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Phenology and frugivory of large-fruited species in northern New Zealand and the impacts of introduced mammals.

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A thesis submitted for the degree of Doctor of Philosophy in Biological Science.
School of Biological Sciences, University of Auckland, 2002

Abstract

This thesis investigated the reproductive phenology, fruit features, dispersal and seed predation of native New Zealand fleshy-fruited species, concentrating mainly on fruits larger than 10-mm in diameter borne by trees. There are several species with large tree-borne fruit in New Zealand and they currently only have one seed disperser (kereru, *Hemiphaga novaeseelandiae*). Historical evidence suggests that kereru might have been the sole effective disperser for most of the Quaternary. Thus the New Zealand large-fruited frugivore system is relatively simple. It might, therefore be possible to test whether competition amongst large-fruited species for dispersers has resulted in character displacement in the timing of ripe fruit presentation. With this in mind I examined the timing of ripe fruit presentation – the phenological patterns – and nutrient complementarity of fruit species known to contribute to the kereru diet.

Introduced mammals have impacted significantly on New Zealand forest ecosystems, including fruit production. An experiment was designed to measure the level of mammalian fruit consumption. Three paired forest patches, with similar topography, aspect and forest type, were selected. Mammalian pests were suppressed in three forest patches, but left unchanged at the paired site. This allowed comparison of fruit production and fruit phenology at sites with and without pest suppression. The effects of mammal pests on kereru, other bird species and some insect species were also investigated.

Showing that phenological patterns have statistically significant character displacement has proved difficult in the past. It was considered that significant differences might be obtained if phenological patterns were broken down in to the most important character displacement attributes. These were thought to be: (1) order of ripe fruit presentation amongst species; (2) peak fruit production should be greater than could be expected by chance; (3) synchronicity of fruit production within species; (4) lack of significant overlap between species competing for the same resource.

The two sites with the longest phenological record and best level of pest suppression were used to investigate whether character displacement occurs amongst large-fruited species. The fruiting pattern of large-fruited species in northern New Zealand was more akin to tropical forests with year round fruit supply, than to temperate forest with more seasonal fruiting. The order of fruiting tended to be consistent between years at both sites. Fruit was not produced throughout the year by individual species, but tended to occur in defined peaks. A combination Simpson Index and Monte Carlo parametric bootstrap method was used to confirm that the fruiting peaks were non-random.

The theory of competitive displacement amongst co-existing species requires that little or no overlap should occur in the production of ripe fruits by competing species. This means that the period of ripe fruit presentation for one species should not overlap significantly with ripe fruit production of another species. This was tested by modifying a formula developed by Augspurger (1983) that considers the phenological state of an individual in the context of what all other individuals of that same species (for synchrony) or other species (for overlap) are doing over the same period. A further development was the generation of critical values against which the values for individual species could be compared.

Species tended to be more synchronous than asynchronous in the presentation of ripe fruits but only one species was consistently more synchronous than the calculated critical value at both sites. Two other species at Whitford Bush exceeded the critical synchrony value and several other species from both sites came close to exceeding the synchrony value. Despite synchrony values being generally smaller than expected species tended to not overlap significantly with other species in some or all years. Character displacement, in the form of timing of ripe fruit presentation, was demonstrated for most species. However, it is not possible to conclude that this has come about through co-evolution, solely, with the frugivorous kereru.

Fruit nutritional analysis of a range of (mostly) large-fruited species gave rise to six 'fruit types' that clustered on size, lipid content, sugar and moisture content, carbohydrate or protein content. These categories and the nutritional values obtained for New Zealand fruits tended to agree with overseas studies. Compared to overseas fruits, a generalist description of New Zealand fruits could be "relatively small, moist, fibrous but nutritionally poor fruits". In the forests of Auckland, fruit is available throughout the year. Reasonable quantities of high-lipid fruits are available throughout most

of the year, except for parts of summer, and there is little overlap between lipid-rich species. High-sugar fruits are most common during summer and autumn.

Kereru were shown to use fruit species as they become seasonally available. However, they preferred large lipid-rich fruits, which can amount to 40% or more of the diet at one time and possibly up to 80% of the diet fed to chicks. Taraire (*Beilschmiedia tarairi*) and nikau (*Rhopalostylis sapida*) were the most preferred of the lipid-rich fruits. Nikau is also a calcium-rich fruit. Puriri (*Vitex lucens*), a large sugar-rich fruit, was a common dietary item, eaten throughout the year, even when the fruit was relatively scarce. Kahikatea (*Dacrycarpus dacrydioides*; small and sugar-rich) was eaten by kereru when large quantities of ripe fruit were available. The timing and nutrition of the fruiting species was generally complementary, with different nutritional components available from species fruiting simultaneously. Observational data indicate that kereru generally prefer large-fruits over small fruits. The greatest numbers of feeding observations were of kereru taking fruits that were too large to be taken by other extant bird species.

Fruit species were available and eaten throughout the period that foliage (e.g. kowhai *Sophora* spp.) was also eaten. Kowhai leaves and other sources of foliage have higher concentrations of nitrogen than most fruits. Thus perhaps a switch to utilizing foliage is not so much due to a lack of food but more an issue of nutrient complementarity, during the periods of egg development and nesting.

Possum (*Trichosurus vulpecula*) and rodent (*Rattus* spp., *Mus musculus*) control was reflected in the number of possums and/or rodents caught in forest patches at the end of the study. Long-term pest mammal suppression resulted in no trappable possums, rats or mice. Sites lacking mammal suppression had moderate to high numbers of possums and rodents. Possum numbers were lower at one site with partial possum suppression but lacking rodent suppression. Rodent (rats and mice) numbers were generally too low to make valid comparisons but appeared somewhat elevated at the site with partial possum suppression.

Possum droppings were more frequent in seedfall traps at sites with no systematic possum suppression. Rodent droppings had less clearly defined patterns and showed more seasonal variability than possum droppings. The data for number of pest-mammal droppings in seedfall traps generally support the mammal trapping data.

Possums and rodents had adverse effects on fruit production at sites without pest suppression. Suppression of possum and rodent numbers resulted in more fruit production, less fruit damaged, more fruits maturing and more fruits consumed by birds that void the seed unharmed. Pest suppression also ensured that ripe fruits were available throughout the year, supporting resident native frugivores. Partial possum control resulted in both the production of more fruits and proportionally more possum and rodent damaged fruits. Mammal pests showed preference for energy rich fruits such as taraire, and nikau, which are also preferred by kereru.

Pest suppression generally increased the number of traps with insect or kereru droppings, except at the site with partial pest suppression where the occurrence of insect droppings was relatively low. It is not possible to determine whether the benefits to these species are solely through a reduction in possum numbers or through a combination of reduced possum and rodent numbers.

Bird encounter rates were generally greater at sites where pest-mammals were suppressed, especially for frugivorous birds. This increased encounter rate is unlikely to be solely due to behavioral changes in the bird population since the proportion of consumed fruits also increased. Other factors, such as forest patch size and forest patch isolation, are also thought to be important in determining bird numbers. Some forest patches seemed to have insufficient kereru to consume and disperse available crops of large fruit.

The timing of fruit production and the nutrient content of the fruits resulted in some fruits being more attractive (e.g. high energy food source, or important seasonal nutritional component) to frugivores than others. These fruits were consumed more often by both seed dispersers (kereru) and seed predators (possums and rodents). Predation of fruits has negative consequences for the survival and fecundity of the kereru and long-term implications for the survival of these large-fruited tree species.

The interrelationships between ripe fruit production, disperser availability and predator impact has implications for managing forests and pest and kereru populations. Management will also need to consider the plant species composition since there are fewer large-fruited species at southern latitudes and higher altitudes. At northern latitudes pest suppression may be less successful because fruit is available virtually throughout the year and pest species may not be food limited. Fewer large-fruited species are found at more southerly or higher locations and might result in 'windows' of food shortage that can be utilized for delivering toxic baits. Being able to predict unusually large or small fruiting events would thus be very useful for conservation management.

Acknowledgements

To my parents who bought the ladder with which to elevate myself and to George van Meeuwen for being this girl's best friend.

A special thanks to all the landowners who welcomed me onto their properties. Without access to your land this thesis would never have happened. Thank you; Val and Arthur Dunn, Mick and Joan Clout, John Smith and Ann Pacey, the Robertson family, the Tolhopf family, Department of Conservation Auckland and the Auckland Regional Council

I'd also like to thank my extremely helpful and patient supervisors and advisors; Mick Clout, John Ogden and Bill Lee. None of us realised what a monster we had by the tail/tale, thank you for sticking it out with me.

Thank you Department of Conservation Wanganui for allowing me some study time and giving me your friendship and support.

As I toiled, I occasionally remembered to note down the people that helped me. If I've neglected to thank you in the list below then please believe that I am grateful for any help and advice you gave me.

Mum for helping me set up Remiger's and Val's Bush and helping to sort seed samples for a couple of months. And for the hundreds of cloth bags that she sewed.

Dad for his help with SAS and the Simpson analysis.

Colin for helping me with PC computer support and converting data into readable forms.

Sandra Anderson for technical support and bird counts.

Emmanuelle Jousellin for coming out from France to count kohekohe flowers in relation to possum browse and helping to set up Robertson's Bush. Stephanie Gueguen (also from France) who undertook some seed dispersal work at Wenderholm Regional Park and Mireille Höeft from Germany for helping me in field.

Murray Bansall-Adam for putting together the first lot of seedfall traps and helping to set up Whitford Bush.

Barry Green, Ross Gaastra and all the other staff at Wenderholm Regional Park.

Tim Lovegrove and Brenda Green for arranging support for me through the Auckland Regional Council.

Brenda and Terry Greene, Barry Green, Sandra Jones and Emmanuelle Jousellin for helping with observer variability study.

Bill Lee for allowing me to help him on the kakapo project.

Henry Wopereis who helped me set up Loch Amber, and Val's Bush.

Thanks also to Carlos Jordano, Colin Ogle and Ralph Powlesland for helpful suggestions.

Dad, Mum, Colin and Henry for helping lug all the seedfall traps back out of the bush again.

The librarians, especially the Bioscience librarians, whose job description must read "can perform three miracles before breakfast, and recognize stressed students by email."

Allen Rodrigo, Diane Brunton, Ross Ihaka for statistical advice and guidance.

This thesis was sponsored by Telecom, World Wildlife Fund for Nature, Robert C. Bruce Trust, Forest & Bird, Auckland Regional Council and the Auckland University.

Thank you all for your support

Astrid Dijkgraaf

Table of Contents

ABSTRACT	II
ACKNOWLEDGEMENTS	V
TABLE OF CONTENTS	VI
TABLES	XIV
FIGURES	XVI
PHOTOS	XIX
CHAPTER 1. INTRODUCTION.....	2
1.1. HISTORY OF FRUGIVORE STUDIES	2
1.2. NEW ZEALAND SITUATION.....	4
1.2.1. <i>General history of NZ</i>	4
1.2.2. <i>New Zealand Flora</i>	5
1.2.3. <i>New Zealand Fauna</i>	6
1.2.4. <i>New Zealand frugivore systems</i>	7
1.2.5. <i>Effect of introductions to New Zealand</i>	11
1.3. THE STIMULUS FOR THIS STUDY	12
1.4. FOCUS, THESIS STRUCTURE AND AIMS	14
1.4.1. <i>Focus</i>	14
1.4.2. <i>Thesis structure and aims</i>	15
Chapter 1: Introduction	15
Chapter 2: Review of key native and exotic species in the current frugivore system	15
Chapter 3: Methods and site description	15
Chapter 4: Validation of site selection and methods	15
Chapter 5: Fruiting patterns of indigenous species	15
Chapter 6: Nutritional characteristics, utilisation by kereru and success in attracting dispersers for various fruiting species	15
Chapter 7: Impacts of possums and rodents	15
Chapter 8: Discussion and conclusions	16
CHAPTER 2. KEY NATIVE AND EXOTIC SPECIES IN THE CURRENT FRUGIVORE SYSTEM.....	18
2.1. KARAKA	18
Taxonomy.....	18
Distribution, description and growth habit.....	18
Phenology.....	19
2.2. KOHEKOHE.....	19
Taxonomy.....	19
Distribution, description and growth habit.....	19
Phenology.....	20
2.3. PURIRI	20

	Taxonomy.....	20
	Distribution, description and growth habit.....	20
	Phenology.....	21
2.4.	TAWA.....	24
	Taxonomy.....	24
	Distribution, description and growth habit.....	24
	Phenology.....	25
2.5.	TARAIRE.....	25
	Taxonomy.....	25
	Distribution, description and growth habit.....	25
	Phenology.....	26
2.6.	MANGEAO.....	26
	Taxonomy.....	26
	Distribution, description and growth habit.....	27
	Phenology.....	27
2.7.	TAWAPOU.....	27
	Taxonomy.....	27
	Distribution, description and growth habit.....	27
	Phenology.....	27
2.8.	MIRO.....	28
	Taxonomy.....	28
	Distribution, description and growth habit.....	28
	Phenology.....	28
2.9.	PIGEONWOOD.....	28
	Taxonomy.....	28
	Distribution, description and growth habit.....	29
	Phenology.....	29
2.10.	OTHER IMPORTANT SPECIES.....	29
2.10.1.	<i>Nikau</i>	29
2.10.2.	<i>Kahikatea</i>	30
2.10.3.	<i>Titoki</i>	30
2.11.	NEW ZEALAND PIGEON – KERERU.....	30
2.11.1.	<i>Plant species utilised by kereru</i>	32
	Fruits.....	32
	Foliage.....	32
	Fungi and other food types.....	32
2.12.	FRUIT PREDATORS.....	32
2.12.1.	<i>Possums</i>	32
2.12.2.	<i>Rodents</i>	34

CHAPTER 3. SAMPLING DESIGN, METHODS AND STUDY SITE DESCRIPTIONS.38

3.1.	INTRODUCTION.....	38
3.2.	SAMPLING DESIGN.....	38
3.3.	PHENOLOGICAL SAMPLING METHODS.....	39
3.3.1.	<i>Presence/absence classification</i>	39
3.3.2.	<i>Intensity scales</i>	40
3.3.3.	<i>Direct counts</i>	40
3.3.4.	<i>Seedfall traps</i>	41
3.4.	FOREST SAMPLING METHODS.....	41
3.4.1.	<i>Random sampling</i>	41
3.4.2.	<i>Transects</i>	42
3.4.3.	<i>Marked trees</i>	42
3.4.4.	<i>Selection of phenology methods for this study</i>	42
3.5.	DESCRIPTION OF METHODS.....	42
3.5.1.	<i>Selection of trees</i>	43

3.5.2.	<i>Ground fall</i>	43
3.5.3.	<i>Maturity scale</i>	43
3.5.4.	<i>Number per cubic metre</i>	43
3.5.5.	<i>Seedfall traps</i>	44
	Description.....	44
	Positioning of seedfall traps.....	45
	Sample collection.....	45
	Categorising seedfall litter.....	45
3.6.	MAMMALIAN SEED PREDATOR NUMBERS.....	46
3.7.	BIRD COUNTS.....	47
3.8.	SITE SELECTION AND DESCRIPTION.....	47
3.8.1.	<i>Site selection</i>	47
3.8.2.	<i>Wenderholm Regional Park</i>	50
3.8.3.	<i>Loch Amber Bush</i>	50
3.8.4.	<i>Whitford Bush</i>	52
3.8.5.	<i>Robertson's Bush</i>	52
3.8.6.	<i>Remiger's Bush</i>	54
3.8.7.	<i>Val's Bush</i>	54
CHAPTER 4. VALIDATION OF SITE SELECTION AND METHODS.....		56
4.1.	PLANT SPECIES SIMILARITY BETWEEN SITES.....	56
4.1.1.	<i>Results</i>	56
4.1.2.	<i>Effect on further work</i>	58
4.2.	SWITCHING TRAPS AT WENDERHOLM REGIONAL PARK.....	58
4.2.1.	<i>Results</i>	58
4.2.2.	<i>Conclusion</i>	60
4.2.3.	<i>Effect on further work</i>	60
4.3.	COMPARISON BETWEEN METHODS.....	60
4.3.1.	<i>Method</i>	61
4.3.2.	<i>Results</i>	61
4.3.3.	<i>Conclusions</i>	65
CHAPTER 5. FRUITING PATTERNS OF LARGE-FRUITED NATIVE SPECIES.....		68
5.1.	INTRODUCTION.....	68
5.2.	STATISTICAL TESTING FOR CHARACTER DISPLACEMENT.....	72
5.3.	CHAPTER STRUCTURE.....	73
5.4.	DATA USED IN THIS CHAPTER.....	73
5.5.	OBSERVED FRUITING PHENOLOGIES.....	73
5.5.1.	<i>Results</i>	74
	Tawa.....	74
	Karaka.....	74
	Puriri.....	74
	Kohekohe.....	74
	Tarairé.....	77
	Comparison between the sites.....	77
5.5.2.	<i>Discussion</i>	77
	Karaka.....	77
	Kohekohe.....	77
	Puriri.....	78
	Tarairé.....	78
	Tawa.....	78
5.6.	FRUITING SEQUENCE.....	78
5.6.1.	<i>Data used</i>	78
5.6.2.	<i>Analysis</i>	79

5.6.3.	<i>Results</i>	79
5.6.4.	<i>Discussion</i>	80
5.7.	TESTING FOR RANDOMNESS.....	83
5.7.1.	<i>Fruit weight and numbers for all traps and all fleshy fruits</i>	83
5.7.1.1.	Data used.....	83
5.7.1.2.	Analysis.....	83
5.7.1.3.	Results and discussion.....	84
5.7.2.	<i>Number of target fleshy fruits to fall into target traps</i>	84
5.7.2.1.	Data used.....	84
5.7.2.2.	Analysis.....	89
5.7.2.3.	Results.....	89
	Karaka.....	89
	Kohekohe.....	93
	Puriri.....	93
	Taraire.....	93
	Tawa.....	93
5.7.2.4.	Discussion.....	93
5.8.	FRUITING SYNCHRONY.....	93
5.8.1.	<i>Synchrony and overlap formulae</i>	95
5.8.2.	<i>Hypotheses to be tested</i>	98
5.8.3.	<i>Data used</i>	98
5.8.4.	<i>Results for Wenderholm Regional Park</i>	98
5.8.4.1.	Within-species synchrony.....	101
5.8.4.2.	Species overlap.....	103
5.8.5.	<i>Results for Whitford Bush</i>	106
5.8.5.1.	Within-species synchrony.....	108
5.8.5.2.	Species overlap.....	108
5.8.6.	<i>Comparison between the sites</i>	111
5.9.	CONCLUDING DISCUSSIONS.....	113
5.9.1.	<i>Description of fruit phenology</i>	113
5.9.2.	<i>Fruiting sequence</i>	113
5.9.3.	<i>Randomness</i>	114
5.9.4.	<i>Synchrony</i>	114
5.9.5.	<i>Overlap between species</i>	116
5.9.6.	<i>Character displacement</i>	117
5.10.	CONCLUSIONS.....	118

CHAPTER 6. NUTRITIONAL CHARACTERISTICS, UTILISATION BY KERERU AND SUCCESS IN ATTRACTING DISPERSERS FOR VARIOUS FRUITING SPECIES.....122

6.1.	INTRODUCTION.....	122
6.2.	NUTRITIONAL ANALYSIS.....	123
6.2.1.	<i>Method</i>	123
6.2.2.	<i>Results</i>	124
6.2.2.1.	Fruit nutritional characteristics.....	128
6.2.2.2.	Fruit 'types'.....	128
6.3.	COMPARISON WITH OTHER NEW ZEALAND STUDIES.....	135
6.3.1.	<i>Data used</i>	135
6.3.2.	<i>Results</i>	135
6.4.	COMPARISON WITH OVERSEAS SPECIES.....	137
6.4.1.	<i>Method</i>	137
6.4.2.	<i>Results</i>	137
6.4.3.	<i>Conclusions</i>	141
6.5.	NUTRITIONAL AVAILABILITY AND UTILISATION.....	141
6.5.1.	<i>Relative abundance of fleshy-fruited species</i>	141
6.5.1.1.	Data used.....	141
6.5.1.2.	Results.....	144
6.5.2.	<i>Fruit utilisation by kereru, with particular reference to fruit nutrition</i>	144

6.5.2.1.	Data used	144
6.5.2.2.	Results from this study.	148
6.5.2.3.	Results from Wenderholm Regional Park 1988-1989 data.....	148
6.5.2.4.	Results from Wenderholm Regional Park 1993-1994 data.....	151
6.5.2.5.	Comparison of all three studies.....	151
6.5.3.	<i>Fruit consumption as a measure of attractiveness of fruit species to dispersers.</i> ..	152
6.5.3.1.	Data used	152
6.5.3.2.	Results	153
	Nikau	153
	Tawa	154
	Karaka	154
	Puriri.....	154
	Miro.....	157
	Kahikatea.....	157
	Tawapou	157
	Kohekohe	157
	Taraire	157
	Pigeonwood.....	158
	Supplejack	158
6.6.	CONCLUDING DISCUSSIONS.....	158
6.6.1.	<i>Fruit nutrition</i>	158
6.6.2.	<i>Seasonality of fruit nutrition</i>	159
6.6.3.	<i>Utilisation by kereru</i>	160
6.6.4.	<i>Success of plant species in attracting dispersers</i>	161
6.7.	CONCLUSIONS	161
 CHAPTER 7. IMPACTS OF POSSUMS AND RODENTS		164
7.1.	GENERAL BACKGROUND.....	164
7.2.	SUPPRESSION OF MAMMALS. THE HISTORY OF EACH SITE.....	164
	Wenderholm Regional Park	164
	Loch Amber Bush	165
	Whitford Bush	167
	Robertson's Bush	167
	Remiger's Bush	168
	Val's Bush	168
7.3.	EFFECT ON MAMMAL PRESENCE	169
7.3.1.	<i>Possum and rodent numbers.</i>	169
	Results	170
	Discussion	173
7.3.2.	<i>Mammal droppings</i>	174
	Data used	174
	Method	174
	Results	177
	Discussion	178
7.4.	EFFECT ON FRUIT AVAILABILITY.....	179
7.4.1.	<i>Overall fruit production.</i>	179
	Data used	179
	Results	180
	Discussion	180
7.4.2.	<i>Fruit consumption and predation by species</i>	189
	Data used	189
	Analysis.....	189
	Results	189
	Discussion	201
7.4.3.	<i>Overall patterns of fruit production between paired sites.</i>	202
	Data used	202

Analysis.....	202
Results	202
Discussion	208
7.5. EFFECT ON OTHER ANIMAL SPECIES.....	209
7.5.1. <i>Non-mammalian droppings</i>	209
Data used.....	209
Data analysis.....	209
Results	209
Discussion	213
7.5.2. <i>Bird species abundance</i>	213
Data used.....	213
Data analysis.....	214
Results	214
Discussion	223
7.6. CONCLUDING DISCUSSIONS.....	223
7.6.1. <i>Effect of pest suppression on mammal presence</i>	223
7.6.2. <i>Effect on fruit availability</i>	223
7.6.3. <i>Effect on other animal species</i>	224
7.7. CONCLUSIONS	225
CHAPTER 8. INTERACTION OF LARGE-FRUITED SPECIES, SEED DISPERSERS AND SEED PREDATORS.....	228
8.1. INTRODUCTION.....	228
8.2. FRUIT PHENOLOGY OF LARGE FRUITED SPECIES	228
8.2.1. <i>Effect on kereru populations</i>	231
8.2.2. <i>Effect on possums and rodent populations</i>	232
8.2.3. <i>Interaction between species</i>	235
8.2.4. <i>Food webs</i>	236
8.2.5. <i>Implications for management of the large-fruited species-frugivore system</i>	240
8.3. CONCLUSIONS AND FURTHER RESEARCH OPPORTUNITIES.....	242
REFERENCES	245
APPENDIX 3.1 - DESCRIPTIONS OF MATURITY STAGES FOR SELECTED SPECIES..	264
APPENDIX 3.2 - EXAMPLE OF PHENOLOGY DATA COLLECTION FORM.....	270
APPENDIX 3.3 - DESCRIPTIONS FOR SEEDFALL TRAP CONTENTS	271
APPENDIX 3.4 - DESCRIPTION OF TOXINS.....	276
APPENDIX 3.5 SCHEMATIC DIAGRAM FOR CONSTRUCTION OF SEEDFALL TRAPS	277
APPENDIX 4.1 COMMON AND SCIENTIFIC NAMES OF PLANT SPECIES	278
APPENDIX 5.1 - SYNTAX USED FOR SIMPSON ANALYSES	278

APPENDIX 5.2 SYNCHRONY ANALYSIS OF PHENOLOGY TREES	285
APPENDIX 5.3 GENERAL LINEAR MODELS PROCEDURE FOR ASPECTS OF SYNCHRONY ANALYSIS.....	290
General Linear Models Procedure for Wenderholm data.....	290
Wenderholm PROP	290
Wenderholm DURATN	291
Wenderholm DAYS	293
Wenderholm WITHINSP	295
General Linear Models Procedure for Whitford data.....	297
Whitford PROP	297
Whitford DURATN.....	298
Whitford DAYS	299
Whitford WITHINSP	301
General Linear Models Procedure for Both sites	302
Both PROP	302
Both DURATN.....	304
APPENDIX 5.4 SYNCHRONY OF THE FRUITING POPULATION VERSUS THE WHOLE POPULATION.	307
APPENDIX 6.1 COLLECTION OF FRUIT FOR NUTRITIONAL ANALYSIS.....	311
APPENDIX 6.2 FRUIT-FLESH CHARACTERISTICS AND PHYSICAL ATTRIBUTES OF A RANGE OF FRUIT OF SPECIES, ARRANGED ACCORDING TO CLUSTER ANALYSIS.....	313
APPENDIX 6.3 DISCRIMINANT ANALYSIS OF NUTRITIONAL CLUSTER ANALYSIS	314
Using discriminant analysis to check the cluster analysis of fruit nutritional characteristics (physical attributes excluded), grouped by fruit traits. Data not transformed.....	314
Using discriminant analysis to check the cluster analysis of fruit nutritional characteristics (physical attributes included), grouped by fruit traits. Data normalised.	316
Using discriminant analysis to check the cluster analysis of fruit species (physical attributes excluded), grouped by fruit nutritional characteristics. Data not transformed.	317
Using discriminant analysis to check the cluster analysis of fruit species (physical attributes included, but not as separate cluster), grouped by fruit nutritional characteristics. Data either not transformed or normalised.	318
Using discriminant analysis to check the cluster analysis of fruit species (physical attributes included as separate cluster), grouped by fruit nutritional characteristics. Data are normalised.....	319
APPENDIX 6.4 ; REFERENCES USED BY JORDANO (1995)	321
APPENDIX 7.1 WEIGHTS AND SEX OF POSSUMS CAUGHT DURING FINAL TWO WEEKS OF STUDY.....	323

APPENDIX 7.2 SYNTAX USED TO ANALYSE VARIOUS ASPECTS OF MAMMALIAN PREDATOR PRESENCE.....	324
A. Number of droppings.....	324
Site nested within pest suppression.....	324
Differences between sites.....	324
B. Predation, consumption and production of fruit.....	325
APPENDIX 7.3 SAS OUTPUT FOR PEST SPECIES DROPPINGS.	326
Possum droppings analysis - Site nested within suppression.....	326
Possum droppings analysis - Differences between sites.....	327
Rat droppings analysis - Site nested within suppression.....	328
Rat droppings analysis - Differences between sites.....	329
Rodent droppings analysis - Site nested within suppression.....	329
Rodent droppings analysis - Differences between sites.....	331
APPENDIX 7.4 SAS OUTPUT; PREDATION AND CONSUMPTION OF FRUITS BETWEEN SITE PAIRS.	332
Wenderholm and Loch Amber –number of mature fruits.....	332
Wenderholm and Loch Amber –number of immature fruits.....	333
Wenderholm and Loch Amber –number of predated fruits.....	334
Wenderholm and Loch Amber –number of unpredated fruits.....	335
Wenderholm and Loch Amber –number of consumed fruits.....	336
Wenderholm and Loch Amber –number of insect predated fruits.....	337
Wenderholm and Loch Amber –number of possum predated fruits.....	338
Wenderholm and Loch Amber –number of fruits predated by rodents.....	339
Wenderholm and Loch Amber –number of fruits predated by unknown agents.....	340
Whitford and Robertson’s –number of mature fruits.....	341
Whitford and Robertson’s –number of immature fruits.....	342
Whitford and Robertson’s –number of predated fruits.....	343
Whitford and Robertson’s –number of unpredated fruits.....	344
Whitford and Robertson’s –number of consumed fruits.....	345
Whitford and Robertson’s –number of insect predated fruits.....	346
Whitford and Robertson’s –number of possum predated fruits.....	347
Whitford and Robertson’s –number of fruits predated by rodents.....	348
Whitford and Robertson’s –number of fruits predated by unknown agents.....	349
Remiger’s and Val’s –number of mature fruits.....	350
Remiger’s and Val’s –number of immature fruits.....	351
Remiger’s and Val’s –number of predated fruits.....	352
Remiger’s and Val’s –number of unpredated fruits.....	354
Remiger’s and Val’s –number of consumed fruits.....	355
Remiger’s and Val’s –number of insect predated fruits.....	356
Remiger’s and Val’s –number of possum predated fruits.....	357
Remiger’s and Val’s –number of fruits predated by rodents.....	358
Remiger’s and Val’s –number of fruits predated by unknown agents.....	359
APPENDIX 7.5 SAS OUTPUT FOR NON-PEST SPECIES DROPPINGS.	361
Insect (excluding weta) droppings analysis - Site nested within suppression.....	361
Insect (excluding weta) droppings analysis - Differences between sites.....	362
Pigeon droppings analysis - Site nested within suppression.....	363
Pigeon droppings analysis - Differences between sites.....	364
Weta droppings analysis - Site nested within suppress.....	
Weta droppings analysis - Differences between sites.....	

APPENDIX 7.6 SAS OUTPUT FOR TOTAL NUMBER OF BIRDS NOTED PER SPECIES AND PER VISIT TO EACH SITE.....367

Number of kereru seen per visit- Site nested within suppression.....	367
Number of tui seen per visit- Site nested within suppression.....	369
Number of rosella seen per visit- Site nested within suppression.....	370
Number of silvereyes seen per visit- Site nested within suppression.....	371
Number of blackbirds seen per visit- Site nested within suppression.....	372
Number of thrushes seen per visit- Site nested within suppression.....	373
Number of myna seen per visit- Site nested within suppression.....	374
Number of fantails seen per visit- Site nested within suppression.....	375
Number of harriers seen per visit- Site nested within suppression.....	376
Number of pukeko seen per visit- Site nested within suppression.....	377
Number of kingfishers seen per visit- Site nested within suppression.....	378
Number of warblers seen per visit- Site nested within suppression.....	379
Number of finches seen per visit- Site nested within suppression.....	380
Number of magpies seen per visit- Site nested within suppression.....	381
Number of pheasants seen per visit- Site nested within suppression.....	382
Number of skylarks seen per visit- Site nested within suppression.....	383
Number of swallows seen per visit- Site nested within suppression.....	384

APPENDIX 7.7 SAS OUTPUT FOR FLOCK SIZE PER SPECIES AND PER SITE.....386

Flock size of kereru per site.....	386
Flock size of tui per site.....	388
Flock size of rosella per site.....	389
Flock size of silvereyes per site.....	390
Flock size of blackbirds per site.....	392
Flock size of thrushes per site.....	393
Flock size of myna per site.....	395
Flock size of harriers per site.....	396
Flock size of pukeko per site.....	397
Flock size of kingfishers per site.....	399
Flock size of warblers per site.....	400
Flock size of fantails per site.....	402
Flock size of finches per site.....	403
Flock size of magpies per site.....	404
Flock size of pheasants per site.....	406
Flock size of skylarks per site.....	408
Flock size of swallows per site.....	409

APPENDIX 8.1: SOME KEY REFERENCES USED IN THE CONSTRUCTION OF THE FOOD WEB.....411

APPENDIX 8.2: - OTHER RESEARCH QUESTIONS412

Tables

Table 1.1: Extinct and extant terrestrial forest seed dispersers of New Zealand, with some indications of size, gape width and postulated or known diet.....	8
Table 1.2: Larger-fruited tree species presented by minimum transverse fruit diameter classes.....	12
Table 1.3: First appearance dates in fossil records for large-fruited genera of interest.....	13
Table 3.1: Sample design; summary of site pairs and levels of pest suppression.....	38
Table 3.2: Set up dates of phenology sites.....	45

Table 3.3: Classification of fruits and flowers, within species, in samples collected from seedfall traps.....	46
Table 4.1: Summary of species found during Point Centred Quarters surveys at each site.....	57
Table 4.2: Czekanowski similarity coefficients for species composition for all sites.....	58
Table 4.3: Summary of Chi-square comparisons between trap designs for bulked samples.....	59
Table 4.4: Average number of fruits from focus species per seedfall traps per sampling occasion before and after trap switch at Wenderholm Regional Park.....	60
Table 4.5: Comparisons of average seedfall numbers versus counts per cubic metre.....	61
Table 4.6: Comparisons of different phenological methods for individual trees with target traps.....	63
Table 5.1: Total number of target species fruits to fall into conspecific seedfall traps at Wenderholm Regional Park and Whitford Bush for each of three years.....	80
Table 5.2: Number of visits when ripe fruit was sighted at Wenderholm Regional Park.....	101
Table 5.3: Duration of fruiting and synchrony of trees with one or more ripe fruits at Wenderholm Regional Park.....	102
Table 5.4: Overlap and critical overlap values for sample species at Wenderholm Regional Park....	105
Table 5.5: Occurrence of ripe fruit at Whitford Bush for the duration of the study.....	106
Table 5.6: Duration of fruiting and synchrony of trees with one or more ripe fruits at Whitford Bush.....	109
Table 5.7: Overlap and critical overlap values for sample species at Whitford Bush.....	110
Table 5.8: Synchrony results obtained by Augspurger (1983) for flowering phenology of six shrub species.....	115
Table 6.1: Fruit-flesh nutritional composition for a range of larger-fruited species. Data are not transformed.....	125
Table 6.1a: Variability in nutritional characteristics for five kahikatea trees. Data are not transformed.....	125
Table 6.2: Physical measurements of simple fruits for a range of larger-fruited species.....	126
Table 6.2a: Physical measurements of complex fruits for a range of larger-fruited species.....	126
Table 6.3: Comparison of fruit nutritional characteristics with some other studies.....	136
Table 6.4: Average fruit nutritional and structural characteristics from other studies as compiled by Jordano (1995).....	138
Table 6.4 Continued: Average fruit nutritional and structural characteristics from other studies as compiled by Jordano (1995).....	139
Table 6.5: Comparison of large (>10mm) bird dispersed New Zealand fruit with large overseas bird, mixed (mammal and bird), and mammal-dispersed fruit.....	140
Table 6.6: Observations of fruit consumption by bird species.....	145
Table 6.7: Feeding observations and consumption of fruit by kereru in three different studies.....	146
Table 6.8: Chi-square comparison of number of consumed and uneaten fruits per fortnightly sampling period.....	153
Table 7.1: Rats and mice captured per 100 trap nights at Wenderholm Regional Park.....	165
Table 7.2 Average weight and number of possums caught.....	170
Table 7.3: Summary of index trapping at all sites.....	171
Table 7.4: Number of rodents caught during the extinction trapping session.....	173
Table 7.5: Average number of seedfall traps at Remiger's Bush containing possum or rodent droppings during the three periods with different levels of possum control.....	178
Table 7.6: Differences between paired sites in fruit predation, bird consumption and fruit production.....	203
Table 7.7: A posteriori Tukey's HSD means for fruit predation, bird consumption and fruit production at paired sites.....	204
Table 7.8: ANOVA of number of frugivorous bird species observations per site visit.....	215
Table 7.9: ANOVA of number of non-frugivorous bird species observations per site visit.....	215
Table 7.10: ANOVA of 'flock size' for frugivorous species at each site.....	218
Table 7.11: ANOVA of 'flock size' for non-frugivorous species at each site.....	219
Table 6.3.1: Summary of canonical discriminant functions of fruit nutritional characteristics (physical attributes excluded), grouped by fruit traits. Data not transformed.....	314
Table 6.3.2: Discriminant analysis Wilks' lambda of fruit nutritional characteristics (physical attributes excluded), grouped by fruit traits. Data not transformed.....	315

Table 6.3.3: Summary of canonical discriminant functions of fruit nutritional characteristics (physical attributes included), grouped by fruit traits. Data normalised.	316
Table 6.3.4: Discriminant analysis Wilks' lambda of fruit nutritional characteristics (physical attributes included), grouped by fruit traits. Data normalised.	316
Table 6.3.5: Summary of canonical discriminant functions of fruit species (physical attributes excluded), grouped by fruit nutritional characteristics. Data not transformed.	317
Table 6.3.6: Discriminant analysis Wilks' lambda of fruit species (physical attributes excluded), grouped by fruit nutritional characteristics. Data not transformed.	317
Table 6.3.7: Summary of canonical discriminant functions of fruit species (physical attributes included), grouped by fruit nutritional characteristics. Data not transformed.	318
Table 6.3.8: Discriminant analysis Wilks' lambda of fruit species (physical attributes included), grouped by fruit nutritional characteristics. Data not transformed.	319
Table 6.3.9: Summary of canonical discriminant functions of fruit species (physical attributes included as separate cluster), grouped by fruit nutritional characteristics. Data not transformed.	320
Table 6.3.10: Discriminant analysis Wilks' lambda of fruit species (physical attributes included as a separate group), grouped by fruit nutritional characteristics. Data not transformed. ...	320

Figures

Figure 3.1 Map of Auckland showing location of the study sites.	39
Figure 4.1: R-square values from linear regressions between various phenology methods	62
Figure 4.2: Number of target fruits caught in all and in target traps at Wenderholm Regional Park. ..	63
Figure 5.1: Number of fruits, from large fruited species, caught in seedfall traps at Wenderholm Regional Park.	75
Figure 5.2: Number of fruits, from large fruited species, caught in seedfall traps at Whitford Bush. ...	76
Figure 5.3: Timing of fruit fall for individual trees during three consecutive years at Wenderholm Regional Park (25 th to 75 th percentiles).	81
Figure 5.4: Timing of fruit fall for individual trees during three consecutive years at Whitford Bush (25 th to 75 th percentiles).	82
Figure 5.5a: Simpson plot of weight of all fleshy-fruits to fall in seedfall traps at Wenderholm Regional Park.	85
Figure 5.5b: Total weight of all fleshy-fruits to fall in seedfall traps at Wenderholm Regional Park. ..	85
Figure 5.6a: Simpson plot of number of all fleshy-fruits to fall in seedfall traps at Wenderholm Regional Park.	86
Figure 5.6b: Total number of all fleshy-fruits to fall in seedfall traps at Wenderholm Regional Park.	86
Figure 5.7a: Simpson plot of weight of all fleshy-fruits to fall in seedfall traps at Whitford Bush.	87
Figure 5.7b: Total weight of all fleshy-fruits to fall in seedfall traps at Whitford Bush.	87
Figure 5.8a: Simpson plot of number of all fleshy-fruits to fall in seedfall traps at Whitford Bush ...	88
Figure 5.8b: Total number of all fleshy-fruits to fall in seedfall traps at Whitford Bush	88
Figure 5.9: Flow diagram of Monte Carlo procedure for estimating parameters for target fruits to fall into target traps.	90
Figure 5.10: Simpson analysis for number of target fruits to fall in seedfall traps at Wenderholm Regional Park.	91
Figure 5.11: Simpson analysis for number of target fruits to fall in seedfall traps at Whitford Bush. ..	92
Figure 5.12: Species synchrony sums the occasions that individual trees have fruit simultaneously ..	94
Figure 5.13: Species overlap sums the occasions that individuals from one species overlap with fruiting occasions of other species	94
Figure 5.14: The magnitude of overlap with other species should be viewed in proportion to the number of competing species (Pianka 1974).	96
Figure 5.15: Illustration of the chance of overlap between species in the same habitat.	97
Figure 5.16: Occasions that phenology trees at Wenderholm Regional Park had one or more ripe fruits.	99
Figure 5.17: Occasions that phenology trees at Whitford Bush had one or more ripe fruits.	100

Figure 5.18: A posteriori Tukey's HSD test for different fruiting synchrony variables at Wenderholm Regional Park.	103
Figure 5.19: Mean length of fruiting (fortnights) and synchrony analysis for large fruited-species at Wenderholm Regional Park	104
Figure 5.20: Mean length of fruiting (fortnights) and synchrony analysis for large-fruited species at Whitford Bush	107
Figure 5.21: A posteriori Tukey's HSD for different fruiting synchrony variables at Whitford Bush.....	107
Figure 5.22 Average critical overlap values ($X_{S(o)}$) for species at both sites using different measures of fruit phenology length (\bar{F}_s).	112
Figure 5.23: Overlap between hypothetically synchronously and asynchronously fruiting species. .	116
Figure 5.24: Comparison of amplitude overlap versus linear overlap.	117
Figure 6.1: Cluster analysis of fruit nutritional characteristics, grouped by fruit traits.	127
Figure 6.2: Cluster analysis of fruit species, grouped by nutritional characteristics.	130
Figure 6.3: Nutritional characteristics of fruits, grouped according to cluster results.	131
Figure 6.3 cont: Nutritional characteristics of fruits, grouped according to cluster results (page 2)..	132
Figure 6.3 cont: Physical characteristics of fruits, grouped according to cluster results.	133
Figure 6.4: Mean fruit characteristics for fruit 'types' presented as averages for cluster 'categories'. .	134
Figure 6.5: Observations of relative abundance for each fruit species throughout a generalised year.	142
Figure 6.6: Availability of fruits throughout a generalised year by nutritional fruit 'types'.....	143
Figure 6.7: Observed availability and nutritional fruit 'type' throughout the year compared with kereru behaviour and seed deposition over all sites during this study.	147
Figure 6.8: Availability and nutritional value of fruits throughout the year compared with observed kereru feeding and nesting in 1988/89.	149
Figure 6.9: Availability and nutritional value fruits throughout the year compared with observed kereru feeding and nesting in 1993/94.	150
Figure 6.10: Number of consumed and uneaten fruits to fall into seedfall traps, summed over all sites by sampling fortnight	155
Figure 6.11: Relative abundance of fruits (observation and seed deposition) and kereru feeding observations.....	156
Figure 7.1: Number of possums killed per annum at Wenderholm Regional Park	164
Figure 7.2: Number of rats and mice per 100 trap nights at Wenderholm Regional Park.....	166
Figure 7.3: Locality map of Wenderholm Regional Park and Loch Amber Bush.....	166
Figure 7.4: Locality map of Whitford Bush and Robertson's Bush	167
Figure 7.5: Locality map of Remiger's Bush and Val's Bush	168
Figure 7.6: Trapping grid layout for small and larger sites.	169
Figure 7.7: Number of possums trapped per site.	172
Figures 7.8 a to c: Number of seedfall traps at each site containing one or more possum droppings. .	175
Figures 7.9 a to c: Number of seedfall traps at each site containing one or more rodent droppings. .	176
Figure 7.10: A posteriori Tukey's Studentized Range (HSD) test for mammalian droppings in seedfall traps by site.	177
Figure 7.11: Number of mature, damaged fruits found in seedfall traps at Wenderholm Regional Park.....	181
Figure 7.12: Number of mature, undamaged fruits found in seedfall traps at Loch Amber Bush.....	183
Figure 7.13: Number of mature, undamaged fruits found in seedfall traps at Whitford Bush	184
Figure 7.14: Number of mature, undamaged fruits found in seedfall traps at Robertson's Bush.....	185
Figure 7.15: Number of mature, undamaged fruits found in seedfall traps at Remiger's Bush	186
Figure 7.16: Number of mature, undamaged fruits found in seedfall traps at Val's Bush	188
Figure 7.17: Predation and consumption of Kohekohe fruits	191
Figure 7.18: Predation and consumption of Taraire fruits	192
Figure 7.19: Predation and consumption of Karaka fruits.....	193
Figure 7.20: Predation and consumption of Puriri fruits	194
Figure 7.21: Predation and consumption of Tawa fruits.....	195
Figure 7.22: Predation and consumption of Pigeonwood fruits.....	196
Figure 7.23: Predation and consumption of Nikau fruits.....	197

Figure 7.24: Predation and consumption of Kahikatea fruits	198
Figure 7.25: Predation and consumption of Rewarewa seed capsules.....	199
Figure 7.26: Comparison between levels of predation, bird consumption and fruit production for Wenderholm Regional Park and Loch Amber Bush.	205
Figure 7.27: Comparison between levels of predation, bird consumption and fruit production for Whitford Bush and Robertson's Bush.	206
Figure 7.28: Comparison between levels of predation, bird consumption and fruit production for Remiger's Bush and Val's Bush.....	207
Figure 7.29 a to c: Number of traps at each site containing one or more insect dropping.....	210
Figure 7.30 a to c: Number of traps at each site containing one or more weta dropping.	211
Figure 7.31 a to c: Number of traps at each site containing one or more kereru dropping.....	212
Figure 7.32: A posteriori Tukey's Studentized Range (HSD) test for non-mammalian dropping in seedfall traps by site.	213
Figure 7.33: Average number of observations (seen or heard) of frugivorous bird species per site visit.	216
Figure 7.34: Average number of observations (seen or heard) of non-frugivorous bird species per site visit.	217
Figure 7.35: Number of frugivorous birds at Wenderholm Regional Park and Loch Amber Bush, grouped by flock size	220
Figure 7.36: Number of frugivorous birds at Whitford Bush and Robertson's Bush, grouped by flock size	221
Figure 7.37: Number of frugivorous birds at Remiger's Bush and Val's Bush, grouped by flock size.....	222
Figure 8.1 Approximate latitudinal limits for species with large fruits and large flowers.	234
Figure 8.2 Simplified food web for functional groups in forest remnants in the Auckland area (northern New Zealand).	237
Figure 8.3 Interaction web for large-fruited species and frugivores.....	240
Figure 5.4.1: Comparison of population synchrony values ($Z_s^{(sp)}$) for all monitored trees (whole population) and $Z_s^{(sp)}$ for fruiting trees only (fruiting population).	308
Figure 5.4.2: Linear regression of number of trees failing to fruit plotted against synchrony values for fruiting population only.	309
Figure 5.4.3: Linear regression of number of trees failing to fruit plotted against synchrony values for entire population.	310
Figure 6.3.1: Discriminant analysis of nutritional clusters; physical parameters excluded, data not transformed.....	314
Figure 6.3.2: Discriminant analysis of nutritional clusters; physical parameters included, data normalised.	316
Figure 6.3.3: Discriminant analysis of fruit species clusters; physical parameters excluded, data not transformed.....	317
Figure 6.3.4: Discriminant analysis of fruit species clusters; physical parameters included, data not transformed.....	318
Figure 6.3.5: Discriminant analysis of fruit species clusters; physical parameters included as a separate cluster, data not transformed.	319

Photos

Photo 3.1: Aerial view of location and relationship of the 4 northern sites.....	48
Photo 3.2: Aerial photograph showing forested headland at Wenderholm Regional Park.....	48
Photo 3.3: Site map of Wenderholm Regional Park and Loch Amber Bush, and their relationship to each other.	49
Photo 3.4: Site map of Whitford Bush and Robertson's Bush and their relation to each other.....	51
Photo 3.5: Site map of Remiger's Bush and Val's Bush and their relation to each other	53
Photo 4.1: The two trap 'designs'.....	59