})$ were: (2) G_3 young-at-foot survival/transition; (4) P_4 subadult survival; and (5) G_4 subadult survival/transition. Smaller (co)contributions were associated with: (1) late pouch young and young-at-foot survival/transition; (3) late pouch young survival/transition and subadult survival; (6)(i) subadult survival/transition and prime-aged adult survival and (ii) young-at-foot survival/transition and old adult survival (two peaks); (7)(i) prime-aged adult survival and (ii) subadult and old adult survival (two peaks); and (8) old adult survival. 190

List of tables

Table 2.1. Total rainfall (mm) at Lyndhurst Station, 30km from Black Rock, in each season for each year between 1986 and 1997, and the long-term (100 year) average rainfall for each season. The percentage of annual total rainfall in each season is given in parentheses. The superscript "*a*" indicates that the value is the percentage of the long-term mean annual rainfall. Years are season years (i.e. each year begins with the onset of the wet season (as defined by Jones 1987)); seasons are defined in Section 2.1.3.1........21

Table 2.2. Number of rainfall days at Lyndhurst Station (30km from Black Rock) in each season for each year between 1986 and 1997, and the long-term (100 year) average number of rainfall days for each season. The percentage of annual total rainfall days in each season is given in parentheses. The superscript "*a*" indicates that the value is the percentage of the long-term mean annual number of rainfall days. Years are season years (i.e. begin with onset of wet season (Jones 1987)); seasons are defined in Section 2.1.3.1. 23

Table 2.3 Correlations between the Southern Oscillation Index (SOI), rainfall ($\log_2$), and temperature (°C) environmental variables recorded near Black Rock between 1986 and 1997 over lag periods of the preceding three, six, nine, and 12 months. Rainfall was the cumulative sum and the other variables were averaged over the previous *lag* months. *P*-values for the test for non-zero correlation are given in italics below each correlation coefficient. Significant correlations (α = 0.05) are bolded. 27

Table 2.4. Number of traps and spatial arrangement of the trapping grid at Black Rock between 1986 and 1997. 28

Table 2.5. Codes for determining the lactation status of female *P. assimilis* teats. From Spencer (1996). 30

Table 2.6. The age ranges of transition between the developmental stages of *P. assimilis* pouch young at Black Rock. Adapted from Spencer (1996). 30

Table 3.1. Bias, precision, and accuracy of estimated ages of captive *P. persephone* pouch young from simulated field data. All parameters varied randomly between individual animals in the nonlinear model, and individual profiles varied linearly from the beta-spline (df = 3) mean profile. SD, standard deviation; MSE, mean square error.....48

Table 4.1. Estimated prediction error sums of squares, and bias, precision and accuracy of predicted of body mass using each of four morphometric length measures. Estimates were based on cross-validation for each individual (*n* = 56), and summed over individuals. SD, standard deviation; $\sqrt{}$MSE, root mean square error. 63

Table 4.2. Model selection summary statistics for differences in the complexity of random deviations in body mass from individual animals about a natural-spline (df = 9) mean relationship between head length (*ln* mm) and body mass (*ln* kg) for *P. assimilis* at Black Rock. The best supported model is bolded. df, degrees of freedom; BIC, Bayesian Information Criterion; Δ BIC, the difference in BIC from the minimum BIC model; Deviance, -2*log likelihood for model; % Var, percentage variance explained by the model........65

Table 4.3. Model selection summary statistics for the smoothness of the mean relationship between head length (*ln* mm) and body mass (*ln* kg) for *P. assimilis* at Black Rock. Natural splines with between nine and two degrees of freedom were assessed. The best supported model (df = 6) is bolded. df, degrees of freedom; BIC, Bayesian Information Criterion; Δ BIC, the difference in BIC from the minimum BIC model; Deviance, -2*log likelihood for model; % Var, percentage variance explained by the model. 66

Table 4.4. Model selection summary statistics for differences in the complexity of random deviations in body mass from individual animals about a natural-spline (df = 6) mean relationship between head length (*ln* mm) and body mass (*ln* kg), conditional on temporal and environmental variation, for *P. assimilis* at Black Rock. The best supported model includes constant deviations between individual animals (bolded). df, degrees of freedom; BIC, Bayesian Information Criterion; Δ BIC, the difference in BIC from the minimum BIC model; Deviance, -2*log likelihood for model; % Var, percentage variance explained by the model. 66

Table 4.5. Model selection summary statistics for temporal, environmental and sex differences in body mass conditional on body size for *P. assimilis* at Black Rock. The covariates were included in a model with a natural spline (df = 6) for the relationship between mass and size. Models with strong support are bolded. df, degrees of freedom; BIC, Bayesian Information Criterion; Δ BIC, the difference in BIC from the minimum BIC model; Deviance, -2*log likelihood for model; % Var, additional percentage variance explained by the covariates. Y, year; SN, season; S, sex; R, cumulative rainfall over lag period; SOI, mean Southern Oscillation Index over lag period; T, mean maximum temperature over lag period; subscripts show the lag period for environmental covariates. 67

Table 5.1. Chi-square goodness-of-fit test statistics for the components of TEST 2 and TEST 3 for each sex and the pooled sexes for *P. assimilis* at Black Rock using Program U-CARE. The negative normalised signed-statistic associated with Test 2.Ct indicated a trap-happy behavioural response to capture. Degrees of freedom are given in parentheses; *P*-values for tests are given in italics. 88

Table 5.2. Chi-square goodness-of-fit test statistics for the components of TEST 2 and TEST 3 for a two age-class by sex model for *P. assimilis* at Black Rock using Program U-CARE. The negative normalised signed-statistic associated with Test 2.Ct indicated a trap-happy behavioural response to capture for adult females and all males. Degrees of freedom are given in parentheses; *P*-values for tests are given in italics. 90

Table 5.3. Model selection summary statistics for factors affecting the probability of recapture in Cormack-Jolly-Seber (CJS) capture-recapture models. Best supported models are bolded. The model for time-dependent recapture rates that also depend on past capture history and differ with sex and age at marking had highest support. ϕ, survival; *p*, recapture probability, Y, year; SN, season; S, sex; AC, age-class; t, sampling occasion; m, captured on previous sampling occasion; E, trap effort ($\log_2$ number of trap nights). AIC_c, Akaike's Information Criterion corrected for small sample bias; Weight, AIC_c weights; Likelihood, relative model likelihood; df, degrees of freedom (i.e. number of parameters in the model). 91

Table 5.4 Model selection statistics for factors affecting the probability of recapture in generalised linear mixed-models. Best supported models are bolded. Models for time- or year-dependent recapture rates that also depended on past capture history and differed with sex and age at marking had highest support. ρ, recapture probability. df = degrees of freedom; $\mathrm{AIC_c}$, Akaike's Information Criterion; $\Delta\ \mathrm{AIC_c}$, the difference in $\mathrm{AIC_c}$ from the minimum $\mathrm{AIC_c}$ model; w_i represents the relative model weight; % Var, percentage variance explained by the model. T, sampling occasion; M, captured on previous sampling occasion; ID, individual animal; Y, year; SN, season; S, sex; ACm, age-class at marking; A, age in years; t, sampling occasion; E, trap effort ($\log_2$ number of trap nights); P, minimum number known alive (i.e. population size); s, indicates a smooth term with specified degrees of freedom. 94

Table 6.1. The assumptions underlying the Cox proportional hazards models used for the analysis of pre-weaning survival of *P. assimilis* at Black Rock, and descriptions of how these assumptions were addressed. 117

Table 6.2. Pouch young sex ratios for *P. assimilis* at Black Rock depending on the sex of the previous pouch young. Birth sex ratio did not depend on the sex of the previous pouch young ($\chi^2 = 2.1$, df = 2, $P = 0.35$). Proportions of column totals are given in italics...... 122

Table 6.3. Pouch young sex ratios for *P. assimilis* at Black Rock depending on the sex of the previous pouch young (PY) and the environmental conditions at birth where: (a) the previous pouch young survived; and (b) did not survive to pouch emergence. Birth sex ratio did not depend on the survival of the previous pouch young to pouch emergence ($\chi^2 = 1.97$, df = 1, $P = 0.16$), or on the interaction between sex and survival of the previous pouch young ($\chi^2 = 0.83$, df = 2, $P = 0.66$), and these relationships were independent environmental conditions at the time of birth ($\chi^2 = 1.03$, df = 4, $P = 0.91$). Proportions of column totals or subtotals are given in italics. 123

Table 6.4. Summary results describing proximate factors that influenced sex ratio variation and the probability of survival at each life history stage between birth and weaning for *P. assimilis* at Black Rock. Accordance with the Trivers-Willard hypothesis, that predicts the sex ratio of offspring will vary depending on the parent's ability to allocate resources if the cost of producing offspring of each sex differs, are also described. $\propto$ represents the proportion of the specified sex; ↑ and ↓ represent increases and decreases in the specified variable, respectively; SOI, Southern Oscillation Index; $\bar{X}$ sex ratios are probability of male offspring. 141

Table 7.1. Model selection summary for factors affecting subadult and adult survival and transition between the stages for *P. assimilis* at Black Rock. The recapture model was fixed. Only models with AIC_c weights >0.001 are displayed. *SA*, subadult survival; *A*, adult survival; *p*, recapture probability; γ, probability of transition from subadult to adult stage. Y, year; S, sex; AC, age-class; R_i, cumulative rainfall over preceding *i* months; SOI_i, mean Southern Oscillation Index over preceding *i* months; P, population size; t, sampling occasion; m, captured on previous sampling occasion. AIC_c, Akaike's Information Criteria corrected for small sample bias; NP, number of parameters in the model. 178

Table 7.2. Model selection summary for factors affecting subadult, prime-aged adult and old adult survival and transition between the stages for *P. assimilis* at Black Rock. The recapture model was fixed. *SA*, subadult survival; P*A*, prime-aged adult survival; O*A*, old adult survival; *p*, recapture probability; γ_{12}, probability of transition from subadult to prime-aged adult stage; γ_{23}, probability of transition from prime-aged adult to old adult stage. Y, year; S, sex; AC, age-class; R_i, cumulative rainfall over preceding *i* months; SOI_i, mean Southern Oscillation Index over preceding *i* months; P, population size; t, sampling occasion; m, captured on previous sampling occasion. AIC_c, Akaike's Information Criteria corrected for small sample bias; NP, number of parameters in the model. 180

Table 7.3. The 100 day population projection matrix (Equation 7.1) representing mean survival and transition probabilities and fertilities for female *P. assimilis* at Black Rock. EPY, early pouch young; LPY, late pouch young; YAF, young-at-foot; SA, subadult; PA, prime-aged adult; OA, old adult. 184

Table 7.4. The estimated annual population rate of change ($\hat{\lambda}$) and intrinsic rate of increase ($r = ln\,\hat{\lambda}$) from the projection model for female *P. assimilis* at Black Rock. 95% confidence intervals were calculated from the estimated variance in $\hat{\lambda}$ 184

Table 7.5. Sensitivities (S) and elasticities (E) of $\hat{\lambda}$ to changes in the population projection matrix elements for female *P. assimilis* at Black Rock. EPY, early pouch young; LPY, late pouch young; YAF, young-at-foot; SA, subadult; PA, prime-aged adult; OA, old adult. 185

Table 7.6. The stable stage distribution and stage-specific reproductive value and stage-specific life expectancy for female *P. assimilis* at Black Rock. Standard errors for the life expectancy are presented in parentheses. 186

Table 7.7. The value of the lower-level vital rates and their standard error (SE) and coefficient of variation (CV), and the sensitivity and elasticity of population growth rate to each vital rate for female *P. assimilis* at Black Rock. Bolded values indicate substantial components of each variable. 187

Table 7.8. Percentage contributions to $V(\hat{\lambda})$ summed over all elements for each life history stage (Equation 7.1) for female *P. assimilis* at Black Rock. The largest contributions are bolded. Note that positive and negative contributions cancelled out in calculating these summations; negative co-contributions from subadult survival and subadult transition reduced the percentage contributions of these matrix elements. EPY, early pouch young; LPY, late pouch young; YAF, young-at-foot; SA, subadult; PA, prime-aged adult; OA, old adult. 191

Table 7.9. The among year covariances (x 10^{-2}) of the lower-level vital rates for female *P. assimilis* at Black Rock. Large covariances are bolded. ϕ_1, early pouch young survival; ϕ_2, late pouch young survival; ϕ_3, young-at-foot survival; ϕ_4, subadult survival; ϕ_5, prime-aged adult survival; ϕ_6, old adult survival; γ_3, transition to subadult; γ_4, transition to prime-aged adult; γ_5, transition to old adult; b_5, prime-aged adult fecundity; b_6, old adult fecundity; v_5, prime-aged adult sex ratio; v_6, old adult sex ratio. 192

Table 7.10. The contributions (x10^{-4}) of the covariances among the lower-level vital rates to $V(\hat{\lambda})$ for female *P. assimilis* at Black Rock. Large contributions are bolded. ϕ_1, early pouch young survival; ϕ_2, late pouch young survival; ϕ_3, young-at-foot survival; ϕ_4, subadult survival; ϕ_5, prime-aged adult survival; ϕ_6, old adult survival; γ_3, transition to subadult; γ_4, transition to prime-aged adult; γ_5, transition to old adult; b_5, prime-aged adult fecundity; b_6, old adult fecundity; v_5, prime-aged adult sex ratio; v_6, old adult sex ratio. 193

Table B.1. Example contingency table of observed counts of *P. assimilis* at one sampling occasion (t) at Black Rock for RELEASE TEST 2. Numbers in italics are residual deviations from expected cell counts. One cell had an expected count < 2, therefore inference was based on an exact test. 274

Table B.2. Example contingency table of observed counts of *P. assimilis* at one sampling occasion (t) at Black Rock for RELEASE TEST 3.Sr. Numbers in italics are residual deviations from expected cell counts. Two cells had an expected count < 2, therefore inference was based on an exact test. 275

Table B.3. Example contingency table of observed counts of *P. assimilis* at one sampling occasion (*t*) at Black Rock for RELEASE TEST 3.Sm. Numbers in italics are residual deviations from expected cell counts. One cell had an expected count < 2, therefore inference was based on an exact test. 275

Table C.1. Model selection statistics for the generalised linear mixed-model analysis of temporal factors on the sex ratio at birth. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 276

Table C.2. Model selection statistics for the generalised linear mixed-model analysis of temporal factors on the sex ratio at birth. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 277

Table C.3. Model selection statistics for the generalised linear mixed-model analysis of (a) maternal factors, and (b) maternal factors including condition index, on the sex ratio at birth. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 278

Table C.4. Model selection statistics for the analysis of temporal variation in juvenile survival among individuals at birth. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 279

Table C.5. Model selection statistics for the analysis of (a) environmental variation and (b) different cumulative lag periods of the Southern Oscillation Index (SOI) on the hazard rate among individuals at birth. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 280

Table C.6. Model selection statistics for the effects of (a) maternal factors, and (b) maternal factors including maternal condition on variation in the hazard of mortality among individuals at birth. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 281

Table C.7. Model selection statistics for the time-dependent analysis of temporal variation in the hazard among individuals. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 282

Table C.8. Model selection statistics for the time-dependent analysis of environmental variation in the hazard rate among individuals. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 283

Table C.9. Model selection statistics for the time-dependent analysis of (a) maternal factors, and (b) maternal factors, including maternal condition, in the hazard rate among individuals. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 284

Table C.10. Model selection statistics for the generalised linear mixed-model analysis of temporal factors on the sex ratio at permanent emergence from the pouch. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 285

Table C.11. Model selection statistics for the generalised linear mixed-model analysis of environmental factors on the sex ratio variation at permanent emergence from the pouch. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 286

Table C.12. Model selection statistics for the generalised linear mixed-model analysis of maternal factors on the sex ratio variation at permanent emergence from the pouch. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols.287

Table C.13. Model selection statistics for the time-dependent analysis of temporal variation in the hazard rate from PEP to weaning among individuals. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 288

Table C.14. Model selection statistics for the time-dependent analysis of environmental variation in the hazard rate from PEP to weaning among individuals. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 289

Table C.15. Model selection statistics for the time-dependent analysis of maternal variation in the hazard rate from PEP to weaning among individuals. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 290

Table C.16. Model selection statistics for the generalised linear mixed-model analysis of temporal factors in the sex ratio at weaning. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 291

Table C.17. Model selection statistics for the generalised linear mixed-model analysis of environmental factors in the sex ratio at weaning. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 292

Table C.18. Model selection statistics for the generalised linear mixed-model analysis of maternal factors in the sex ratio at weaning. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 293

Table C.19. Model selection statistics for the generalised linear mixed-model analysis of temporal factors in the age at weaning. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 294

Table C.20. Model selection statistics for the generalised linear mixed-model analysis of environmental factors in the age at weaning. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 295

Table C.21. Model selection statistics for the generalised linear mixed-model analysis of maternal factors in the age at weaning. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 296

Table C.22. Model selection statistics for the generalised linear mixed-model analysis of maternal and environmental factors in the age at weaning. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 296

Table C.23. Model selection statistics for the generalised linear mixed-model analysis of environmental factors in the body mass at weaning. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 297

Table C.24. Model selection statistics for the generalised linear model analysis of maternal and environmental factors in the body mass at weaning. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 298

Table D.1. Model selection statistics for the linear model analysis of sex, body mass, environmental conditions and random temporal variation in the age at sexual maturity. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols.299

Table D.2 Model selection statistics for the linear model analysis of sex, environmental conditions and random temporal variation in the age at sexual maturity. df = degrees of freedom; AIC = Akaike's Information Criteria; ∆ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 301

Table D.3 Model selection statistics for the linear model analysis of sex, body mass, environmental conditions and residual body mass at weaning (adjusted for age at weaning) in the age at sexual maturity. df = degrees of freedom; AIC = Akaike's Information Criteria; Δ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 302

Table D.4 Model selection statistics for the time-dependent analysis of sex, age-class and random temporal variation in the hazard rate from weaning to death among individuals. df = degrees of freedom; AIC = Akaike's Information Criteria; Δ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols.303

Table D.5 Model selection statistics for the time-dependent analysis of temporal variation in the hazard rate between sexes and age-classes from weaning to death among individuals. df = degrees of freedom; AIC = Akaike's Information Criteria; Δ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols.304

Table D.6 Model selection statistics for the time-dependent analysis of environmental, density and body mass variation in the hazard rate between sexes and age-classes from weaning to death among individuals. df = degrees of freedom; AIC = Akaike's Information Criteria; Δ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 306

Table D.7 Model selection statistics for the time-dependent analysis of environmental, density, body mass and body condition variation in the hazard rate between sexes and age-classes from weaning to death among individuals. df = degrees of freedom; AIC = Akaike's Information Criteria; Δ AIC = the difference in AIC from the minimum AIC model; w_i represents the relative model weight; % Var = percentage variance explained by the model. See Methods section for model symbols. 307