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The Textural Discontinuity Hypothesis and its relation to nomadism, migration, decline, and competition

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The Textural Discontinuity Hypothesis and its relation to
nomadism, migration, decline, and competition

by

Aaron L. ALAI

A THESIS

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The Textural Discontinuity Hypothesis and its relation to nomadism, migration, decline, and competition

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The causes of nomadism, migration, and decline in vertebrates are debated issues in the ecological sciences. Literature suggests nomadism may arise in species that specialize in granivory, nectivory, or the utilization of rodent outbreaks. Migration is thought to arise as a result of the exploitation of certain scarce or variable food resources. Species decline is hypothesized to be the result of many different factors as well; large species, island species and specialists may be more prone to decline.

A fresh perspective regarding the causes for species nomadism, migration, and decline is being investigated utilizing the ideas within the Textural Discontinuity Hypothesis. The Textural Discontinuity Hypothesis stems from complex systems analysis and posits that body mass distributions form aggregations within ecological systems, and that those body mass aggregations reflect discontinuous distributions of resources. Additionally scientists have posited that species at the edges of body mass aggregations may be exposed to highly variable resources. Literature indicates nomadic and declining bird species populations occur at the edges of body mass aggregations more frequently than expected. Migratory bird species also may be located at the edges

of body mass aggregations more frequently than expected. The morphological spacing of species within aggregations may yield clues regarding species interactions.

The distribution of species within a body mass aggregation would have low variance if species within an aggregation interact with each other strongly – morphological overdispersion has been documented in many animal communities and reflects strong competitive interactions among species.

I analyzed nomadism, migration, and decline in South African birds using an information-theoretic approach. I assembled a series of plausible models based upon suggested or theoretically predictive characteristics. Additionally, I used a series of Monte Carlo simulations to investigate the distribution of species within aggregations, in terms of body mass.

Results suggest that a combination of species characteristics, including the distance to the edge of a body mass aggregation, explain the complex phenomena of nomadism, migration and decline. Generally there was no single model supported, and often many models were in the confidence set, providing only weak inference. Within body mass aggregations, there is more variance among species than null expectations, thus with my dataset morphological overdispersion is not present within body mass aggregations. Nomadism, migration, and decline are complex phenomena which incorporate different species characteristics, perhaps explaining why such debate still exists over the causes of these phenomena.

DEDICATION

This thesis is dedicated to my insightful advisor Dr. Craig Allen and to my supportive committee members; Dr. Andrew Tyre for his combination of statistical and ecological guidance, and to Dr. Kathy Hanford for her assistance with statistical dilemmas. This thesis is also dedicated to my friends and lab mates who put up with me talking about discontinuities in complex systems all the time.

TABLE OF CONTENTS

TITLE PAGE	i
ABSTRACT.....	iii
DEDICATION.....	iv
LIST OF TABLES.....	vii
LIST OF FIGURES	xix
PREFACE.....	xxii
CHAPTERS	
I. OVERVIEW	1
Literature Cited	10
II. SOUTH AFRICAN BIRD SPECIES AND THE STRUCTURE OF THEIR BODY MASS DISTRIBUTIONS	13
Introduction.....	13
Methods.....	19
Results.....	22
Discussion	36
Literature Cited	40
III. SOUTH AFRICAN MIGRATORY BIRD SPECIES AND THEIR LOCATION WITHIN DISCONTINUOUS AGGREGATIONS.....	42
Introduction.....	42
Methods.....	47
Results.....	51
Discussion	80
Literature Cited	84
IV. SOUTH AFRICAN PREDICTORS OF NOMADIC BIRD SPECIES AND THEIR LOCATION WITHIN DISCONTINUOUS AGGREGATIONS	86
Introduction.....	86
Methods.....	92
Results.....	96
Discussion	122
Literature Cited	126

V.	A TEST OF ALTERNATIVE MODELS PREDICTING DECLIN IN SOUTH AFRICAN BIRDS	128
	Introduction.....	128
	Methods.....	132
	Results.....	135
	Discussion	152
	Literature Cited	155
VI.	SMMARY	157
	Literature Cited	163

LIST OF TABLES

2.1	The number of body mass aggregations in South African bird species by habitat and ecosystem, including and excluding aquatic species. The number of aggregations was determined by Bayesian Classification And Regression Tree analyses	24
2.2	Variance in inter species spacing within aggregations in South African agricultural habitats. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation	25
2.3	Variance in inter species spacing within aggregations in the South African Fynbos ecosystem. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation	26
2.4	Variance in inter species spacing within aggregations in South African grassland habitats. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation	27
2.5	Variance in inter species spacing within aggregations in the South African Karoo ecosystem. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation	28
2.6	Variance in inter species spacing within aggregations in South African lagoon habitats. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation	29
2.7	Variance in inter species spacing within aggregations in the South African Namib ecosystem. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation	30

List of Tables (Continued)

2.8	Variance in inter species spacing within aggregations in South African semi-arid habitats. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation	31
2.9	Variance in inter species spacing within aggregations in South African savanna habitats. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation	32
2.10	Variance in inter species spacing within aggregations in South African wetland habitats. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation	33
2.11	Variance in inter species spacing within aggregations in South African woodland habitats. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation	34
2.12	Summation of body mass aggregation rank against Monte Carlo simulations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 – 1000 indicates high variance within the actual body mass aggregation. Body mass aggregations were too small for the analysis if they contained three or fewer species' body masses.....	35
3.1	The number of body mass aggregations and species per habitat in South African birds including and excluding aquatic species. The aggregations were determined with Bayesian Classification And Regression Tree analysis.....	53

List of Tables (Continued)

- 3.2 Agricultural habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 22% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption54
- 3.3 Karoo ecosystem. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 19% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption56
- 3.4 Namib ecosystem. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 11% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption58

List of Tables (Continued)

- 3.5 Grassland habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 27% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.59
- 3.6 Savanna habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 16% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption61
- 3.7 Wetland habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 19% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption63

List of Tables (Continued)

- 3.8 Woodland habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 18% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption65
- 3.9 Semi-arid habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 15% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption67
- 3.10 Fynbos ecosystem. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 26% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption69
- 3.11 Logistic Regression composite migration model for South African birds located in agricultural habitats. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption71

List of Tables (Continued)

- 3.12 Logistic Regression composite migration model for South African birds located in the Karoo ecosystem. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.....72
- 3.13 Logistic Regression composite migration model for South African birds located in the Namib ecosystem. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption73
- 3.14 Logistic Regression composite migration model for South African birds located in grassland habitats. Aerial = aerial substrate, edge = distance to the closest edge of a body mass aggregation, fruit = frugivorous, ground = ground substrate, plantparts = plant part consumption, seeds = granivory, terrinverts = terrestrial invertebrate consumption.....74
- 3.15 Logistic Regression composite migration model for South African birds located in savanna habitats. Aerial = aerial substrate, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, seeds = granivory, terrinverts = terrestrial invertebrate consumption.....75
- 3.16 Logistic Regression composite migration model for South African birds located in wetland habitats. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, ground = ground substrate, habitatrich = habitat richness, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.....76
- 3.17 Logistic Regression composite migration model for South African birds located in woodland habitats. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.....77

List of Tables (Continued)

3.18	Logistic Regression composite migration model for South African birds located in semi-arid habitats. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, habitatrich = habitat richness, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.....	78
3.19	Logistic Regression composite migration model for South African birds located in the Fynbos ecosystem. Edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, habitatrich = habitat richness, seeds = granivory, substratumrich = substrate richness	79
4.1	The number of body mass aggregations and species per habitat in South African birds, including and excluding aquatic species. Aggregations were determined with Bayesian Classification And Regression Tree analysis	98
4.2	Models predicting nomadism in South African birds inhabiting the Karoo ecosystem. Nomadic species account for 20% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.....	99
4.3	Models predicting nomadism in South African birds inhabiting savanna habitats. Nomadic species account for 20% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption	101

List of Tables (Continued)

- 4.4 Models predicting nomadism in South African birds inhabiting grassland habitats. Nomadic species account for 18% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption103
- 4.5 Models predicting nomadism in South African birds inhabiting the Namib ecosystem. Nomadic species account for 47% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.....105
- 4.6 Models predicting nomadism in South African birds inhabiting woodland habitats. Nomadic species account for 12% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption107
- 4.7 Models predicting nomadism in South African birds inhabiting agricultural habitats. Nomadic species account for 31% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.....109

List of Tables (Continued)

- 4.8 Models predicting nomadism in South African birds inhabiting lagoon habitats. Nomadic species account for 19% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption111
- 4.9 Models predicting nomadism in South African birds inhabiting wetland habitats. Nomadic species account for 14% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption112
- 4.10 Logistic Regression nomadism composite model for South African birds located in the Karoo ecosystem. Edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, nectar = nectivory, seeds = granivory, terrinverts = terrestrial invertebrate consumption.....114
- 4.11 Logistic Regression nomadism composite model for South African birds located in savanna habitats. Edge = distance to the closest edge of a body mass aggregation, foragerich = forage richness, fruit = frugivorous, nectar = nectivory, terrinverts = terrestrial invertebrate consumption.....115
- 4.12 Logistic Regression nomadism composite model for South African birds located in grassland habitats. Aerial = aerial substrate, edge = distance to the closest edge of a body mass aggregation, foragerich = forage richness, ground = ground substrate, terrinverts = terrestrial invertebrate consumption.....116

List of Tables (Continued)

4.13	Logistic Regression nomadism composite model for South African birds located in the Namib ecosystem. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, ground = ground substrate, habitatrich = habitat richness, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.....	117
4.14	Logistic Regression nomadism composite model for South African birds located in woodland habitats. Edge = distance to the closest edge of a body mass aggregation, nectar = nectivory	118
4.15	Logistic Regression nomadism composite model for South African birds located in agricultural habitats. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, nectar = nectivory, plantparts = plant part consumption, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.....	119
4.16	Logistic Regression nomadism composite model for South African birds located in lagoon habitats. Edge = distance to the closest edge of a body mass aggregation, foragerich = forage richness, habitatrich = habitat richness	120
4.17	Logistic Regression nomadism composite model for South African birds located in wetland habitats. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, ground = ground substrate, terrinverts = terrestrial invertebrate consumption.....	121
5.1	The number of body mass aggregations and species per habitat within South African bird species, including and excluding aquatic species. The data are the result of Bayesian classification and regression tree analysis of South African bird species	137
5.2	Grassland Logistic Regression model results of South African bird species. The percentage of declining species is 12%. Models a value of 10% the highest ranked model (bold) are considered plausible explanatory models for decline within South African bird species. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness	138

List of Tables (Continued)

- 5.3 Woodland Logistic Regression model results of South African bird species. The percentage of declining species is 6%. Models a value of 10% the highest ranked model (bold) are considered plausible explanatory models for decline within South African bird species. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness139
- 5.4 Wetland Logistic Regression model results of South African bird species. The percentage of declining species is 10%. Models a value of 10% the highest ranked model (bold) are considered plausible explanatory models for decline within South African bird species. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness140
- 5.5 Agricultural Logistic Regression model results of South African bird species. The percentage of declining species is 5%. Models a value of 10% the highest ranked model (bold) are considered plausible explanatory models for decline within South African bird species. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness.141
- 5.6 Lagoon Logistic Regression model results of South African bird species. The percentage of declining species is 13%. Models a value of 10% the highest ranked model (bold) are considered plausible explanatory models for decline within South African bird species. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness142
- 5.7 Karoo Logistic Regression model results of South African bird species. The percentage of declining species is 3%. Models a value of 10% the highest ranked model (bold) are considered plausible explanatory models for decline within South African bird species. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness143

List of Tables (Continued)

5.8	Savanna Logistic Regression model results of South African bird species. The percentage of declining species is 6%. Models a value of 10% the highest ranked model (bold) are considered plausible explanatory models for decline within South African bird species. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness	144
5.9	Logistic Regression composite decline model for South African birds located in grassland habitats. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, habitatrich = habitat richness, substratumrich = substrate richness	145
5.10	Logistic Regression composite decline model for South African birds located in woodland habitats. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation	146
5.11	Logistic Regression composite decline model for South African birds located in wetland habitats. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness.....	147
5.12	Logistic Regression composite decline model for South African birds located in agricultural habitats. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness	148
5.13	Logistic Regression composite decline model for South African birds located in lagoon habitats. Foodrich = food richness, foragerich = forage richness, substratumrich = substrate richness	149
5.14	Logistic Regression composite decline model for South African birds located in the Karoo ecosystem. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness	150
5.15	Logistic Regression composite decline model for South African birds located in savanna habitats. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation	151

LIST OF FIGURES

1.1	A representation of resources within different spatial and temporal scales (Gunderson and Holling 2002). Events at a small temporal and spatial scale, such as a breeze, and events with large temporal and spatial scales, such as climate change, represent different temporal and spatial scales where resources may be located	2
1.2	A hypothetical representation of organisms distributed throughout a discontinuous distribution of resources within an environment as predicted by the Textural Discontinuity Hypothesis. Organisms are represented by spheres, the diameter of which indicates body mass, and resources are represented by blocks. Each sphere and block set represents a different temporal spatial scale	3
1.3	A representation of potential aggregations within a body mass distribution of a taxon of vertebrates within an ecosystem. Grey bars represent individual aggregations of species with similar body size and black bars within grey bars represent edge species	5
1.4	An aggregation of species with similar body masses. Here species exhibit perfect spacing; thus the variance in distances between adjacent species is low (zero)	7
2.1	A simplified representation of scales of structure and processes within arboreal forests (Peterson et al. 1998). Dispersal, home range, and food choice of animals of different size correspond to different scales of process and structure in the system	15
2.2	A hypothetical representation of the discontinuous distribution of organisms relative to the discontinuous distribution of resources within an environment, as predicted by the Textural Discontinuity Hypothesis. Organisms are represented by spheres, the diameter of which indicates body mass, and resources are represented by blocks. Each sphere and block set represents a different temporal spatial scale	16
2.3	An aggregation of species with similar body masses. Here species exhibit perfect spacing; thus the variance in distances between adjacent species is low (approaching zero)	17
2.4	Histogram of the variance of distances between species within aggregations of all ecosystems and habitats of the South African bird dataset	23

List of Figures (Continued)

2.5	A hypothetical representation of the data describing high variance within a body mass aggregation. Species are spaced irregularly within a body mass aggregation creating uneven variance among species	37
3.1	A representation of resources within different spatial and temporal scales (Gunderson and Holling 2002). Events at a small temporal and spatial scale, such as a breeze, and events with large temporal and spatial scales, such as climate change, represent different temporal and spatial scales in which resources may be located	43
3.2	A hypothetical representation of organisms distributed throughout a discontinuous distribution of resources within an environment as predicted by the Textural Discontinuity Hypothesis. Organisms are represented by spheres, the diameter of which indicates body mass, and resources are represented by blocks. Each sphere and block set represents a different temporal spatial scale	44
3.3	A representation of potential aggregations within a body mass distribution of a taxon of vertebrates from an ecosystem. Grey bars represent individual aggregations of species with similar body size and black bars within grey bars represent edge species	45
4.1	A representation of resources within different spatial and temporal scales (Gunderson and Holling 2002). Events at a small temporal and spatial scale such as a thunderstorm, and events with large temporal and spatial scales such as climate change, represent different temporal and spatial scales in which resources may be located	87
4.2	A hypothetical representation of organisms distributed throughout a discontinuous distribution of resources within an environment as predicted by the Textural Discontinuity Hypothesis. Organisms are represented by spheres, the diameter of which indicates body mass, and resources are represented by blocks. Each sphere and block set represents a different temporal spatial scale	89
4.3	A representation of potential aggregations within a body mass distribution of a taxon of vertebrates from an ecosystem. Grey bars represent individual aggregations of species with similar body size and black bars within grey bars represent edge species	90

List of Figures (Continued)

- 5.1 A representation of structures and processes within different spatial and temporal scales (Gunderson and Holling 2002). Events at a small temporal and spatial scale such as a thunderstorm, and events with large temporal and spatial scales such as climate change, represent different temporal and spatial scales in which resources may be located129
- 5.2 A hypothetical representation of organisms distributed throughout a discontinuous distribution of resources within an environment as predicted by the Textural Discontinuity Hypothesis. Organisms are represented by spheres, the diameter indicates body mass, and resources are represented by blocks. Each sphere and block set represents a different temporal spatial scale.....130
- 5.3 A representation of potential aggregations within a body mass distribution of a taxon of vertebrates from an ecosystem. Grey bars represent individual aggregations of species with similar body size and black bars within grey bars represent edge species131

PREFACE

Tables, figures, and analyses may be redundant in chapters 2-5. The information within these chapters is intended to be a separate journal article and thus require the information to stand alone.

CHAPTER I

OVERVIEW

Ecology as a formal science has existed for roughly a century and is relatively new compared to other sciences, for example chemistry, physics, and mathematics - which have each existed for several centuries longer (McIntosh, 1988; Partington, 1965; Hall, 2002; Boyer, 1991). Because scientists have formally studied the interactions of organisms with their environment for such a brief period of time there are many more phenomena to still be discovered. These new phenomena may be contradictory or dissimilar to the more traditional ideas in ecology. Some of the traditional ideas that helped evolve ecology were poorly demonstrated due to spatial and temporal constraints; but the conclusions made are often assumed to be true and applicable in all ecological systems (Wiens, 1989). For example, in 1988 scientists analyzed over 100 field experiment plot sizes and discovered that half were no larger than 1 meter in diameter (Kareiva, 1988).

The Textural Discontinuity Hypothesis represents a potential paradigm shift in the way we view ecological systems. Correctly interpreted and applied, the hypothesis may reveal critical aspects regarding species interactions even when provided little information about a particular species. The Textural Discontinuity Hypothesis stems from complex systems analysis and posits that the resources in an ecological system are discontinuously distributed across temporal and spatial scales (Holling, 1986). Within a forest system for example (Figure 1.1), different resources exist, each occupying a different spatial and temporal scale (Gunderson & Holling, 2002). A tree crown has a

higher turnover rate and is relatively small when compared to a forest stand. Each scale is discrete, thus creating aggregations of resources, based upon the temporal availability and spatial extent of resources (Burrough, 1981).

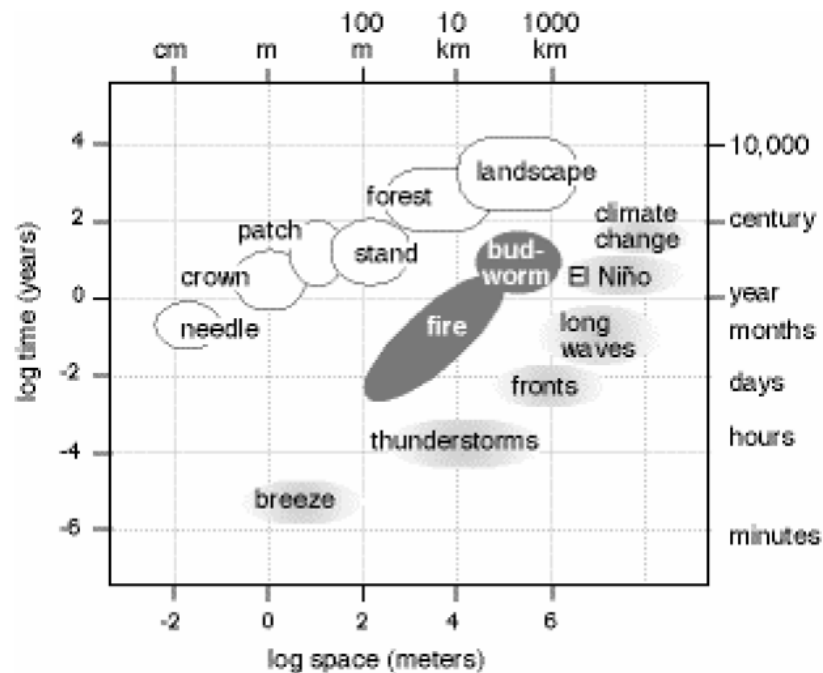


Figure 1.1 A representation of resources within different spatial and temporal scales (Gunderson and Holling 2002). Events at a small temporal and spatial scale, such as a breeze, and events with large temporal and spatial scales, such as climate change, represent different temporal and spatial scales where resources may be located.

There is probably no central tendency that pulls resources into aggregations at different scales; aggregations within the context of the Textural Discontinuity Hypothesis are merely groupings of resources segregated by scale. The aggregations of resources are hypothesized to be the result of a small number processes and structures occurring within different temporal and spatial scales (Carpenter & Leavitt, 1991; Holling et al. 1995).

Organisms take advantage of resources within a landscape, but an organism is limited in the resources it can utilize based on how it perceives its environment (Milne et al. 1989; Holling, 1992; Peters, 1983). Within ecological systems smaller organisms, a mouse for example, will view and utilize resources at a scale relative to its size, and an elephant will do likewise, utilizing resources relative to its own scale of perception (Schmidt-Nielsen, 1984; Peterson, et al. 1998). Thus, just as resources are aggregated, organisms too are aggregated into different temporal and spatial scales dictated by the resources available within a landscape (Figure 1.2).

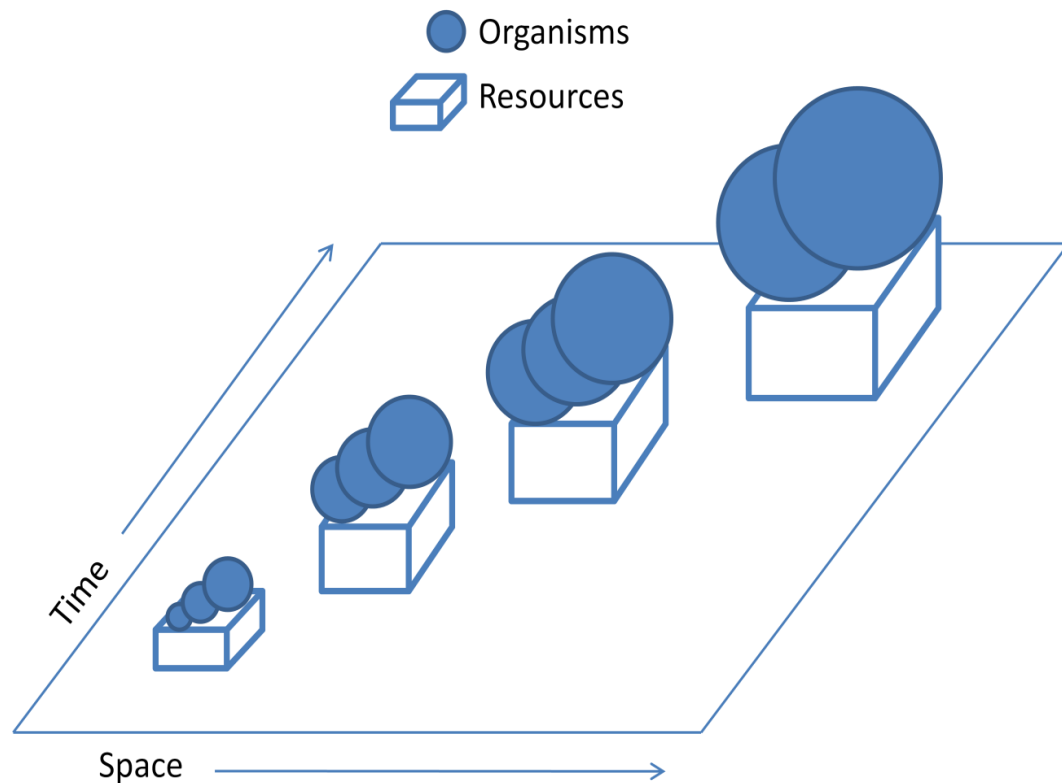


Figure 1.2 A hypothetical representation of organisms distributed throughout a discontinuous distribution of resources within an environment as predicted by the Textural Discontinuity Hypothesis. Organisms are represented by spheres, the diameter of which indicates body mass, and resources are represented by blocks. Each sphere and block set represents a different temporal spatial scale.

The aggregation to which a particular species belongs to within its landscape is determined by the species' average body mass (Holling, 1992). An organism's body mass is allometric to attributes such as metabolic rates, food consumption, life expectancy and is indicative of how that particular organism interacts with its environment (Peters, 1983). The absence of body masses within species distributions is reflective of gaps in resource availability found within the landscape, and discontinuous body mass distributions are assumed to reflect discrete scales of resource distributions (Holling, 1992; Holling et al., 1996).

Other scientist have added to the framework of the Textural Discontinuity Hypothesis by further hypothesizing that resources located at the edges of resource aggregations are disproportionally more variable in their availability when compared to resources towards the center of resource aggregations (Allen et al. 1999). These scientists posit that the transitions between aggregations of resources are transitions between scales, where resource availability is hypothesized to be highly variable (Wiens, 1989; Allen et al. 1999). If organisms reflect aggregations of resources at different temporal and spatial scales, and thus also form aggregations within a landscape, then organisms located at the edges of organism aggregations may exhibit more variability in their life history as well (Figure 1.3) (Allen et al. 1999; Allen & Saunders, 2002; Allen & Saunders, 2006). That is, species located at the edges of aggregations may be prone to migration, nomadism, and species decline because the resources they depend on are highly variable in their availability and species either seek out resources when the resources they depend on are not available, i.e. migrate or become nomadic, or their populations decline.

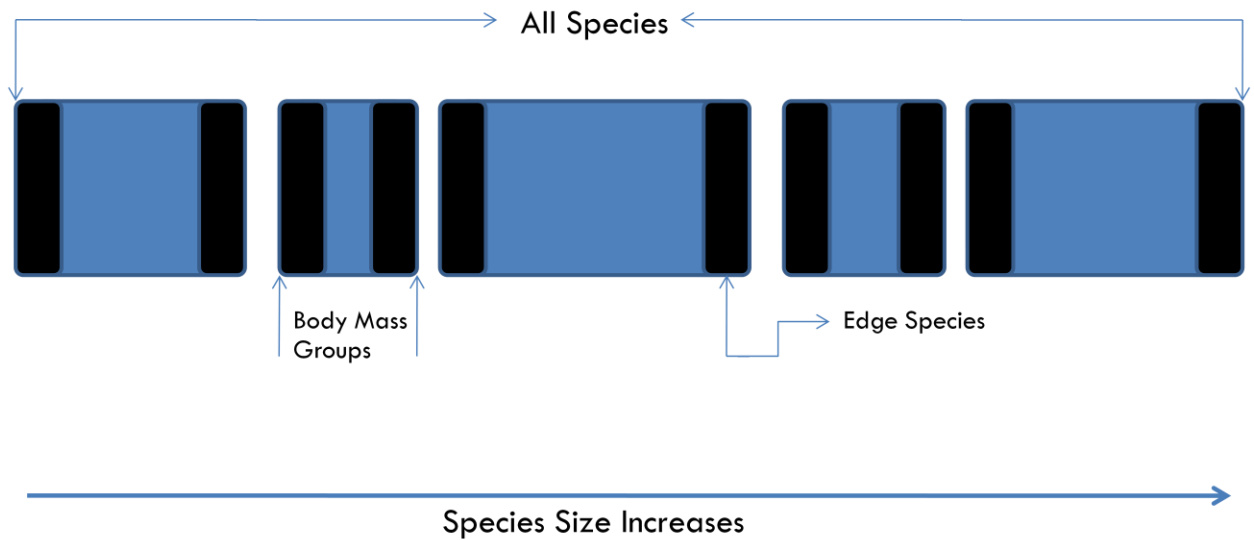


Figure 1.3 A representation of potential aggregations within a body mass distribution of a taxon of vertebrates within an ecosystem. Grey bars represent individual aggregations of species with similar body size and black bars within grey bars represent edge species.

The ideas behind the Textural Discontinuity Hypothesis and variable resource availability within the context of the Textural Discontinuity Hypothesis have been used to examine species within several different ecological systems. The phenomena examined using the Textural Discontinuity Hypothesis are complex, however, and are not always attributed to only the position of species within resource aggregations. Allen and Saunders (2002) reported that nomadic bird species in an Australian climate ecosystem tended to occur at the edges of species aggregations, feed on nectar, and be large. Woinarski (2006), however, concluded that nomadic characteristics exhibited by birds are the result of diet and not a species' location within a resource aggregation. Allen and Saunders (2006) reanalyzed their work and that of Woinarski and came to the same conclusion of their original paper, refuting Woinarski. This example indicates that

species' phenomena can be complex; single attributes such as diet may not be the only explanation for certain observed species' characteristics.

In 1999 scientists examined patterns of extinction and invasion in different taxa in south Florida relative to the species' position within body mass aggregations (Allen et al. 1999). Extinct and invasive species were frequently located at the edges of species aggregations. The authors hypothesized that the edges of species aggregations are transition zones “analogous to phase transitions” where resources are highly variable in their availability. Because of the variability of resource availability species located at the edges of aggregations tended to become extinct or be invasive (Allen et al. 1999).

This thesis consists of four analyses involving the Textural Discontinuity Hypothesis utilizing South African bird species. The data include detailed information for over 700 bird species and utilize the most comprehensive dataset for birds in the continent of Africa. The data were collected by Austin Roberts and colleagues from the Percy Fitzpatrick Institute in Cape Town, and donated for this study by Graeme Cumming, also from the Percy Fitzpatrick Institute in Cape Town. For these analyses the South African bird data set is segregated into 14 non-exclusive habitat categories, bird species within each habitat type are numerically ordered based on body mass, then assigned to aggregations within each habitat type based on where they lay within the array of body masses.

My first chapter analyzes South African habitats/ecosystems for body mass aggregations and then examines the underlying structure within species body mass aggregations; how species within an aggregation are distributed relative to each other. The spacing patterns between individuals within an aggregation may yield clues with

regard to how species interact with each other and their environment. Competition within species aggregations may be responsible for observed spacing of individuals within aggregations; i.e. where species are located relative to each other along a body mass axis (Peterson et al. 1998). I hypothesize that species within a body mass aggregation will more evenly distribute themselves within a body mass aggregation, that is, I expect species within a given size class to have similar variance in the distance separating species in terms of body mass (Figure 1.4). This hypothesis arises from the assumption that species within an aggregation interact with each other more strongly relative to species interactions between aggregations, this high degree of interaction coupled with similarly sized species body masses may result in even spacing within aggregations.

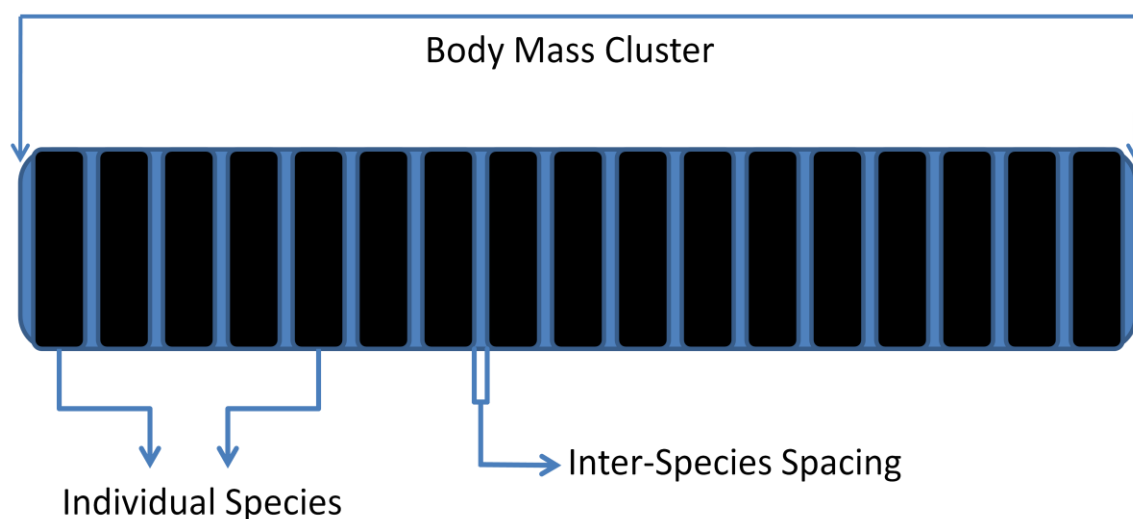


Figure 1.4 An aggregation of species with similar body masses. Here species exhibit perfect spacing; thus the variance in distances between adjacent species is low (zero).

My second chapter examines migratory bird species within the framework of the Textural Discontinuity Hypothesis. Migratory bird species are defined as bird species that travel predictably in response to seasonal changes (Berthold, 2001). The causes of migration, though, are still debated (Rappole et al. 2003). For example, one analysis concluded that Neotropical forest birds were mainly frugivorous/insectivorous (Levey & Stiles, 1992). While recent analysis from Boyle and Conway (2007) indicate that bird species migrate as a response to increased scarcity in resources; and that there are no particular resource types that, when becomes scarce, triggers a migratory response.

My third chapter investigates predictors of nomadism in birds. Nomadic species are species that lack a permanent location, or home, because they seek out and follow non-permanent resources (Dean, 1997). Resources utilized by nomadic species are highly variable and can change both temporally and spatially in their availability (Sinclair, 1984). If species aggregations reflect aggregations of resources, and aggregations of resources have more variable resources located at the edges, then nomadic bird species should be located more frequently at the edges of species aggregations due to highly variable resource availability.

The fourth chapter analyzes predictors of species decline. Some ecological literature suggests that species in decline have larger body masses (Cardillo et al. 2005; Fisher & Owens, 2004). This potential bias towards large species is evident in the International Union for Conservation of Nature and Natural Resources' Red List. Recent literature, however, challenges this traditional approach to the study of species decline by examining populations of species within the context of the Textural Discontinuity Hypothesis (Allen et al. 1999; Forsys & Allen, 1999). I hypothesize highly variable

resource availability reduces the probability of species located closer to the edges of species aggregations to avoid species decline.

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CHAPTER II

SOUTH AFRICAN BIRD SPECIES AND THE STRUCTURE OF THEIR BODY MASS DISTRIBUTIONS

INTRODUCTION

Knowledge regarding interactions among species and their environments is crucial for making management, political and scientific decisions. The knowledge we possess regarding these interactions is limited. Some of the traditional ideas of ecology were prone to spatial and temporal constraints; yet the conclusions made are often assumed to be true and applicable in all ecological systems (Wiens, 1989). For example, a 1988 analysis of over 100 field experimental plots discovered that half were no larger than one meter in diameter (Kareiva, 1988). Experiments conducted at such small spatial extents may not be accurate when applied at larger scales.

The Textural Discontinuity Hypothesis attempts a cross-scale understanding of ecosystem structure and process. (Holling, 1992; Allen et al. 1999; Allen & Saunders, 2002; Allen & Saunders, 2006) Analyzing organisms within the context of the Textural Discontinuity Hypothesis may provide a paradigm shift in the way ecological systems are conceptualized. The hypothesis may reveal critical aspects regarding species interactions even with little information about a particular species. The Textural Discontinuity Hypothesis stems from complex systems science and posits that the resources in an ecological system are discontinuously distributed across different temporal and spatial scales (Holling, 1986). Within an ecological system different resources exist, each occupying a different spatial and temporal scale (Gunderson & Holling, 2002) due to the scale-specific effects of a limited number of key abiotic and biotic processes (Figure 2.1).

The scale-specific effects of key processes create a discontinuous template of resources for animals to exploit (Burrough, 1981; Wiens, 1989; Holling, 1992).

Organisms take advantage of the resources within a landscape, but organisms are limited in the resources they can utilize based upon their perception of the environment (Schmidt-Nielsen 1984; Milne et al. 1989; Holling, 1992; Peters, 1983). Within ecological systems smaller organisms such as mice will view and utilize resources at a scale relative to their size, and elephants will do likewise, utilizing resources relative to their own scale of perception (Peterson et al. 1998). This limitation in resource acquisition is hypothesized to reflect aggregations of resources within the landscape (Holling, 1996; Peterson et al. 1998). Thus, just as resources are aggregated, organisms too are aggregated into different temporal and spatial scales dictated by the resources available within a landscape (Figure 2.2; Holling, 1996).

The aggregation to which a particular species belongs within a given ecosystem is determined by the species' average body mass (Holling, 1992). An organism's body mass is allometric to attributes such as metabolic rates, food consumption and life expectancy, and is indicative of how that particular organism interacts with its environment (Peters, 1983). The absence of body masses within species distributions is reflective of gaps in resource availability found within the landscape, and are assumed to reflect transitions between discrete scales of resource distributions (Holling, 1992; Holling, et al., 1996).

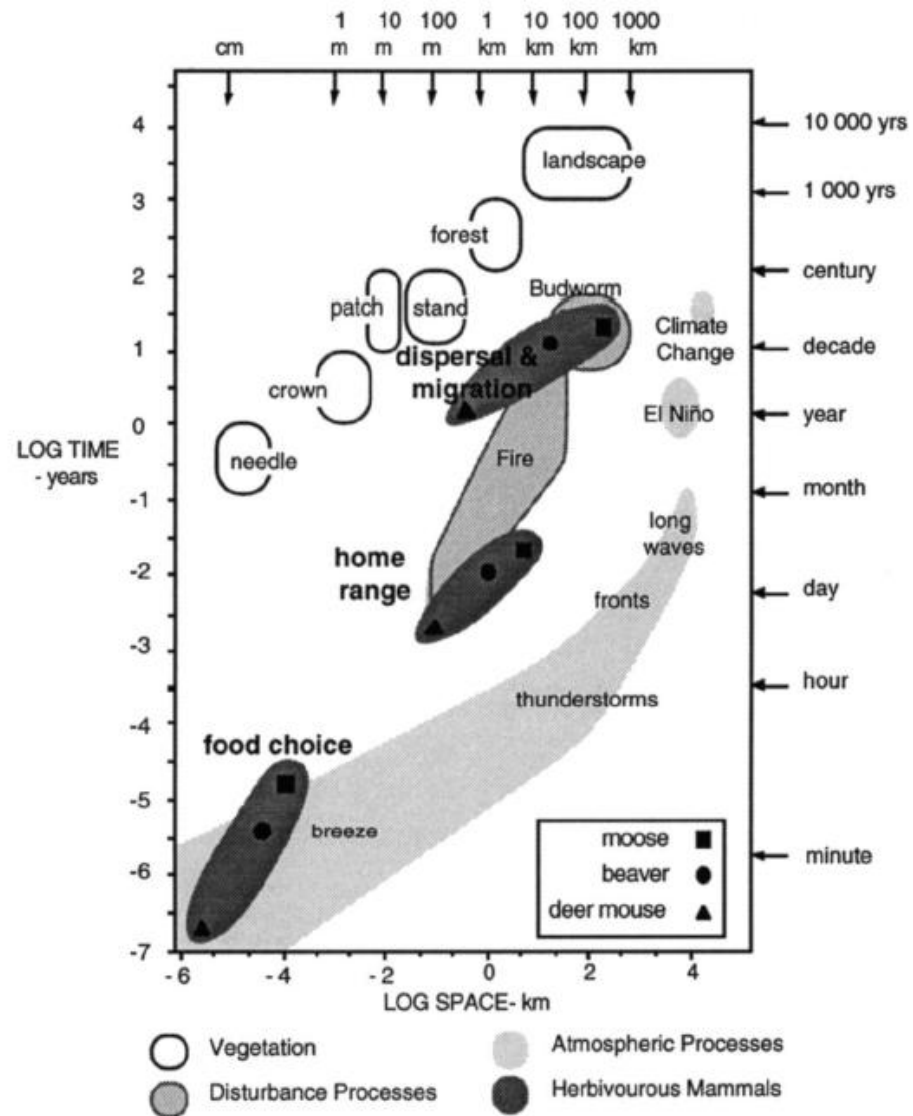


Figure 2.1 A simplified representation of scales of structure and processes within arboreal forests (Peterson et al. 1998). Dispersal, home range, and food choice of animals of different size correspond to different scales of process and structure in the system.

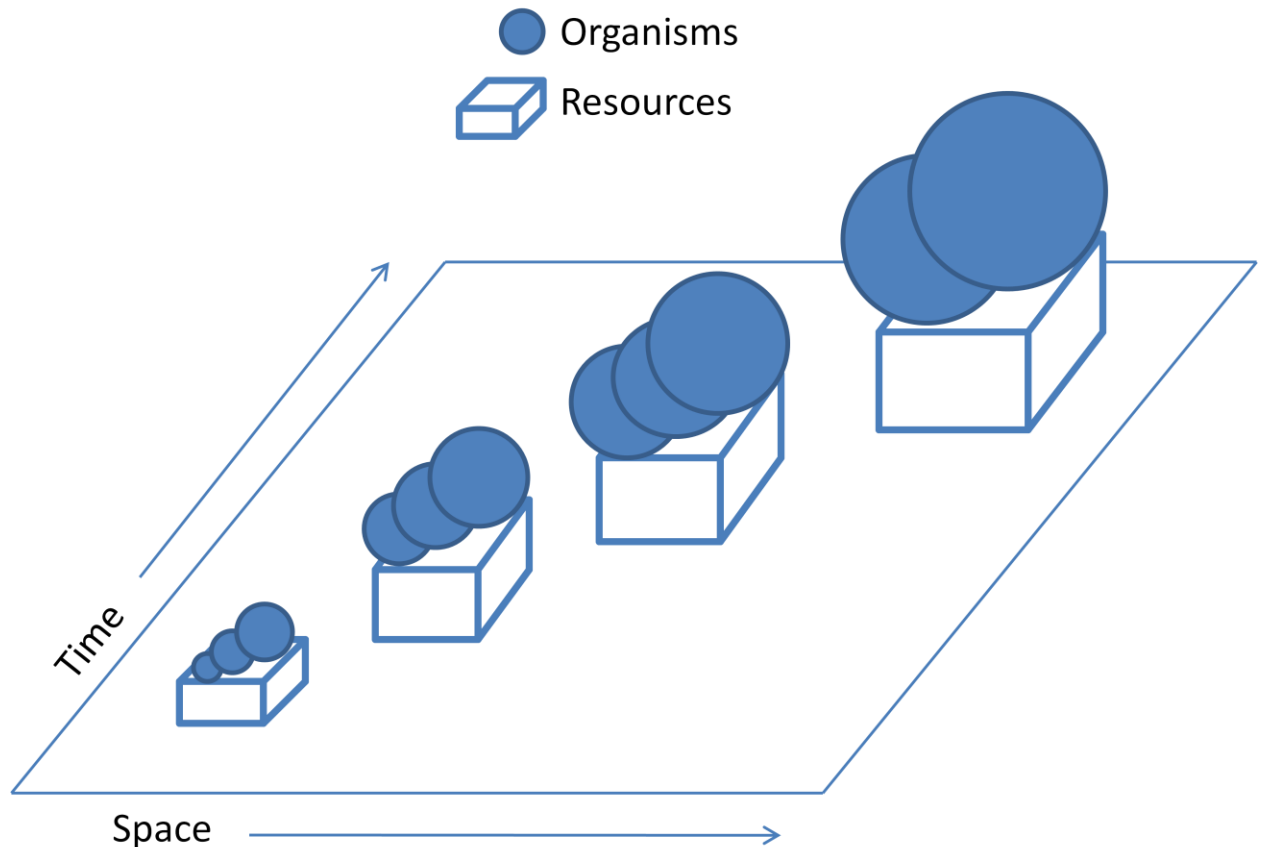


Figure 2.2 A hypothetical representation of the discontinuous distribution of organisms relative to the discontinuous distribution of resources within an environment, as predicted by the Textural Discontinuity Hypothesis. Organisms are represented by spheres, the diameter of which indicates body mass, and resources are represented by blocks. Each sphere and block set represents a different temporal spatial scale.

The spacing between individuals within an aggregation could yield clues about how species interact with each other and their environment. Competition within species aggregations may be responsible for observed spacing of individuals within aggregations; i.e. where species are located relative to each other. Species composition within an aggregation may be the result of morphological overdispersion, where species are morphologically more different from one another than one would expect by chance

(Moulton & Pimm, 1983; Lockwood et al. 1993). Overdispersed morphological differences may space species within an aggregation evenly due to competition.

If species are indeed morphologically overdispersed along a body mass axis, the analysis of spacing within aggregations may provide insight into the forces structuring the assemblages of species communities. I hypothesize that species within a body mass aggregation will more evenly distribute themselves within a body mass aggregation than expected by chance (Figure 2.3). This hypothesis arises from the assumption that species within an aggregation interact with each other more strongly or frequently relative to species interactions between aggregations; and that this strong interaction creates competition among species which in turn creates even spacing among species within an aggregation.

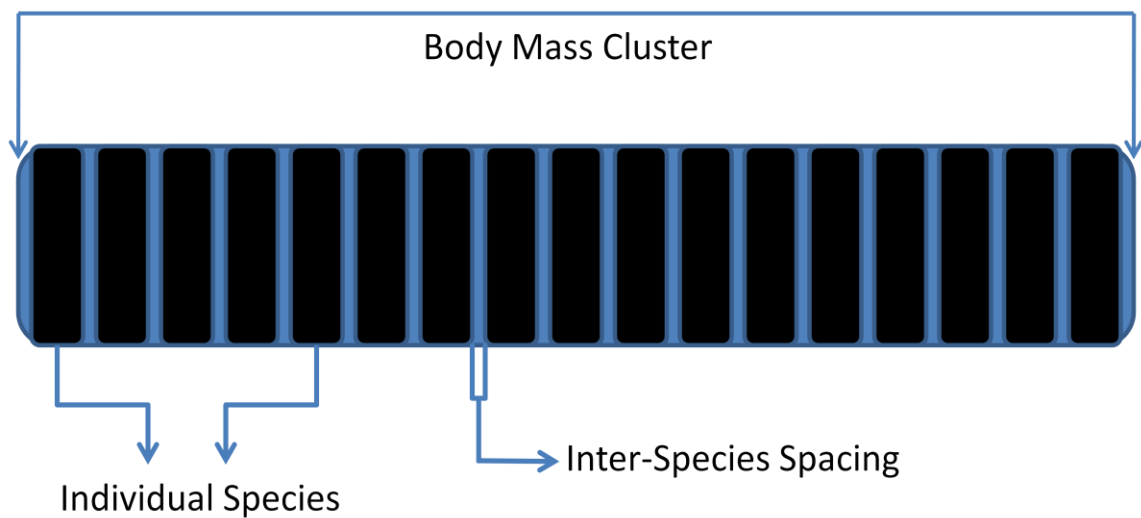


Figure 2.3 An aggregation of species with similar body masses. Here species exhibit perfect spacing; thus the variance in distances between adjacent species is low (approaching zero).

To test this hypothesis I analyzed South African bird species data. The data include more than 700 South African bird species and represent the most comprehensive collection of South African bird species to date. The data were independently collected by Austin Roberts and associates from the Percy Fitzpatrick Institute in Cape Town, and donated for this study by Graeme Cumming also from the Percy Fitzpatrick Institute in Cape Town. I examined the Robert's data set for discontinuities within bird species distributions according to habitats and ecosystems. I then compared results including and excluding aquatic and non-aquatic bird species to determine if any differences in these distributions existed. Finally, I analyzed the variance among species within body mass aggregations by comparing observed aggregations with generated aggregations from a unimodel null.

METHODS

South African bird species lacking sufficient descriptive data (body mass, food consumption, habitat usage etc.) associated with them were removed from the Robert's dataset (n=10). Birds were grouped into habitat/ecosystem-specific assemblages. The Robert's dataset provides four categories to describe a bird's habitat use: main, secondary, occasional use, and not used habitat/ecosystem. In building habitat/ecosystem specific assemblages I included as "present" in a habitat/ecosystem species categorized by Roberts as "main" or "secondary" users of that habitat/ecosystem. The habitats/ecosystems analyzed were agricultural, Fynbos, grassland, Karoo, lagoon, Namib, savanna, semi-arid, wetland, and woodland. The Fynbos, Karoo, and Namib are best described as ecosystems; the others are habitats.

AGGREGATION ANALYSIS

The body masses of species for each ecosystem/habitat were arranged from smallest to largest and log transformed. I used Bayesian Classification And Regression Trees (BCART) to test for and determine the number of aggregations of species body masses within each habitat. BCART examines numerical data for aggregations by creating combinations of observations in order to calculate the largest log integrated likelihood for all combinations of data entered (Chipman et al. 1998). One million iterations of BCART were performed for each habitat to calculate aggregations of species.

I performed two separate analyses one including aquatic species and the other excluding aquatic species. In previous studies aquatic species were excluded from

discontinuity analysis because the food webs of aquatic species are compartmentalized from the surrounding food web (Pimm & Lawton, 1980; Allen et al. 1999). I performed the two different analyses to test the hypothesis that aquatic species have little influence on the body mass distributions. To remove aquatic species from the second set of models for each habitat I removed species that used freshwater invertebrates as a main or secondary food source and species that utilized aquatic substrate. The data sets including aquatic species and excluding aquatic species were then visually inspected for differences.

VARIANCE ANALYSIS

After determining species aggregations, the distance of a species to its next closest neighbor in the species aggregation was calculated. The variance in distances between adjacent species was then calculated for each body mass aggregation. Aggregations consisting of three or fewer species were too small for variance analysis; three species aggregations would have resulted in a variance of only two distances between species. A Pearson Correlation test was used to test for a correlation between aggregation variance and the number of species within an aggregation.

Observed variances were compared against the output of 1,000 simulations drawn from a unimodel null (Crystal Ball, 2009). Simulated aggregations were analyzed for distance between species and the variance between those distances within an aggregation, just as the original data was. Simulated data were drawn from a discrete uniform random distribution with the upper and lower limits constrained by the largest

and smallest observations in the observed data. A discrete uniform random distribution allows an equal chance for each simulated observation to be drawn within each iteration.

Each aggregation's observed variance was ranked among the 1,000 simulated aggregation's variances; where the 1,000th observation represented the simulated aggregation with the largest amount of variance, and the 1st observation represented the simulated aggregation with the smallest amount of variance. If the actual observed variance was between 1 and 500 it was in the lower half of the distribution, and if the actual observed variance was between 501 and 1000 it was in the upper half of the distribution.

If the observed variances fell in the lower half of the distribution of simulated variances ,i.e., inter-species spacing was more even than expected, the hypothesis that competition drives within aggregation structure would be supported. A binomial test was used to test for variances occurring above or below 500 more often than expected by chance.

RESULTS

AGGREGATION ANALYSIS

Discontinuous distributions of body masses were identified for each ecosystem and habitat type (Table 2.1). The numbers of aggregations present when aquatic species were included in analysis ranged from 4 to 12. The numbers of aggregations present when aquatic species were not included in analysis ranged from 5 to 12. Five habitats contained aquatic species. The percentage of aquatic species removed from each of these five habitats ranged from 1.4% (Karoo) to 52% (Lagoon). The aquatic habitats of lagoon and wetland contained the highest percentage of aquatic species. The differences between aggregations identified with aquatic and non-aquatic species was minimal. Even when almost half of the species are aquatic and thus removed (Lagoon) for analysis there is at most one fewer aggregation present in the ecological system. Thus, here after I only present the results of analyses with aquatic species excluded.

VARIANCE ANALYSIS

Although it appears that most aggregations had little variance among species (Figure 2.4) twenty eight aggregations were ranked below the 50th percentile and 38 were ranked above the 50th percentile (Tables 2.2 – 2.12). Fourteen aggregations were too small for analysis. Assuming an equal chance of having a variance below or above the 501th generated aggregation, the probability of 38 aggregations ranked above the 501th generated aggregation is 0.046. There was no correlation between observed variance in species spacing within aggregations and the number of species within an aggregation, $r = -0.191$ ($p = 0.124$).

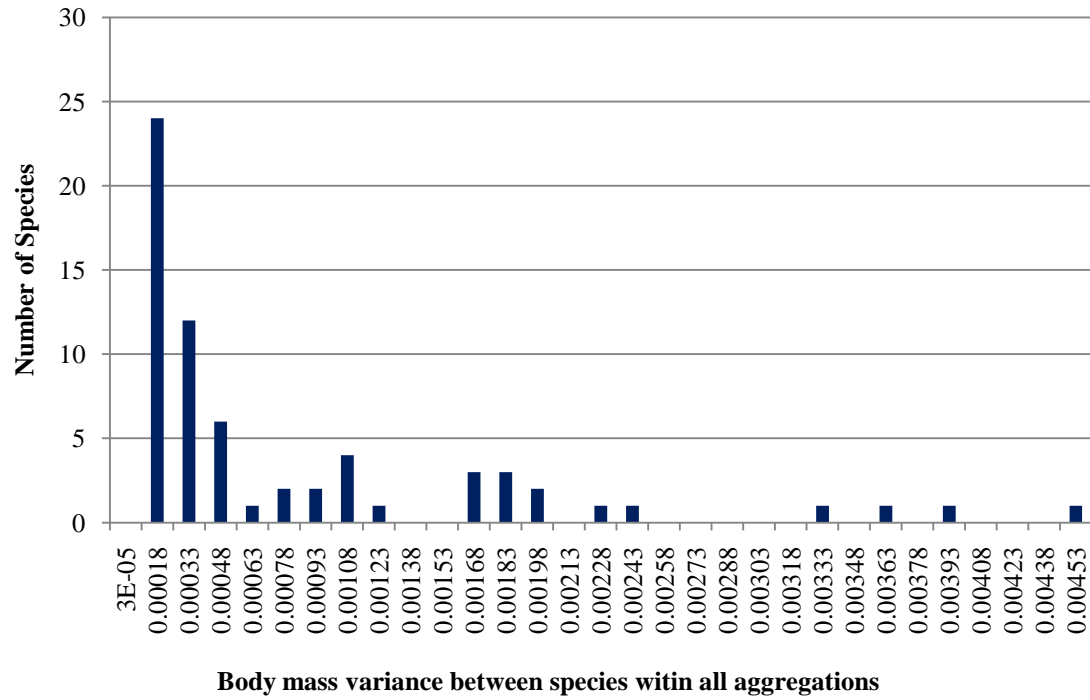


Figure 2.4 Histogram of the variance of distances between species within aggregations of all ecosystems and habitats of the South African bird dataset.

Table 2.1 The number of body mass aggregations in South African bird species by habitat and ecosystem, including and excluding aquatic species. The number of aggregations was determined by Bayesian Classification And Regression Tree analyses.

Habitat Type	Number of aggregations including aquatic species	Number of species including aquatic species	Number of aggregations excluding aquatic species	Number of species excluding aquatic species
Fynbos	7	46	7	46
Karoo	7	70	7	69
Namib	5	19	5	19
Agricultural	10	152	10	145
Grassland	9	106	9	106
Lagoon	5	33	4	16
Savanna	12	214	12	214
Semi-Arid	6	34	6	34
Wetland	9	177	8	108
Woodland	11	254	12	251

Table 2.2 Variance in inter species spacing within aggregations in South African agricultural habitats. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation.

Aggregation Number	Aggregation Variance	Rank	n
1	0.00027	974	23
2	0.00012	1000	24
3	5.99×10^{-5}	185	23
4	0.00016	739	14
5	0.00012	172	16
6	0.00027	111	12
7	0.00024	370	12
8	0.00039	436	13
9	0.0032	821	5
10	Too small	-	3

Table 2.3 Variance in inter species spacing within aggregations in the South African Fynbos ecosystem. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation.

Aggregation Number	Aggregation Variance	Rank	n
1	0.00042	418	9
2	0.00031	905	13
3	0.00079	987	8
4	0.00027	308	7
5	Too small	-	2
6	0.0039	829	6
7	Too small	-	1

Table 2.4 Variance in inter species spacing within aggregations in South African grassland habitats. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation.

Aggregation Number	Aggregation Variance	Rank	n
1	0.00036	540	12
2	0.00021	685	13
3	5.84×10^{-05}	273	28
4	0.00012	584	18
5	0.00074	765	9
6	0.0016	902	5
7	0.00070	942	9
8	0.0019	702	7
9	0.0024	672	5

Table 2.5 Variance in inter species spacing within aggregations in the South African Karoo ecosystem. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation.

Aggregation Number	Aggregation Variance	Rank	n
1	0.00097	978	14
2	0.000312	928	15
3	0.00028	952	19
4	Too small	-	3
5	0.0044	105	4
6	0.0022	930	11
7	Too small	-	3

Table 2.6 Variance in inter species spacing within aggregations in South African lagoon habitats. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation.

Aggregation Number	Aggregation Variance	Rank	n
1	0.0016	464	7
2	Too small	-	1
3	0.0018	656	5
4	Too small	-	3

Table 2.7 Variance in inter species spacing within aggregations in the South African Namib ecosystem. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation.

Aggregation Number	Aggregation Variance	Rank	n
1	Too small	-	3
2	0.0004	390	10
3	Too small	-	2
4	Too small	-	2
5	Too small	-	2

Table 2.8 Variance in inter species spacing within aggregations in South African semi-arid habitats. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation.

Aggregation Number	Aggregation Variance	Rank	n
1	0.0016	868	9
2	0.001	982	11
3	0.00047	317	8
4	Too small	-	1
5	Too small	-	3
6	Too small	-	2

Table 2.9 Variance in inter species spacing within aggregations in South African savanna habitats. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation.

Aggregation Number	Aggregation Variance	Rank	n
1	0.00096	974	10
2	0.00021	996	21
3	3.85×10^{-5}	184	32
4	5.55×10^{-5}	408	27
5	0.00014	724	20
6	0.0001	772	27
7	0.00014	452	13
8	0.00014	375	19
9	0.00021	275	12
10	8.18×10^{-5}	265	12
11	0.00048	511	11
12	.00015	893	10

Table 2.10 Variance in inter species spacing within aggregations in South African wetland habitats. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation.

Aggregation Number	Aggregation Variance	Rank	n
1	0.00021	801	26
2	5.83×10^{-5}	195	26
3	0.00011	689	23
4	0.0004	259	5
5	0.0017	990	7
6	0.0012	495	9
7	0.0017	689	8
8	0.0036	395	4

Table 2.11 Variance in inter species spacing within aggregations in South African woodland habitats. Aggregation variance is a measure of the spread of species within body mass aggregations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 - 1000 indicates high variance within the actual body mass aggregation.

Aggregation Number	Aggregation variance	Rank	n
1	0.00019	848	9
2	6.35×10^{-5}	811	28
3	3.1×10^{-5}	354	35
4	6.32×10^{-5}	346	24
5	4.55×10^{-5}	321	31
6	3.81×10^{-5}	40	27
7	8.05×10^{-5}	970	31
8	8.07×10^{-5}	129	20
9	0.00012	76	18
10	0.00085	966	13
11	0.00099	792	11
12	0.0019	795	4

Table 2.12 Summation of body mass aggregation rank against Monte Carlo simulations. Rank is based on 1000 Monte Carlo simulations of the actual data; a rank of 1 – 500 indicates low variance and a rank of 501 – 1000 indicates high variance within the actual body mass aggregation. Body mass aggregations were too small for the analysis if they contained three or fewer species' body masses.

Habitat Type	Number of Aggregations Below 500	Number of Aggregations Above 500	Number of Too Small Aggregations
Agricultural	5	4	1
Fynbos	2	3	2
Grassland	1	8	0
Karoo	1	4	2
Lagoon	1	1	2
Namib	1	0	4
Savanna	6	6	0
Semi-Arid	1	2	3
Wetland	4	4	0
Woodland	6	6	0
Total	28	38	14

DISCUSSION

Discontinuities in the body mass distributions of South African birds were detected within each ecosystem/habitat; these results support the Textural Discontinuity Hypothesis. Patterns of aggregations between data sets including and excluding aquatic species were similar, suggesting that aquatic species have little influence on the body mass assemblages of terrestrial species and reinforcing the findings of Pimm & Lawton (1980) that suggested aquatic species food webs are compartmentalized from terrestrial food webs.

Body mass aggregations were ranked above the 50th percentile of the null distribution more frequently than expected by chance ($p = 0.046$). This suggests that species spacing within body mass aggregations were more unevenly distributed than expected under a uniform random null (Figure 2.5). These data do not support the hypothesis that morphological overdispersion is occurring within body mass aggregations. The observed variances among species within body mass aggregations may occur if resources are not evenly distributed within body mass aggregations. Resources may be discontinuously distributed throughout the landscape forming aggregations of resources, but these may be aggregations of resources only when compared to surrounding highly variable resources; i.e. the resources outside of an aggregation may be so variable that the resources within an aggregation are less variable in comparison and thus organisms utilizing these resources form aggregations as well .

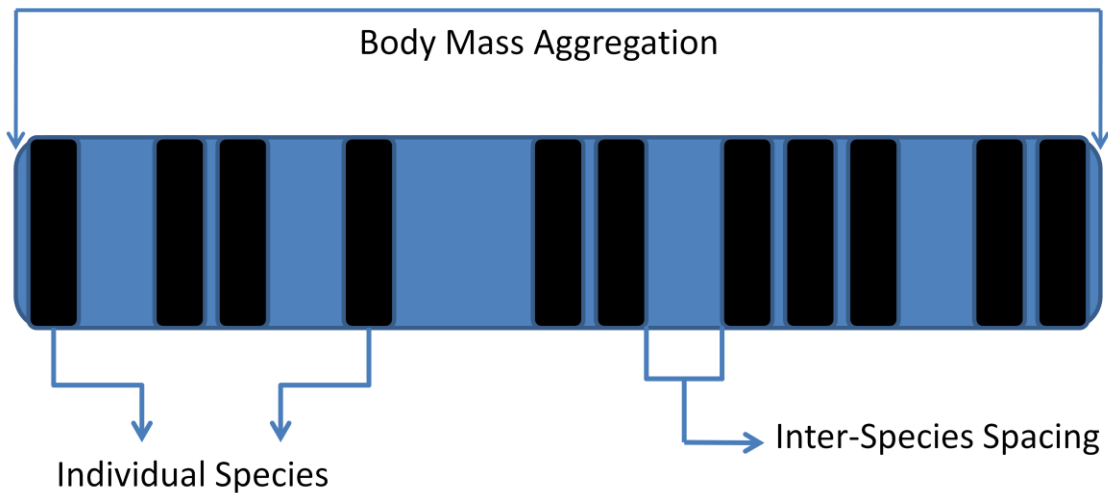


Figure 2.5 A hypothetical representation of the data describing high variance within a body mass aggregation. Species are spaced irregularly within a body mass aggregation creating uneven variance among species.

Competition for resources nonetheless may help structure the distribution of body masses within aggregations. Larger species may have the capacity to utilize more resource types than smaller species; larger species have developmental cycles where the young go through many different size changes, thus utilizing many resource types (May & MacArthur, 1972). Within the context of the Textural Discontinuity Hypothesis and competition the utilization of many resource types by larger species may set them apart in ecological space (within aggregations) more than smaller species who do not utilize as many resource types through development into adulthood. To test if this idea was applicable within body mass aggregations I divided each body mass into two halves (top and bottom) and calculated the variance between species in each half; top halves contained species with smaller body masses and bottom halves contained species with larger body masses. Only aggregations larger than five species were examined because

five or fewer created halves that only contained two species, and the difference between two species has no variance. Aggregations with an odd number of individuals were analyzed twice, each time placing the extra species in the top or bottom half of the aggregation.

Both when the odd numbered species were put in the top and bottom halves of body mass aggregations, the top halves were more variable in species composition ($p = <0.01$ top half and $p = 0.02$ bottom half). The data suggest that smaller species are more spread out within body mass aggregations than are larger species. These results are further reinforced by the fact that there was no correlation between the number of species within a body mass aggregation and the variance of the aggregation.

The ideas behind the Textural Discontinuity Hypothesis suggest that resources are distributed into aggregations within the environment; further scientific inquiry has suggested that species utilization of these resources create aggregations of species within ecological environments. Analysis of the dataset of South African bird species has shown that indeed these species aggregate according to bodymass. It is clear that species are discontinuously dispersed into body mass aggregations, but how the interactions between species affect within aggregation distributions, if at all, is unknown.

Morphological overdispersion is an unlikely candidate for the explanation of species distributions within body mass aggregations; species are not evenly spread out through body mass aggregations. The fact that smaller species tend to be dispersed more variably within body mass aggregations indicates that larger species undergoing a series of size transformations into adulthood is not an explanation for observed body mass aggregation variance. The observed variance within body mass aggregations may be the result of a

more complex set of interactions between species than analyzed here. This set of species interactions may include to some extent competition, but competition alone is insufficient in the explanation of observed species spacing within species aggregations.

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CHAPTER III

SOUTH AFRICAN MIGRATORY BIRD SPECIES AND THEIR LOCATION WITHIN DISCONTINUOUS AGGREGATIONS

INTRODUCTION

Migratory bird species travel in response to seasonal changes in resources (Berthold, 2001). The causes of migration, though, are still debated (Rappole et al. 2003). For example, one analysis concluded that migratory Neotropical forest birds were mainly frugivorous/nectivorous (Levey & Stiles, 1992). Recent analysis (Boyle & Conway, 2007), however, indicate that bird species migrate as a response to increased scarcity in resources; and that there are no particular resource types that, when become scarce, trigger a migratory response. Here I examine the phenomenon of avian migration utilizing the Textural Discontinuity Hypothesis.

The Textural Discontinuity Hypothesis posits that processes and structure within an ecological system, everything from a light breeze to a hurricane and from a twig to a tree, are discontinuously distributed into a distinct and limited number of temporally and spatially scales (Holling, 1986; Holling, 1992). For example, consider a forest system (Figure 3.1; Gunderson & Holling, 2002). A pine tree needle occupies little space and exists for a short duration of time when compared to the tree itself, or a stand of trees. Because each scale is discrete, aggregations of resources exist based upon the resources temporal availability and spatial extent (Holling, 1986; Holling, 1992).

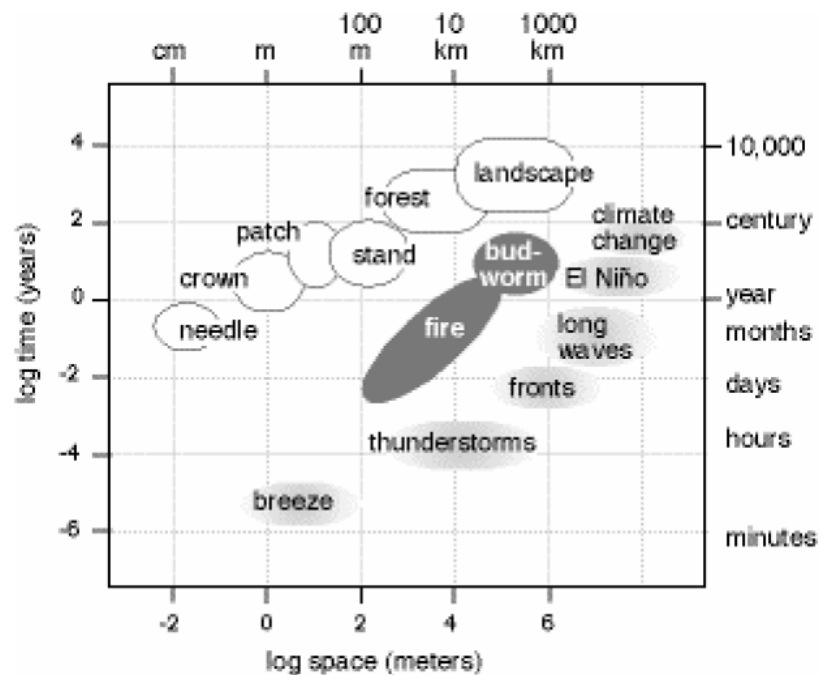


Figure 3.1 A representation of resources within different spatial and temporal scales (Gunderson and Holling 2002). Events at a small temporal and spatial scale, such as a breeze, and events with large temporal and spatial scales, such as climate change, represent different temporal and spatial scales in which resources may be located.

This aggregating of resources into different spatial and temporal scales is hypothesized to be the result of a small number of key assembling processes occurring at different temporal and spatial scales (Carpenter & Leavitt, 1991; Holling et al. 1995). Organisms within an ecosystem may be limited in the resources they use because of their scale of perception (Peters, 1983; Milne et al. 1989; Holling C. S., 1992). For example smaller mammals, such as moles, will perceive their environment at a scale relative to their own size; moles consume earthworms and other small invertebrates that occur within specific temporal and spatial scales similar to their temporal and spatial scale of perception. Just as resources are aggregated within an ecosystem, organisms may form

aggregations that exist at different temporal and spatial scales dictated by the resources available within an ecosystem and the organism's perception of scale (Figure 3.2; Holling, 1992; Peterson et al. 1998).

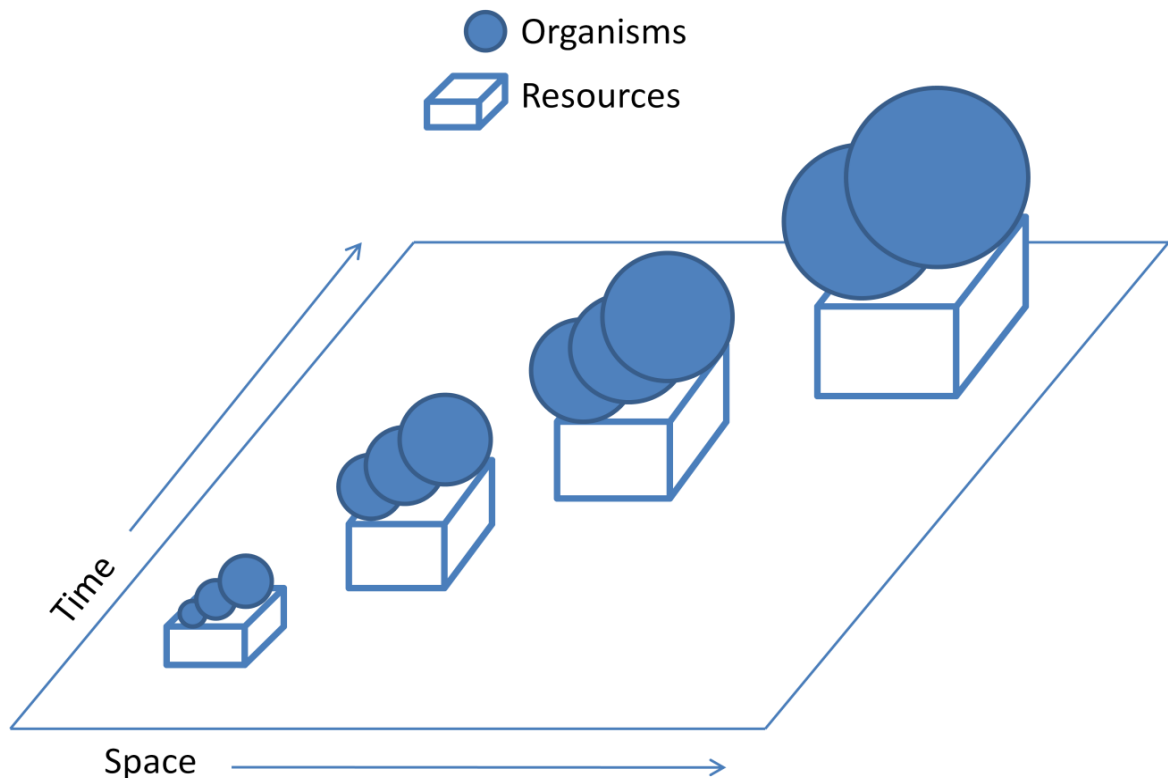


Figure 3.2 A hypothetical representation of organisms distributed throughout a discontinuous distribution of resources within an environment as predicted by the Textural Discontinuity Hypothesis. Organisms are represented by spheres, the diameter of which indicates body mass, and resources are represented by blocks. Each sphere and block set represents a different temporal spatial scale.

The aggregation to which a particular species belongs is identified using the species' average body mass. An organism's body mass is allometric to attributes such as metabolic rates, food consumption, life expectancy, and is indicative of how the organism interacts with its environment (Holling, 1992). The absence of body masses along a body

mass axis is indicative of gaps in resource availability (Holling, 1992; Holling, et al. 1996).

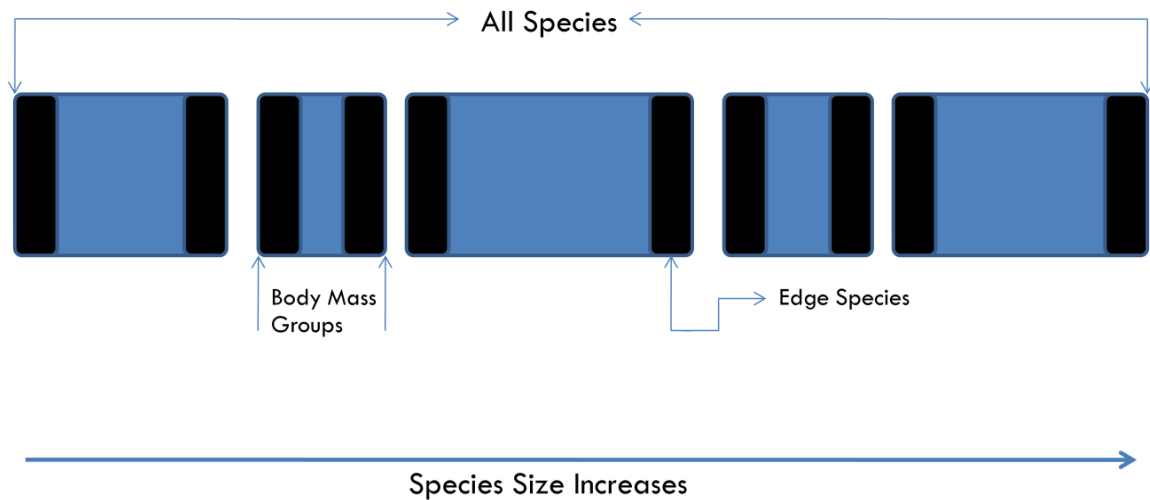


Figure 3.3 A representation of potential aggregations within a body mass distribution of a taxon of vertebrates from an ecosystem. Grey bars represent individual aggregations of species with similar body size and black bars within grey bars represent edge species.

The edge of resource aggregations may represent transition zones, where resources are highly variable in their availability (Allen et al. 1999). If species assemblages reflect aggregations of resources at different temporal and spatial scales, then organisms located at the edges of body mass aggregations may exhibit more variability in their life history because of the hypothetically transient and variable nature of the resources edge species utilize (Figure 3.3; Allen et al. 1999; Allen & Saunders, 2002; Allen & Saunders, 2006). That is, species located at the edges of aggregations may be migration prone because the resources they depend on are highly variable in their availability.

If body mass distributions reflect resource availability and the availability of resources at the edges of resource aggregations are highly variable in space and time then avian species may have evolved a migratory response to utilize these resources. The consumption of specific food items may cause species to migrate as the food item's availability changes temporally and spatially. The capacity of a bird to utilize different habitat, substrate, and foraging techniques may predict migration in birds; less diverse birds may be forced to migrate to find resources. The body mass of bird species may also serve as a predictor of migration; larger species may have a better capacity to store food as fat and thus better prepare themselves for migration. A series of *a priori* models were constructed that could predict migration, each derived from theoretically suggested characters of migratory bird species.

METHODS

The data were independently collected by Austin Roberts and colleagues from the Percy Fitzpatrick Institute in Cape Town, and donated for this study by Graeme Cumming also from the Percy Fitzpatrick Institute in Cape Town. South African bird species that did not have sufficient observational data associated with them were removed from the Robert's dataset ($n = 10$). Birds were grouped into habitat/ecosystem specific assemblages. The Robert's dataset provides four categories to describe a bird's habitat/ecosystem usage: main, secondary, occasional, and not used. In building habitat/ecosystem specific assemblages I included as "present" in a habitat/ecosystem species categorized by Roberts as "main" or "secondary" users of that habitat/ecosystem. The habitat/ecosystems analyzed were agricultural, Fynbos, grassland, Karoo, lagoon, Namib, savanna, semi-arid, wetland, and woodland; hereafter I refer to all of these as "habitats."

The body masses of species were arranged from smallest to largest within each habitat and log transformed. I used Bayesian Classification And Regression Tree analysis (BCART) to test for and then calculate aggregations of species body masses within each habitat. BCART examines numerical data for aggregations by creating combinations of observations in order to calculate the largest log integrated likelihood for all combinations of data (Chipman et al. 1998). One million iterations of BCART were performed for each habitat to calculate aggregations of species.

Up to 25 logistic regression models for each habitat were tested to analyze the relative fit amongst competing models (SAS Institute, 1985). It should be noted that not all habitats have the same number of models associated with them. The lack of dissimilar

model numbers within each habitat is due to a particular species trait having weak presence within a particular habitat. Models with a weight of 10% the highest ranked model were considered to be plausible models for predicting migration (Royall, 1997). AIC_c was used to account for bias in small sample sizes i.e. where the ratio of observations to parameters used was less than 40 (Turkheimer et al. 2003). The models considered were (a) migration = aerial foraging, (b) migration = aquatic foraging, (c) migration = body mass, (d) migration = DTCE (distance to the closest edge of a body mass aggregation), (e) migration = DTCE body mass, (f) migration = DTCE food richness, (g) migration = DTCE forage richness, (h) migration = DTCE freshwater invertebrate consumption, (i) migration = DTCE fruit consumption, (j) migration = DTCE habitat richness, (k) migration = DTCE habitat richness food richness forage richness substratum richness, (l) migration = DTCE nectar consumption, (m) migration = DTCE plant part consumption, (n) migration = DTCE granivory, (o) migration = DTCE substratum richness, (p) migration = DTCE terrestrial invertebrate consumption, (q) migration = food richness, (r) migration = forage richness, (s) migration = freshwater invertebrate consumption, (t) migration = freshwater invertebrate consumption aquatic substrate, (u) migration = fruit consumption, (v) migration = ground substrate, (w) migration = habitat richness, (x) migration = nectivory, (y) migration = plant part consumption, (z) migration = granivory, (a1) migration = substratum richness, (b1) migration = terrestrial invertebrate consumption, and (c1) migration = terrestrial invertebrate consumption ground substrate.

The model parameters aerial substrate, aquatic substrate, and ground substrate describe a bird's preferred foraging substrate. Different foraging habits may influence a

bird's migration behavior because different resources might have different temporal and spatial availability linked to a type of foraging method. Granivory, nectivory, frugivory, freshwater invertebrate, plant part, and terrestrial invertebrate consumption represent resources that may vary in their temporal and spatial availability, thus influencing migration. Some studies have suggested that the availability of specific food resources can contribute to species migration (Levey & Stiles, 1992). Food, forage, habitat, and substrate richness are included parameters, because having specialist characteristics may lead to migration. If resource depletion causes migration (Boyle & Conway, 2007); then one would expect to see migratory species as specialists lacking the capacity to take advantage of a wide variety of resources resulting in migrating.

The body mass parameter is included because size affects the scale of resources used (Holling, 1992) and this may limit a bird's ability to utilize less variable resources. The distance to closest edge of a body mass aggregation model parameter describes a species location relative to the edges of a body mass aggregation; this parameter may indicate species exposed to highly variable resource availability (Allen et al. 1999). Because the distance to the closest edge of a body mass aggregation may indicate species exposed to highly variable resources (Allen et al. 1999) and migratory species may be migratory due to resource depletion (Boyle & Conway, 2007), the DTCE parameter was included with other parameters to determine if a combination of resource variability and specializing or generalizing in resource utilization explained migration. For example habitat rich species may be located near the edges of body mass aggregations DTCE, because utilizing many different habitats may allow those species to compensate for variable resource availability.

The distance to closest edge is determined by calculating the difference between each species in that body mass aggregation and the edge defining species of the distribution. Global models were not included in the analysis because they did not have any ecological significance. Aquatic species were identified by the usage of freshwater invertebrates as a main or secondary food sources and the usage of aquatic substrate; models including these parameters were removed for the analysis without aquatic species. In previous studies using the Textural Discontinuity Hypothesis (Allen et al. 1999) aquatic species were removed from model analysis. Removing aquatic species was done because aquatic species are thought to have compartmentalized food webs, meaning they might have little influence in the composition of terrestrial food webs (Pimm & Lawton, 1980).

RESULTS

Discontinuous distributions of body masses were identified for each South African habitat type (Table 3.1). The number of aggregations present when aquatic species are excluded from analysis ranged from 4 to 12. The numbers of aggregations present when aquatic were included in analysis ranged from 5 to 12. Five habitats contained aquatic species. The percentage of aquatic species removed from each of these five habitats ranged from 1.4% (Karoo) to 52% (Lagoon). The aquatic habitats of lagoon and wetland contained the highest percentage of aquatic species removed. Six models had enough aquatic species to include an aquatic species parameter. Only one habitat, wetlands, had enough birds utilizing freshwater invertebrates to include the consumption of freshwater invertebrates as a model parameter. The differences between aggregation formation of aquatic and non-aquatic species appears to be minimal. Even when almost half of the species are aquatic and thus removed (Lagoon) for analysis there is at most one fewer aggregation present in the habitat. Therefore, I discuss the results of analysis with aquatic species removed.

The percentages of migratory species for each habitat are as follows: 26% (n = 12 Fynbos), 19% (n = 13 Karoo), 11% (n = 2 Namib), 22% (n = 32 agricultural), 27% (n = 29 grassland), 16% (n = 35 savanna), 15% (n = 6 semi-arid), 19% (n = 21 wetland), and 18% (n = 42 woodland). The percentage of plausible models, or models that were within 10% the weight of the highest weighted model, for each habitat ranged from 27% (savanna) to 91% (wetland). The percentage of plausible models explaining migration for Karoo, Fynbos, and Namib ecosystems ranged from 79%, 43%, and 46%,

respectively. Because of weak inference amongst models, model averaging was performed for each habitat's set of plausible model parameters (Tables 3.11 – 3.19).

The parameters aerial, body mass, fruit consumption, and nectar were all negative within the confidence set of models. The distance to the closest edge of a body mass aggregation was negative 30 times and positive four times within the confidence set of models. A negative and significant result indicates that as a species decreased its distance from the edge of an aggregation it is more likely to be nomadic, i.e. as a species approaches the edge of an aggregation it has a higher likelihood of being a nomadic species.

Species utilizing fewer substrate types were identified as migratory within the confidence set of models. The parameters ground, plant parts, and seeds were positive indicating a possession of these traits among migratory species. The direction of the parameters foodrich, foragerich, and habitatrich were varied throughout different habitats. Composite models indicate that within the Karoo ecosystem and woodland migratory species tended to utilize many different habitats. The composite models also show a tendency for bird species in the Karoo and Fynbos ecosystems not to utilize fruit. Migratory species within the Fynbos did tend to be granivorous and utilize many different foraging techniques. Also within the composite models migratory savanna species tended to not be aerial feeders or utilize many different substrate for feeding.

Table 3.1. The number of body mass aggregations and species per habitat in South Africa birds including and excluding aquatic species. The aggregations were determined with Bayesian classification and regression tree analysis.

Habitat Type	Number of Aggregations Including Aquatic Species	Number of Species Including Aquatic Species	Number of Aggregations Excluding Aquatic Species	Number of Species Excluding Aquatic Species
Agricultural	10	152	10	145
Fynbos	7	46	7	46
Grassland	9	106	9	106
Karoo	7	70	7	69
Lagoon	5	33	4	16
Namib	5	19	5	19
Savanna	12	214	12	214
Semi-Arid	6	34	6	34
Wetland	9	177	8	108
Woodland	11	254	12	251

Table 3.2. Agricultural habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 22% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.2	152.64	intercept only	-1.25	0.2
0.12	153.67	terrinverts	-0.86	0.58
0.07	154.67	seeds	0.58	0.41
0.06	155.01	fruit	-0.50	0.44
0.05	155.19	habitatrich	0.24	0.19
0.04	155.68	bodymass	-0.44	0.72
0.04	155.69	edge	-0.02	0.05
		terrinverts	-0.87	0.58
0.04	155.58	terrinverts	-0.89	0.59
		ground	0.19	0.63
0.04	155.79	plantparts	0.5	0.8
0.04	156.05	substratumrich	-0.34	0.41
0.03	156.17	foodrich	-0.14	0.20
0.03	156.2	foragerich	0.26	0.34
0.03	156.38	edge	-0.03	0.05
		seeds	0.63	0.42
0.03	156.47	aerial	-0.44	0.72

Table 3.2 (continued). Agricultural habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 22% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.03	156.67	edge	-0.01	0.05
0.02	157.07	edge	-0.01	0.05
		fruit	-0.5	0.44
0.02	157.28	edge	-0.01	0.05
		habitatrich	0.24	0.19
0.02	157.69	edge	0.0	0.05
		bodymass	-0.32	0.32
0.01	157.86	edge	-0.01	0.05
		plantparts	0.50	0.80
0.01	158.13	edge	-0.01	0.05
		substratumrich	-0.33	0.41
0.01	158.19	edge	-0.01	0.05
		foragerich	0.27	0.35
0.01	158.27	edge	-0.01	0.05
		foodrich	-0.14	0.2
0.01	158.62	edge	-0.012	0.05
		nectar	-0.36	0.86
0	161.65	edge	-0.01	0.051
		foragerich	0.26	0.35
		foodrich	-0.22	0.23
		habitatrich	0.27	0.2
		substratumrich	-0.35	0.42

Table 3.3. Karoo ecosystem. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 19% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.16	66.96	intercept only	-1.46	0.31
0.12	67.61	fruit	-1.14	0.68
0.09	68.04	habitatrich	0.39	0.22
0.07	68.65	nectar	-1.57	1.05
0.06	69.08	bodymass	-0.68	0.53
0.05	69.19	substratumrich	-0.94	0.66
0.05	69.22	edge	-0.05	0.06
		fruit	-1.17	0.68
0.05	69.25	seeds	0.87	0.71
0.04	69.94	edge	-0.04	0.06
		habitatrich	0.38	0.22
0.04	69.99	edge	-0.06	0.06
		nectar	-1.79	1.1
0.03	70.33	terrinverts	0.04	1.16
0.03	70.4	edge	-0.07	0.07
		substratumrich	-1.16	0.71
0.03	70.31	edge	-0.06	0.06
		seeds	1.01	0.73
0.03	70.52	foragerich	0.43	0.54

Table 3.3 (continued). Karoo ecosystem. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 19% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.03	70.67	edge	-0.04	0.06
0.02	70.81	ground	0.45	0.75
0.02	71.12	foodrich	-0.13	0.29
0.02	70.94	aerial	-0.39	1.20
0.02	71.05	edge	-0.04	0.07
		bodymass	-0.67	0.55
0.01	72.03	edge	-0.04	0.06
		terrinvets	0.15	1.18
0.01	72.3	terrinvets	0.03	1.17
		ground	0.4	0.75
0.01	72.36	edge	-0.04	0.06
		foragerich	0.41	0.54
0.01	73.66	edge	-0.04	0.06
		foodrich	-0.13	0.31
0.01	72.72	edge	-0.07	0.07
		foragerich	0.46	0.57
		foodrich	-0.45	0.4
		habitatrich	0.41	0.25
		substratumrich	-1.08	0.77

Table 3.4. Namib ecosystem. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 11% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.42	13.54	intercept only	-2.14	0.75
0.22	14.84	foodrich	2.41	1.51
0.08	16.9	terrinvets	1.18	1.52
0.05	17.89	substratumrich	-2.01	1.6
0.05	17.81	edge	-0.12	0.28
		foodrich	2.94	2.18
0.05	17.97	bodymass	-0.96	1.82
0.04	18.02	habitatrich	0.3	0.49
0.04	18.24	edge	0.06	0.16
0.02	19.69	edge	0.13	0.19
		substratumrich	-2.40	1.81
0.02	20.16	edge	0.23	0.29
		terrinvets	2.60	2.72
0.01	21.19	edge	0.03	0.16
		bodymass	-0.89	1.89
0.01	21.22	edge	0.04	0.17
		habitatrich	0.26	0.51
0	25.13	edge	-0.04	0.35
		foodrich	4.2	4.31
		habitatrich	-0.79	1.13
		substratumrich	-1.50	2.48

Table 3.5. Grassland habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 27% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.22	122.07	fruit	-1.72	1.24
0.13	123.21	terrinvets	0.02	0.72
		ground	0.54	0.77
0.08	124.04	edge	-0.03	0.06
		fruit	-1.74	1.25
0.07	124.33	aerial	-0.52	0.77
0.07	124.33	ground	0.52	0.77
0.07	124.36	seeds	0.29	0.46
0.07	124.52	intercept only	-0.98	0.22
0.06	124.59	plantparts	-0.32	0.74
0.06	124.77	terrinvets	0.01	0.72
0.03	126.4	edge	-0.04	0.06
		plantparts	-0.52	0.82
0.02	126.47	edge	-0.01	0.06
		seeds	0.27	0.47
0.02	126.59	foragerich	0.62	0.43
0.02	126.79	edge	-0.02	0.06
		terrinvets	-0.02	0.72
0.01	127.77	bodymass	-0.29	0.32

Table 3.5 (continued). Grassland habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 27% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.01	128.1	foodrich	-0.2	0.28
0.01	128.55	substratumrich	0.16	0.53
0.01	128.56	habitatrich	-0.05	0.18
0.01	128.74	edge	-0.01	0.06
0.01	128.58	edge	-0.01	0.06
		foragerich	0.61	0.43
0	129.86	edge	-0.01	0.06
		bodymass	-0.29	0.32
0	130.26	edge	0.0	0.06
		foodrich	-0.2	0.29
0	130.65	edge	-0.01	0.06
		substratumrich	0.16	0.53
0	130.68	edge	-0.01	0.06
		habitatrich	-0.04	0.18
0	134.19	edge	0.0	0.06
		foragerich	0.74	0.45
		foodrich	-0.29	0.31
		habitatrich	-0.07	0.2
		substratumrich	0.13	0.54

Table 3.6. Savanna habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 16% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.29	184.78	aerial	-1.56	0.49
0.18	185.76	edge	-0.15	0.06
		substratumrich	-0.9	0.38
0.09	187.12	edge	-0.16	0.06
		foragerich	-0.35	0.39
		foodrich	-0.43	0.25
		habitatrich	0.09	0.18
		substratumrich	-1.01	0.39
0.07	187.73	edge	-0.15	0.06
		terrinvets	-0.98	0.64
0.06	188.05	edge	-0.15	0.06
		foodrich	-0.36	0.22
0.06	188.07	edge	-0.14	0.06
		seeds	0.74	0.46
0.03	189.12	edge	-0.14	0.06
0.02	189.75	substratumrich	-0.83	0.38
0.02	189.81	edge	-0.13	0.06
		bodymass	-0.33	0.28
0.02	189.82	edge	-0.14	0.06
		plantparts	0.57	0.78
0.02	190	edge	-0.14	0.06
		fruit	0.36	0.58

Table 3.6 (continued). Savanna habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 16% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.02	190.29	edge	-0.14	0.06
		foragerich	-0.34	0.37
0.02	190.5	edge	-0.13	0.06
		nectar	-0.16	1.15
0.02	190.38	intercept only	-1.63	0.18
0.01	191.13	edge	-0.14	0.06
		habitatrich	-0.01	0.18
0.01	191.11	terrinverts	-0.84	0.64
		ground	0.66	0.43
0.01	191.43	terrinverts	-0.93	0.63
0.01	191.44	ground	0.71	0.42
0.01	191.88	seeds	0.64	0.45
0.01	192.15	foodrich	-0.31	0.22
0.01	192.21	bodymass	-0.41	0.28
0	193.1	plantparts	0.57	0.77
0	193.31	nectar	-0.23	1.13
0	193.52	fruit	0.25	0.57
0	193.65	foragerich	-0.3	0.36
0	194.34	habitatrich	0.05	0.17

Table 3.7. Wetland habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 19% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.2	107.12	terrinvts	-1.61	1.07
		ground	-0.16	0.63
0.19	107.23	aerial	-0.94	0.68
0.08	108.87	intercept only	-1.35	0.24
0.08	108.84	ground	0.06	0.62
0.07	109.1	terrinvts	-1.6	1.06
0.07	109.31	edge	-0.08	0.06
		terrinvts	-1.55	1.07
0.04	110.46	edge	-0.09	0.06
		habitatrich	-0.41	0.27
0.03	110.78	edge	-0.08	0.06
0.03	111	habitatrich	-0.36	0.27
0.02	111.49	foragerich	-0.74	0.62
0.02	111.34	edge	-0.08	0.06
		foragerich	-0.72	0.62
0.02	111.69	edge	-0.09	0.06
		substratumrich	0.55	0.49
0.02	111.94	edge	-0.09	0.06
		bodymass	-0.38	0.4

Table 3.7 (continued). Wetland habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 19% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.02	112.04	edge	-0.08	0.06
		seeds	0.33	0.54
		seeds	0.34	0.53
0.02	112.22			
0.02	112.08	substratumrich	0.44	0.48
0.02	112.24	edge	-0.08	0.06
		foodrich	-0.24	0.3
0.02	112.11	edge	-0.08	0.06
		plantparts	-0.4	0.89
0.02	112.24	plantparts	-0.46	0.87
0.02	112.25	foodrich	-0.24	0.3
0.01	112.29	bodymass	-0.29	0.37
0	115.47	edge	-0.1	0.06
		foragerich	-0.37	0.66
		foodrich	-0.03	0.33
		habitatrich	-0.38	0.29
		substratumrich	0.49	0.53

Table 3.8. Woodland habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 18% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.16	228.84	seeds	0.92	0.5
0.13	229.19	intercept only	-1.57	0.17
0.11	229.59	terrinverts	-1.01	0.63
0.08	230.16	aerial	-0.91	0.49
0.08	230.26	habitatrich	0.34	0.18
0.06	230.88	edge	-0.01	0.05
		seeds	0.92	0.5
0.06	230.9	plantparts	1.13	1.05
0.05	231.23	terrinverts	-1.01	0.63
		ground	0.02	0.35
0.04	231.66	edge	0.0	0.05
		terrinverts	-1.01	0.63
0.03	232.09	nectar	-0.05	0.8
0.03	232.3	edge	-0.01	0.05
		habitatrich	0.34	0.18
0.02	232.95	edge	0.01	0.05
		plantparts	1.14	1.05
0.02	233	fruit	-0.22	0.44
0.02	233.02	substratumrich	-0.27	0.34

Table 3.8 (continued). Woodland habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 18% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.02	233.19	ground	0.08	0.35
0.02	233.22	bodymass	-0.16	0.27
0.02	233.44	foragerich	-0.14	0.34
0.02	233.54	foodrich	-0.06	0.2
0.01	233.59	edge	-0.01	0.05
0.01	234.14	edge nectar	-0.01 -0.05	0.05 0.8
0.01	235.03	edge fruit	-0.01 -0.23	0.05 0.44
0.01	235.05	edge substratumrich	-0.01 -0.27	0.05 0.34
0.01	235.28	edge bodymass	0.0 -0.16	0.05 0.27
0.01	235.48	edge foragerich	-0.01 -0.14	0.05 0.34
0.01	235.58	edge foodrich	-0.01 -0.05	0.05 0.2
0	236.91	edge foragerich foodrich habitatrich substratumrich	-0.01 -0.2 -0.18 0.39 -0.31	0.05 0.35 0.23 0.19 0.35

Table 3.9. Semi-arid habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 15% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.45	32.08	intercept only	-1.54	0.45
0.08	35.59	seeds	1.02	1.16
0.08	35.64	foodrich	-0.67	0.78
0.07	35.89	bodymass	0.52	0.65
0.06	36.01	terrinverts	0.95	1.32
0.05	36.33	fruit	-0.51	1.25
0.05	36.38	habitatrich	-0.12	0.36
0.05	36.49	edge	0.0	0.09
0.02	38.14	edge seeds	0.01 1.04	0.09 1.17
0.02	38.21	edge foodrich	0.01 -0.67	0.09 0.78
0.02	38.41	edge bodymass	0.02 0.57	0.09 0.68
0.02	38.59	edge terrinverts	0.0 0.95	0.09 1.32
0.01	38.9	edge fruit	-0.01 -0.55	0.1 1.33

Table 3.9 (continued). Semi-arid habitats. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 15% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.01	38.96	edge	0.0	0.09
		habitatrich	-0.12	0.36
0.01	40.96	edge	0.01	0.09
		foodrich	-0.65	0.8
		habitatrich	-0.04	0.41

Table 3.10. Fynbos ecosystem. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 26% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.22	51.8	foragerich	1.76	0.75
0.06	54.35	seeds	1.61	0.85
0.12	52.95	intercept only	-1.04	0.33
0.09	53.65	edge	0.07	0.09
		foragerich	1.75	0.76
0.11	53.08	fruit	-1.42	0.76
0.08	53.9	edge	0.14	0.13
		foragerich	2.5	0.99
		foodrich	-1.1	0.63
		habitatrich	0.73	0.36
		substratumrich	-0.1	0.9
0.06	54.51	edge	0.09	0.1
		seeds	1.66	0.87
0.04	55.16	edge	0.1	0.09
		fruit	-1.55	0.79
0.04	55.27	habitatrich	0.31	0.21
0.02	56.17	ground	0.85	0.76
0.02	56.27	nectar	-0.92	0.85
0.02	56.38	bodymass	-0.58	0.62
0.02	56.8	edge	0.07	0.09

Table 3.10 (continued). Fynbos ecosystem. Results from analysis of alternative models predicting migratory behavior in South African birds. Migratory species account for 26% of birds analyzed. Models within a value of 10% the highest ranked model (bold) are considered plausible explanatory models for migration within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.02	56.68	foodrich	-0.33	0.42
0.02	56.72	substratumrich	-0.54	0.7
0.02	56.78	edge	0.09	0.09
		habitatrich	0.32	0.22
0.02	56.83	aerial	-1.1	1.46
0.01	57.98	edge	0.09	0.09
		bodymass	-0.62	0.63
0.01	58.22	edge	0.06	0.09
		nectar	-0.82	0.87
0.01	58.33	edge	0.08	0.09
		foodrich	-0.36	0.42
0.01	58.54	edge	0.07	0.09
		substratumrich	-0.52	0.7

Table 3.11. Logistic Regression composite migration model for South African birds located in Agricultural habitats. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	-1.04	0.97	0.56	-2.65
aerial	-0.07	0.13	0.14	-0.27
bodymass	-0.41	0.62	0.61	-1.43
edge	-0.01	0.05	0.07	-0.1
foodrich	-0.14	0.2	0.19	-0.48
foragerich	0.26	0.35	0.83	-0.31
fruit	-0.5	0.45	0.24	-1.24
ground	0.04	0.14	0.27	-0.19
habitatrich	0.24	0.19	0.56	-0.08
nectar	-0.36	0.86	1.07	-1.78
plantparts	0.5	0.8	1.81	-0.81
seeds	0.6	0.41	1.28	-0.09
substratumrich	-0.34	0.41	0.34	-1.01
terrinverts	-0.87	0.58	0.09	-1.83

Table 3.12. Logistic Regression composite migration model for South African birds located in the Karoo ecosystem. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	-0.78	1.74	2.12	-3.68
aerial	-0.05	0.16	0.22	-0.32
bodymass	-0.68	0.54	0.22	-1.58
edge	-0.05	0.06	0.06	-0.16
foodrich	-0.19	0.32	0.34	-0.73
foragerich	0.43	0.54	1.34	-0.47
fruit	-1.15	0.68	-0.01	-2.28
ground	0.43	0.75	1.69	-0.82
habitatrich	0.39	0.22	0.76	0.02
nectar	-1.65	1.07	0.14	-3.44
seeds	0.92	0.72	2.12	-0.29
substratumrich	-1.02	0.69	0.14	-2.18
terrinverts	0.06	1.17	2.02	-1.89

Table 3.13. Logistic Regression composite migration model for South African birds located in the Namib ecosystem. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	-3.29	3.14	2.14	-8.72
bodymass	-0.95	1.83	2.22	-4.12
edge	0.03	0.25	0.45	-0.4
foodrich	2.51	1.66	5.38	-0.35
substratumrich	-2.08	1.66	0.79	-4.96
terrinvets	1.51	1.88	4.77	-1.75

Table 3.14. Logistic Regression composite migration model for South African birds located in Grassland habitats. Aerial = aerial substrate, edge = distance to the closest edge of a body mass aggregation, fruit = frugivorous, ground = ground substrate, plantparts = plant part consumption, seeds = granivory, terrinverts = terrestrial invertebrate consumption.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	0.17	2.16	3.75	-3.42
aerial	-0.17	0.27	0.28	-0.62
edge	-0.02	0.06	0.08	-0.12
fruit	-1.73	1.25	0.34	-3.8
ground	0.54	0.77	1.81	-0.74
plantparts	-0.38	0.77	0.9	-1.66
seeds	0.29	0.46	1.05	-0.48
terrinvets	0.01	0.72	1.21	-1.18

Table 3.15. Logistic Regression composite migration model for South African birds located in Savanna habitats. Aerial = aerial substrate, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, seeds = granivory, terrinverts = terrestrial invertebrate consumption.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	0.12	1.4	2.42	-2.19
aerial	-1.56	0.49	-0.75	-2.37
edge	-0.15	0.06	-0.04	-0.25
foodrich	-0.4	0.24	0	-0.79
foragerich	-0.35	0.39	0.29	-0.98
habitatrich	0.08	0.19	0.38	-0.23
seeds	0.73	0.46	1.48	-0.03
substratumrich	-0.93	0.39	-0.28	-1.58
terrinverts	-0.96	0.64	0.1	-2.02

Table 3.16. Logistic Regression composite migration model for South African birds located in Wetland habitats. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, ground = ground substrate, habitatrich = habitat richness, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	-0.19	1.35	2.06	-2.43
aerial	-0.99	0.72	0.21	-2.19
bodymass	-0.34	0.39	0.31	-0.99
edge	-0.09	0.06	0.01	-0.18
foodrich	-0.21	0.31	0.31	-0.73
foragerich	-0.71	0.63	0.34	-1.75
ground	-0.09	0.64	0.97	-1.15
habitatrich	-0.39	0.28	0.07	-0.85
plantparts	-0.43	0.88	1.04	-1.9
seeds	0.34	0.53	1.22	-0.55
substratumrich	0.5	0.49	1.32	-0.32
terrinverts	-1.6	1.07	0.17	-3.37

Table 3.17. Logistic Regression composite migration model for South African birds located in Woodland habitats. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	-1.77	1.35	0.45	-3.99
aerial	-0.47	0.34	0.09	-1.03
bodymass	-0.17	0.27	0.28	-0.61
edge	-0.01	0.05	0.08	-0.09
foodrich	-0.07	0.21	0.28	-0.42
foragerich	-0.15	0.34	0.41	-0.7
fruit	-0.22	0.44	0.5	-0.94
ground	0.01	0.04	0.07	-0.06
habitatrich	0.34	0.18	0.64	0.04
plantparts	1.13	1.05	2.86	-0.6
seeds	0.92	0.5	1.75	0.09
substratumrich	-0.27	0.35	0.3	-0.84
terrinverts	-1.01	0.63	0.02	-2.04

Table 3.18. Logistic Regression composite migration model for South African birds located in Semi-arid habitats. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, habitatrich = habitat richness, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	-1.7	1.22	0.37	-3.76
bodymass	0.53	0.66	1.65	-0.59
edge	0.01	0.09	0.16	-0.15
foodrich	-0.67	0.78	0.65	-1.98
fruit	-0.52	1.27	1.63	-2.67
habitatrich	-0.11	0.37	0.51	-0.73
seeds	1.03	1.17	3	-0.94
terrinverts	0.96	1.32	3.18	-1.27

Table 3.19. Logistic Regression composite migration model for South African birds located in the Fynbos ecosystem. Edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, fruit = frugivorous, habitatrich = habitat richness, seeds = granivory, substratumrich = substrate richness.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	-2.15	2.16	1.48	-5.77
edge	0.09	0.1	0.27	-0.08
foodrich	-0.87	0.68	0.27	-2
foragerich	1.88	0.83	3.28	0.48
fruit	-1.47	0.77	-0.17	-2.76
habitatrich	0.53	0.36	1.14	-0.08
seeds	1.63	0.85	3.06	0.19
substratumrich	-0.22	0.86	1.23	-1.68

DISCUSSION

Discontinuities within body mass axes were identified within each habitat; these results confirm the results of other studies (Allen et al. 1999; Havlicek & Carpenter, 2001; Allen et al. 2002) that suggest that discontinuities in body mass distributions are common. Body mass aggregations between data sets including and excluding aquatic species were similar, suggesting that aquatic species have little influence on the body mass assemblages of terrestrial species and reinforcing the findings of Pimm & Lawton (1980) where they suggested aquatic species food webs are compartmentalized from terrestrial food webs.

Only a weak inference amongst models was possible in the analysis. The percentage of migratory species in any given analysis was considerably less than ideal for logistic regression. The application of the Textural Discontinuity Hypothesis is traditionally used to examine species within large ecosystems (Allen et al. 1999; Allen et al. 2002). Applying the Textural Discontinuity Hypothesis to habitats may be a possible explanation as to the weak inference amongst models. The percentage of plausible models for each habitat/ecosystems ranged from 27% ($n = 7$ savanna) to 91% ($n = 18$ woodland); but the percentage of plausible models explaining migration for Karoo, Fynbos, and Namib ecosystems ranged from 79%, 43%, and 46%, respectively. The ecosystems analyzed did not perform better than the habitats analyzed in terms of improving the level of inference. The number of species within ecosystems appears to be smaller than in some habitats, but there was no correlation between the number of plausible models and the number of species within a habitat ($p = 0.37$). Also no correlation existed between the number of migratory species in each habitat and the number of plausible models ($p = 0.30$). These data suggest that there is no difference

between habitats and ecosystems in terms of applying the Textural Discontinuity Hypothesis.

Model averaging indicates that there is an assortment of different species characteristics influencing migration and that each different habitat has a different array of characteristics that influence migration. No single set of parameters is applicable to all habitats, indicating that the catalysts for migration may depend on the region being examined. The composite models indicate that in the savanna habitat migratory species tend to be at the edges of body mass aggregations. Savanna migratory bird species also tended not to aerial feed as indicated by the composite models. In woodland habitats and the Karoo ecosystem more habitat rich species tended to be migratory; perhaps these results indicate that migratory bird species have a large capacity to utilize a wider array of habitats than do non-migratory species. In the savanna habitats migratory species tended not to utilize more substrate than their non-migratory counterparts; utilizing fewer substrates may lead birds to migrate to find usable substrate.

Also in the composite models the consumption of grain was positively associated with migration in the Fynbos ecosystem and woodland habitat. The consumption of grains by migratory birds may be the result of compensating for fluctuations in fat storage (Levey & Stiles 1992). In the composite models of the Karoo ecosystem migratory species did not tend to utilize fruit which is contrary to the work of Levey and Stiles (1992) which suggests migratory bird species tend to utilize fruit. Although the composite models often include zero in the confidence intervals, model parameters alone in each habitat may indicate what type of parameters drive migratory behavior.

The model parameters species aerial foraging, fruit, and nectar were always negative. Negative fruit, nectar, and terrestrial invertebrate consumption suggest that South African migratory bird species tend to avoid such resources; they also tend not to utilize aerial foraging but do foraging on the ground. These data are also in conflict with other data (Levey & Stiles, 1992) that indicate nectivorous birds tend to be migratory. The results may be context specific and indicate that predictors of migratory behavior are not applicable to all environments.

Distance to the closest edge of a body mass aggregation was negative a majority of the time. These data reinforce the initial hypothesis that bird species located at the edge of body mass aggregations will tend to exhibit migratory characteristics. These bird species might reflect resource availability and bird species at the edges of body mass aggregations may indicate highly variable resources which could be a result of transitions of resources between aggregations of resources. The results for model parameters food richness, forage richness, habitat richness, and plant part and terrestrial invertebrate consumption are mixed. These results are less absolute than previous results and suggest that diversity in bird species has little to do with predicting migrants in the habitats analyzed.

The data as a whole suggest that successfully singling out one characteristic to explain migration is unlikely. Migration is more than likely a complex phenomenon and a phenomenon that should be viewed within the context of interacting bird species and their environment. Overall, migratory behavior in South African birds involves proximity to the edge of a body mass aggregation, habitat richness, substrate richness, aerial foraging, and fruit, nectar, and grain consumption. Although no single predictor of

migration was better than the rest, the data do not suggest a lack of predictive species characteristics. The data suggest that, instead, many different factors contribute to South African avian species migration, which may explain why such controversy still exists over the reasons for avian species migration.

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CHAPTER IV

SOUTH AFRICAN PREDICTORS OF NOMADIC BIRD SPECIES AND THEIR LOCATION WITHIN DISCONTINUOUS AGGREGATIONS

INTRODUCTION

Little is known about what species characteristics predict nomadism within birds. Nomadic species lack a permanent location or home because they follow nonpermanent and unpredictable resources (Dean, 1997). Resources utilized by nomadic species are highly variable and can change both temporally and spatially in their availability (Sinclair, 1984). Granivory may explain avian nomadism within the Karoo (Dean, 1997) ecosystem of South Africa. Other analyses suggest that avian nomadism occurs because of granivory, nectivory, or as a response to rodent outbreaks (Davis, 1984). Or, body mass patterns reflecting discontinuous resource distributions within an environment may contribute to nomadism (Allen & Saunders 2002 & 2006). The use of body mass patterns as a predictor for nomadism follows from the Textural Discontinuity Hypothesis and represents a potential paradigm shift in the way scientists view ecological systems, and can provide scientists a different perspective when trying to understand the causes of nomadism in avian species.

The Textural Discontinuity Hypothesis stems from complex systems analysis and posits that the structure and processes in an ecological system, everything from thunderstorms to cold fronts, from blades of grass to grasslands, are discontinuously distributed in respect to temporal and spatial scales (Holling, 1986; Holling, 1992). Within a forest system (Figure 4.1) for example, different structures and processes exist each occupying a different spatial and temporal scale (Peterson et al. 1998). The forest crown has a higher turnover rate and is relatively small when compared to the forest

itself. Each scale is discrete, thus creating aggregations of resources, based upon their temporal availability and spatial extent.

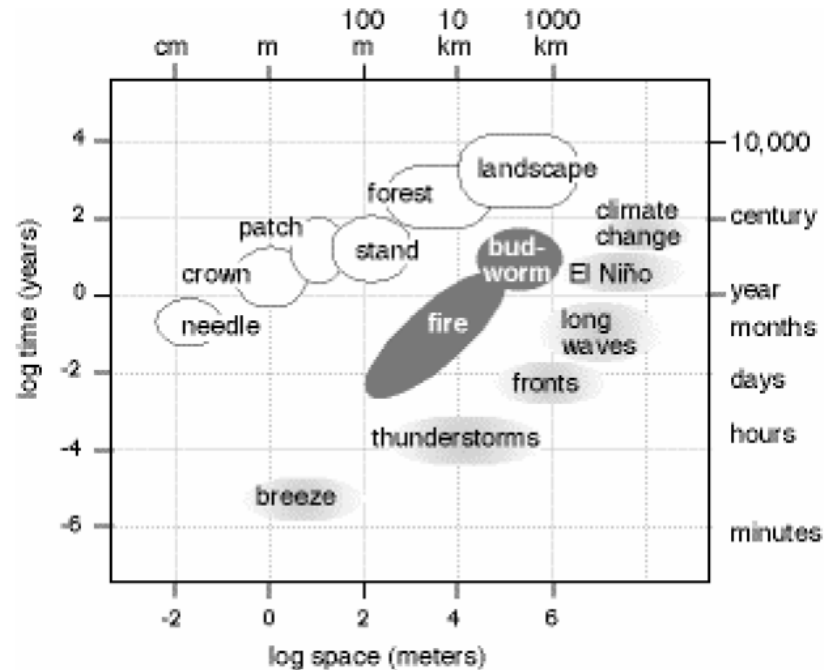


Figure 4.1 A representation of resources within different spatial and temporal scales (Gunderson and Holling 2002). Events at a small temporal and spatial scale such as a thunderstorm, and events with large temporal and spatial scales such as climate change, represent different temporal and spatial scales in which resources may be located.

There is probably no central tendency that pulls structures and processes into aggregations at different scales; aggregations within the context of the Textural Discontinuity Hypothesis are merely groupings of resources segregated by scale. These aggregations of resources are hypothesized to be the result of a small number of key processes occurring at different temporal and spatial scales (Carpenter & Leavitt, 1991; Holling et al.1995).

Organisms exploit resources within the landscape, but an organism is limited in the resources it can utilize based on how it perceives its environment (Peters, 1983; Milne et al. 1989; Holling, 1992; Peterson et al. 1998). For example a small organism such as a shrew will view and utilize resources at a scale relative to its size, such as small insects; a hyena will behave likewise and utilize resources relative to its own scale of perception, such as carrion. This limitation in resource acquisition is hypothesized to reflect aggregations of resources within the landscape (Holling, 1992). Thus, just as resources are aggregated, organisms too are aggregated into different temporal and spatial scales dictated by the resources available within a landscape (Figure 4.2). The result is discontinuous animal body mass distributions, because body mass is allometric with species characteristics including the scale of resource exploitation.

The aggregation to which a particular species belongs is determined by the species' average body mass (Holling, 1992). The absence of body masses within species distributions is reflective of gaps in resource availability found within the landscape, and are assumed to reflect the transition between discrete scales of resource distributions (Holling, 1992; Holling et al. 1996). It has been suggested that resources located at the edges of resource aggregations are more variable in their availability when compared to resources towards the center of resource aggregations (Allen et al. 1999). The transitions between aggregations of resources may be transitions where resource availability is highly variable (Allen et al. 1999). If organisms reflect the scales at which aggregations of resources are present in a system then organisms located at the edges of organism aggregations may exhibit more variability in their life history as well (Figure 4.3). Species located at the edges of aggregations may be prone to nomadism because the

resources they depend on are inherently highly variable in their availability (Allen et al. 1999; Allen & Saunders, 2002; Allen & Saunders, 2006).

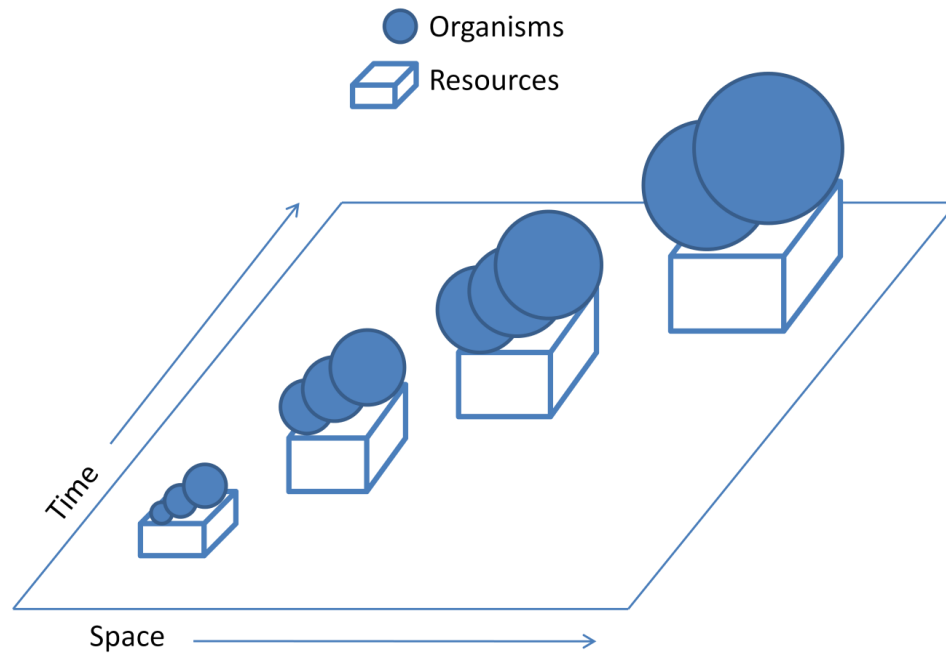


Figure 4.2 A hypothetical representation of organisms distributed throughout a discontinuous distribution of resources within an environment as predicted by the Textural Discontinuity Hypothesis. Organisms are represented by spheres, the diameter of which indicates body mass, and resources are represented by blocks. Each sphere and block set represents a different temporal spatial scale.

Allen and Saunders (2002) used a series of logistic regression models to analyze nomadic bird species in Australia within the context of the Textural Discontinuity Hypothesis. The parameters they used in a series of models were: species body mass, distance to the closest edge of a body mass aggregation, and seed, invertebrate, nectar, or plant diet. Allen and Saunders (2002) concluded that two factors best predicted nomadism in birds; the distance to the edge of a body mass aggregation, and the bird's

diet. Birds closer to the edge body mass aggregations and nectivorous birds were more likely to be nomadic.

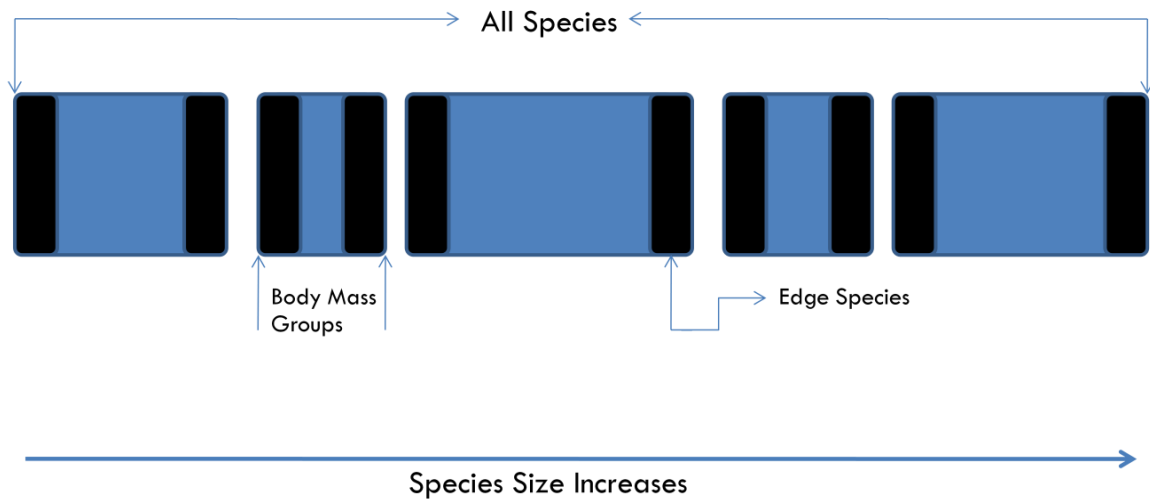


Figure 4.3 A representation of potential aggregations within a body mass distribution of a taxon of vertebrates from an ecosystem. Grey bars represent individual aggregations of species with similar body size and black bars within grey bars represent edge species.

The results of Allen and Saunders (2002) were disputed by Woinarski (2002). Woinarski concluded that nomadic characteristics exhibited by birds are the result of diet and not a species' location within a body mass aggregation. Allen and Saunders (2006) reanalyzed their work and the work of Woinarski (2002) and confirmed the results of their original paper, that nomadism was mainly the result of nectivory and a species position within a body mass aggregation. These results suggest that nomadism is a complex phenomenon arising from interacting species traits. Given the controversy and uncertainty concerning nomadism in birds I use an information-theoretic approach to

analyze South African bird species to sift among alternative competing models predicting nomadism.

METHODS

DATA

I utilized data for more than 700 South African bird species representing the most comprehensive collection of South African bird data. The data were independently collected by Austin Roberts from the Percy Fitzpatrick Institute in Cape Town, and donated for this study by Graeme Cumming also from the Percy Fitzpatrick Institute in Cape Town. A series of *a priori* models were constructed to predict nomadism, each derived from theoretically suggested characteristics of nomadism (Davies, 1984; Sinclair, 1984; Dean, 1997). The models capture variables that change through time and space and variables that indicate high diversity such as food type, foraging type, and habitat type. I conducted identical analyses using a data set excluding and including aquatic species. In previous studies (Allen, Forsys, & Holling, 1999) aquatic species were excluded from model analysis because aquatic species have little influence on the composition of non-aquatic species body mass interactions (Pimm & Lawton, 1980).

South African bird species that did not have sufficient data associated with them were removed from the Robert's dataset. Birds were grouped into habitat specific assemblages. The Robert's dataset provides four categories to describe a bird's habitat: main, secondary, occasional, and not used. In building habitat specific assemblages I included as "present" in a habitat species categorized by Roberts as "main" or "secondary" users of that habitat. The habitats analyzed were agricultural, grassland, lagoon, Karoo, Namib, savanna, wetland, and woodland.

DISCONTINUITY ANALYSIS

Body masses of species were ordered from smallest to largest within each habitat and then log transformed. I used BCART (Bayesian Classification And Regression Tree) analysis to test for and then calculate aggregations of species body masses within each habitat. BCART examines numerical data for aggregations by creating combinations of observations in order to calculate the largest log integrated likelihood for all combinations of data entered into the software (Chipman, 1998). One million iterations of BCART were performed for each habitat to calculate aggregations of species.

MODELS

Up to 29 logistic regression models for each habitat were tested to analyze the relative fit amongst competing models (SAS Institute, 1985). Models with a weight of 10% of the highest ranked model were considered to be plausible models for explaining nomadism (Royall, 1997). AIC_c was used to account for bias in small sample sizes i.e. the ratio of observations to parameters used was less than 40 (Turkheimer et al. 2003). The models considered were (a) nomadism = aerial foraging, (b) nomadism = aquatic foraging, (c) nomadism = body mass, (d) nomadism = DTCE (distance to the closest edge of a body mass aggregation), (e) nomadism = DTCE body mass, (f) nomadism = DTCE food richness, (g) nomadism = DTCE forage richness, (h) nomadism = DTCE freshwater invertebrate consumption, (i) nomadism = DTCE fruit consumption, (j) nomadism = DTCE habitat richness, (k) nomadism = DTCE habitat richness food richness forage richness substratum richness, (l) nomadism = DTCE nectar consumption, (m) nomadism = DTCE plant part consumption, (n) nomadism = DTCE granivory, (o) nomadism =

DTCE substratum richness, (p) nomadism = DTCE terrestrial invertebrate consumption, (q) nomadism = food richness, (r) nomadism = forage richness, (s) nomadism = freshwater invertebrate consumption, (t) nomadism = freshwater invertebrate consumption aquatic substrate, (u) nomadism = fruit consumption, (v) nomadism = ground substrate, (w) nomadism = habitat richness, (x) nomadism = nectivory, (y) nomadism = plant part consumption, (z) nomadism = granivory, (a1) nomadism = substratum richness, (b1) nomadism = terrestrial invertebrate consumption, and (c1) nomadism = terrestrial invertebrate consumption ground substrate.

The model parameters aerial substrate, aquatic substrate, and ground substrate describe a bird's preferred foraging substrate. The characteristics of different foraging substrate may fluctuate temporally; resulting in nomadic behavior because different resources might have different temporal and spatial availability associated to a type of foraging method. Granivory, nectivory, frugivory, and freshwater invertebrate, plant parts, and terrestrial invertebrate consumption represent resources that may vary in their temporally and spatially availability, thus they may also influence nomadism (Davis, 1984; Dean, 1997).

Food, forage, habitat, and substrate richness are included because having specialist characteristics may lead to nomadism. If nomadism is the result of unpredictable resource availability (Dean, 1997) and a species relies on a small set of resources then one would expect nomadic species to seek out their utilized resources for survival.

The body mass parameter is included because size affects the scale of resources used (Holling, 1992) and this may limit a bird's ability to utilize less variable resources.

The distance to closest edge of a body mass aggregation model parameter describes a species location relative to the edges of a body mass aggregation. The distance to the closest edge of a body mass aggregation parameter may indicate species exposed to highly variable resource availability (Allen et al. 1999; Allen & Saunders, 2002 & 2006). The DTCE parameter was included with other parameters to determine if a combination of resource variability and specializing or generalizing in resource utilization explained migration. The distance to closest edge is determined by calculating the difference between each species in that body mass aggregation and the edge defining species of the distribution. Global models were not included in the analysis because they did not have any ecological significance. Aquatic species were identified by the usage of freshwater invertebrates as a main or secondary food sources and the usage of aquatic substrate; models including these parameters were removed for the analysis without aquatic species.

RESULTS

Discontinuous distributions of body masses were identified for each South African habitat/ecosystem type (Table 4.1). The number of aggregations present when aquatic species are excluded from analysis ranged from 4 to 12. The numbers of aggregations present when aquatic species were included in analysis ranged from 5 to 12. Five habitats/ecosystems contained aquatic species. The percentage of aquatic species removed from each of these five habitats/ecosystems ranged from 1.4% (n = 1 Karoo) to 52% (n = 33 Lagoon). The aquatic habitats of lagoon and wetland contained the highest percentage of aquatic species removed. The differences in patterns among body mass distributions with aquatic and non-aquatic species was minimal. Even where 50% of the species are aquatic, and thus removed (Lagoon) for analysis, there was at most one fewer aggregation present. Thus, for the remainder of the results section I will only discuss the results of analysis with aquatic species removed.

Nomadic species for each habitat/ecosystem are as follows: 47% (n = 9 Namib), 20% (n = 14 Karoo), 31% (n = 24 agricultural), 18% (n = 19 grassland), 19% (n = 3 lagoon), 20% (n = 43 savanna), 14% (n = 15 wetland), and 12% (n = 31 woodland). Generally, there were multiple plausible models predicting nomadism in each habitat/ecosystem. The percentage of models included in the confidence set ranged from 8.7% (woodland) to 65% (Namib) (Tables 4.2 – 4.9). Because of weak inference amongst models, model averaging was performed for each habitat's set of plausible model parameters (Tables 4.10 – 4.17).

Within the composite set of models migratory species utilized ground substrate in the Karoo ecosystem; utilized many foraging techniques in the savanna and agricultural

ecosystems, consumed fruit in savanna habitats, tended not to consume nectar in the woodland and savanna habitats; were closer to the edges of body mass aggregations in the agricultural habitat; and tended to be larger in the wetlands habitat. Within the confidence set of models distance to the closest edge of a body mass aggregation, nectivory, and granivory were all negative, indicating that as a species decreased its distance from the edge of an aggregation it is more likely to be nomadic and that nectivores and granivores tended to not be nomadic. Terrestrial invertebrate, fruit, and plant part consumption and substrate richness were positive predictors of nomadism. The parameters body mass, aerial, food richness, forage richness, habitat richness, and ground substrate were inconsistent in confidence set models. In some habitats they were positive and in others these parameters were negative.

Table 4.1. The number of body mass aggregations and species per habitat in South African birds, including and excluding aquatic species. Aggregations were determined with Bayesian classification and regression tree analysis.

Habitat Type	Number of Aggregations Including Aquatic Species	Number of Species Including Aquatic Species	Number of Aggregations Excluding Aquatic Species	Number of Species Excluding Aquatic Species
Agricultural	10	152	10	145
Grassland	9	106	9	106
Karoo	7	70	7	69
Lagoon	5	33	4	16
Namib	5	19	5	19
Savanna	12	214	12	214
Wetland	9	177	8	108
Woodland	11	254	12	251

Table 4.2. Models predicting nomadism in South African birds inhabiting the Karoo ecosystem. Nomadic species account for 20% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.23	68.29	fruit	1.34	1.09
0.2	68.57	terrinvets	0.00	1.21
		ground	1.43	0.7
0.11	69.79	terrinvets	0.04	1.16
0.08	70.31	ground	1.34	0.69
0.08	70.39	edge	0.0	0.06
		fruit	1.34	1.09
0.07	70.55	intercept only	-1.37	0.3
0.04	71.69	nectar	-1.47	1.05
0.03	72.57	foodrich	-0.39	0.34
0.03	72.33	edge	0.0	0.06
		terrinvets	0.04	1.17
0.02	73.37	seeds	-0.02	0.61
0.02	73.58	edge	-0.02	0.06
		nectar	-1.54	1.07
0.01	73.79	foragerich	0.34	0.53
0.01	73.82	bodymass	-0.17	0.43
0.01	73.93	habitatrich	-0.05	0.23

Table 4.2 (continued). Models predicting nomadism in South African birds inhabiting the Karoo ecosystem. Nomadic species account for 20% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.01	73.94	edge	-0.01	0.06
0.01	74.53	edge foodrich	-0.01 -0.4	0.05 0.34
0.01	75.62	edge seeds	-0.01 -0.23	0.06 0.62
0.01	75.82	edge foragerich	-0.01 0.33	0.06 0.53
0	76.07	edge bodymass	-0.01 -0.16	0.06 0.44
0	76.14	edge habitatrich	-0.01 -0.05	0.07 0.23
0	78.58	edge foragerich foodrich habitatrich	-0.01 0.46 -0.47 0.01	0.06 0.55 0.38 0.25

Table 4.3. Models predicting nomadism in South African birds inhabiting savanna habitats. Nomadic species account for 20% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.4	207.8	fruit	1.3	0.75
0.18	209.4	edge	-0.04	0.05
		fruit	1.34	0.76
0.11	210.34	nectar	-1.85	0.93
0.05	212.07	edge	-0.03	0.05
		nectar	-1.84	0.93
0.05	212.1	foragerich	0.67	0.26
0.05	212.18	terrinvets	0.57	0.42
		ground	-0.07	0.46
0.04	212.61	terrinvets	0.67	0.41
0.02	213.91	edge	-0.03	0.05
		foragerich	0.67	0.26
0.02	214.33	edge	-0.02	0.05
		foragerich	0.85	0.28
		foodrich	-0.24	0.19
		habitatrich	0.18	0.17
		substratumrich	0.71	0.42
0.02	214.33	intercept only	-1.37	0.17
0.01	214.43	seeds	-0.32	0.36
0.01	214.58	edge	-0.02	0.05
		terrinvets	0.68	0.41

Table 4.3 (continued). Models predicting nomadism in South African birds inhabiting savanna habitats. Nomadic species account for 20% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.01	214.69	aerial	0.43	0.65
0.01	215.07	ground	-0.15	0.46
0.01	216.13	edge seeds	-0.03 -0.29	0.05 0.36
0.01	216.24	substratumrich	0.56	0.39
0	217.51	habitatrich	0.15	0.15
0	218.14	edge substratumrich	-0.02 0.55	0.05 0.39
0	218.12	foodrich	-0.09	0.17
0	218.16	edge	-0.02	0.05
0	218.39	bodymass	0.01	0.24
0	219.47	edge habitatrich	-0.02 0.14	0.05 0.16
0	219.9	edge foodrich	-0.03 -0.1	0.05 0.17
0	220.22	edge bodymass	-0.03 0.03	0.05 0.24

Table 4.4. Models predicting nomadism in South African birds inhabiting grassland habitats. Nomadic species account for 18% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.26	96.74	terrinvets	1.14	0.7
		ground	1.15	0.8
0.19	97.34	foragerich	1.22	0.48
0.16	97.7	edge	0.03	0.07
		foragerich	1.24	0.48
0.07	99.33	ground	1.16	0.78
0.06	99.53	aerial	0.42	1.1
0.06	99.81	intercept only	-1.52	0.25
0.04	100.48	terrinvets	1.08	0.69
0.02	101.64	habitatrich	0.3	0.19
0.02	101.71	substratumrich	1.06	0.79
0.02	101.89	seeds	0.48	0.54
0.02	101.91	bodymass	0.46	0.32
0.01	102.58	edge	0.02	0.07
		terrinvets	1.1	0.69
0.01	103.47	foodrich	0.28	0.3

Table 4.4 (continued). Models predicting nomadism in South African birds inhabiting grassland habitats. Nomadic species account for 18% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.01	103.05	edge	0.01	0.07
		foragerich	1.08	0.49
		foodrich	0.01	0.33
		habitatrich	0.23	0.22
		substratumrich	0.93	0.81
0.01	103.74	edge	0.0	0.07
		habitatrich	0.3	0.2
0.01	103.86	edge	0.01	0.07
		substratumrich	1.05	0.79
0.01	103.95	edge	0.012	0.07
0.01	104.04	edge	0.02	0.07
		seeds	0.53	0.55
0.01	103.9	edge	0.01	0.07
		bodymass	0.46	0.32
0	105.21	edge	0.0	0.07
		foodrich	0.28	0.3

Table 4.5. Models predicting nomadism in South African birds inhabiting the Namib ecosystem. Nomadic species account for 47% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.33	27.04	intercept only	-0.11	0.46
0.12	29.02	seeds	-1.66	1.03
0.06	30.6	aerial	-0.25	1.5
0.06	30.42	ground	0.25	1.5
0.06	30.42	bodymass	-0.86	0.83
0.06	30.53	edge	-0.16	0.13
		seeds	-2.13	1.19
0.04	31.24	terrinverts	0.69	1.06
0.04	31.45	habitatrich	-0.21	0.33
0.04	31.46	foodrich	0.42	0.72
0.04	31.53	substratumrich	0.69	1.32
0.03	31.92	edge	-0.08	0.11
0.03	31.6	foragerich	0.45	0.87
0.03	31.6	edge	-0.16	0.12
		bodymass	-1.32	0.97
0.01	33.69	terrinverts	0.34	1.16
		ground	0.34	1.53

Table 4.5 (continued). Models predicting nomadism in South African birds inhabiting the Namib ecosystem. Nomadic species account for 47% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AICw	AIC _c	Model	Estimate	Standard Error
0.01	33.77	edge	-0.11	0.11
		foodrich	0.64	0.77
0.01	34.06	edge	-0.09	0.11
		substratumrich	0.87	1.35
0.01	34.27	edge	-0.07	0.11
		habitatrich	-0.16	0.34
0.01	34.34	edge	-0.08	0.11
		foragerich	0.35	0.89
0.01	34.36	edge	-0.07	0.11
		terrinvets	0.42	1.15
0	40.72	edge	-0.15	0.13
		foragerich	0.83	1.06
		foodrich	1.79	1.12
		habitatrich	-0.34	0.43
		substratumrich	2.58	1.98

Table 4.6. Models predicting nomadism in South African birds inhabiting woodland habitats. Nomadic species account for 12% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.54	182.75	nectar	-1.9	0.64
0.21	184.63	edge nectar	-0.03 -1.89	0.06 0.64
0.05	187.46	intercept only	-1.95	0.19
0.03	188.33	terrinvets	0.77	0.45
0.01	189.97	terrinvets ground	0.78 0.18	0.46 0.4
0.01	190.08	edge terrinvets	-0.03 0.78	0.06 0.46
0.01	190.12	plantparts	0.73	1.05
0.01	190.17	foragerich	0.39	0.32
0.01	190.3	substratumrich	0.46	0.43
0.01	190.97	fruit	0.29	0.56
0.01	190.98	bodymass	0.21	0.28
0.01	191.04	seeds	0.21	0.48
0.01	191.11	ground	0.14	0.39
0.01	191.19	edge	-0.03	0.06
0.01	191.21	habitatrich	0.12	0.21

Table 4.6 (continued). Models predicting nomadism in South African birds inhabiting woodland habitats. Nomadic species account for 12% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.01	191.21	aerial	-0.11	0.65
0.01	191.37	foodrich	-0.09	0.24
0.01	191.93	edge foragerich	-0.03 0.39	0.06 0.32
0.01	192.04	edge plantparts	-0.02 0.69	0.06 1.06
0.01	192.08	edge substratumrich	-0.03 0.46	0.06 0.43
0	192.58	edge bodymass	-0.04 0.23	0.06 0.28
0	192.78	edge seeds	-0.03 0.23	0.06 0.48
0	192.79	edge fruit	-0.03 0.26	0.06 0.57
0	192.96	edge habitatrich	-0.03 0.12	0.06 0.21
0	193.14	edge foodrich	-0.03 -0.08	0.06 0.24
0	195.84	edge foragerich foodrich habitatrich substratumrich	-0.03 0.51 -0.17 0.14 0.56	0.06 0.34 0.26 0.23 0.45

Table 4.7. Models predicting nomadism in South African birds inhabiting agricultural habitats. Nomadic species account for 31% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.29	125.68	edge	-0.15	0.07
		plantparts	0.9	1.08
0.2	126.49	edge	-0.15	0.07
		terrinvets	0.12	0.54
0.09	128.06	edge	-0.15	0.07
		foragerich	0.67	0.39
0.06	128.88	edge	-0.14	0.06
0.04	129.45	plantparts	0.89	1.07
0.04	129.44	intercept only	-1.61	0.22
0.04	129.85	edge	-0.14	0.07
		foodrich	-0.32	0.28
0.03	130.1	terrinvets	0.24	0.52
0.03	130.23	edge	-0.14	0.07
		nectar	-0.82	0.88
0.03	130.25	edge	-0.14	0.06
		bodymass	0.28	0.33
0.03	130.59	edge	-0.14	0.06
		substratumrich	0.3	0.48
0.02	130.89	edge	-0.14	0.07
		seeds	0.15	0.46

Table 4.7 (continued). Models predicting nomadism in South African birds inhabiting agricultural habitats. Nomadic species account for 31% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AICw	AIC _c	Model	Estimate	Standard Error
0.02	130.95	edge	-0.14	0.06
		habitatrich	0.05	0.22
0.01	132.13	foragerich	0.55	0.36
0.01	131.8	terrinvets	0.17	0.54
		ground	0.42	0.63
0.01	131.74	edge	-0.15	0.07
		foragerich	0.77	0.4
		foodrich	-0.37	0.3
		habitatrich	0.12	0.24
		substratumrich	0.29	0.5
0.01	132.28	foodrich	-0.31	0.26
0.01	133.28	nectar	-0.74	0.87
		ground	0.41	0.62
0.01	133.51			
0.01	133.55	aerial	0.62	1.08
0.01	133.68	bodymass	0.16	0.31
0.01	133.72	substratumrich	0.22	0.47
0	133.82	habitatrich	0.07	0.22
0	133.91	seeds	-0.07	0.45

Table 4.8. Models predicting nomadism in South African birds inhabiting lagoon habitats. Nomadic species account for 19% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.62	16.37	intercept only	-1.49	0.64
0.08	20.42	habitatrich	0.91	0.91
0.08	20.49	foragerich	-1.15	1.27
0.07	20.76	edge	-0.1	0.13
0.05	21.28	foodrich	-0.22	0.56
0.05	21.44	bodymass	-0.03	0.97
0.02	23.74	edge foragerich	-0.07 -1.01	0.12 1.31
0.02	23.75	edge habitatrich	-0.07 0.73	0.14 0.93
0.01	24.22	edge bodymass	-0.12 -0.43	0.13 1.07
0.01	24.24	edge foodrich	-0.1 -0.19	0.13 0.5
0	31.99	edge foragerich foodrich habitatrich	-0.01 -1.01 -0.42 1.46	0.15 1.85 0.78 1.3

Table 4.9. Models predicting nomadism in South African birds inhabiting wetland habitats. Nomadic species account for 14% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.37	82.14	bodymass	1.03	0.35
0.16	83.85	terrinvets	1.12	0.65
		ground	-0.89	1.09
0.14	84.0	edge	-0.03	0.06
		bodymass	1.05	0.35
	3			
0.1	84.8	ground	-1.18	1.07
0.05	86.2	aerial	-0.4	0.84
0.03	86.85	intercept only	-1.81	0.28
0.03	87.39	terrinvets	1.19	0.63
0.02	88.18	foodrich	0.49	0.29
0.02	88.29	substratumrich	-0.97	0.62
0.02	88.35	foragerich	0.91	0.55
0.01	89.1	edge	-0.04	0.06
		terrinvets	1.24	0.64
0.01	89.61	plantparts	-0.97	0.89
0.01	89.74	habitatrich	0.28	0.25
0.01	90.11	edge	-0.04	0.06
		foragerich	0.96	0.55

Table 4.9 (continued). Models predicting nomadism in South African birds inhabiting wetland habitats. Nomadic species account for 14% of birds analyzed. Models with a value of 10% the highest ranked model are considered plausible explanatory models for nomadism within South African bird species. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, habitatrich = habitat richness, nectar = nectivory, plantparts = plant part consumption, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

AICw	AIC _c	Model	Estimate	Standard Error
0.01	90.15	edge	-0.03	0.06
		foodrich	0.49	0.29
0.01	90.36	edge	-0.02	0.06
		substratumrich	-0.95	0.62
0.01	90.53	fruit	-0.44	1.15
0.01	90.67	seeds	-0.017	0.59
0	90.76	edge	-0.03	0.06
0	91.57	edge	-0.03	0.06
		plantparts	-0.96	0.89
0	91.79	edge	-0.02	0.06
		habitatrich	0.27	0.25
0	92.4	edge	-0.03	0.06
		fruit	-0.55	1.18
0	92.6	edge	-0.03	0.06
		seeds	-0.02	0.59
0	94	edge	-0.02	0.06
		foragerich	0.58	0.6
		foodrich	0.25	0.33
		habitatrich	0.18	0.27
		substratumrich	-0.7	0.67

Table 4.10. Logistic Regression nomadism composite model for South African birds located in the Karoo ecosystem. Edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, fruit = frugivorous, ground = ground substrate, nectar = nectivory, seeds = granivory, terrinverts = terrestrial invertebrate consumption.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	-2.45	2	0.89	-5.78
edge	0	0.53	0.88	-0.89
foodrich	-0.4	0.34	0.17	-0.97
fruit	1.34	1.09	3.15	-0.48
ground	1.41	0.7	2.57	0.24
nectar	-1.49	1.06	0.28	-3.25
seeds	-0.24	0.61	0.78	-1.26
terrinverts	0.02	1.19	2.01	-1.98

Table 4.11. Logistic Regression nomadism composite model for South African birds located in savanna habitats. Edge = distance to the closest edge of a body mass aggregation, foragerich = forage richness, fruit = frugivorous, nectar = nectivory, terrinverts = terrestrial invertebrate consumption.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	-2.41	2.25	1.3	-6.12
edge	-0.03	0.05	0.06	-0.12
foragerich	0.7	0.27	1.16	0.25
fruit	1.31	0.76	2.56	0.07
nectar	-1.85	0.93	-0.31	-3.38
terrinverts	0.63	0.42	1.32	-0.06

Table 4.12. Logistic Regression nomadism composite model for South African birds located in grassland habitats. Aerial = aerial substrate, edge = distance to the closest edge of a body mass aggregation, foragerich = forage richness, ground = ground substrate, terrinverts = terrestrial invertebrate consumption.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	-3.11	1.25	-1.04	-5.18
aerial	0.1	0.28	0.58	-0.37
edge	0.02	0.07	0.13	-0.09
foragerich	1.22	0.48	2.02	0.43
ground	0.72	0.56	1.64	-0.2
terrinverts	1.13	0.7	2.29	-0.03

Table 4.13. Logistic Regression nomadism composite model for South African birds located in the Namib ecosystem. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, ground = ground substrate, habitatrich = habitat richness, seeds = granivory, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	0.42	1.69	3.34	-2.5
aerial	-0.05	0.28	0.44	-0.53
bodymass	-1.01	0.9	0.55	-2.57
edge	-0.12	0.12	0.09	-0.34
foodrich	0.49	0.74	1.77	-0.8
foragerich	0.44	0.87	1.95	-1.08
ground	0.27	1.51	2.87	-2.34
habitatrich	-0.2	0.33	0.37	-0.78
seeds	-1.81	1.1	0.1	-3.71
substratumrich	0.75	1.34	3.07	-1.58
terrinverts	0.58	1.11	2.49	-1.33

Table 4.14. Logistic Regression nomadism composite model for South African birds located in woodland habitats. Edge = distance to the closest edge of a body mass aggregation, nectar = nectivory.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	0.7	2.02	4.04	-2.64
edge	-0.03	0.06	0.08	-0.13
nectar	-1.9	0.64	-0.84	-2.95

Table 4.15. Logistic Regression nomadism composite model for South African birds located in agricultural habitats. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, nectar = nectivory, plantparts = plant part consumption, substratumrich = substrate richness, terrinverts = terrestrial invertebrate consumption.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	-1.82	1.46	0.59	-4.24
bodymass	0.27	0.33	0.81	-0.28
edge	-0.15	0.07	-0.04	-0.26
foodrich	-0.33	0.28	0.13	-0.79
foragerich	0.67	0.39	1.31	0.03
nectar	-0.8	0.88	0.65	-2.26
plantparts	0.9	1.08	2.68	-0.88
substratumrich	0.29	0.49	1.09	-0.51
terrinverts	0.14	0.54	1.03	-0.75

Table 4.16. Logistic Regression nomadism composite model for South African birds located in lagoon habitats. Edge = distance to the closest edge of a body mass aggregation, foragerich = forage richness, habitatrich = habitat richness.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	-1.45	1.28	0.8	-3.69
edge	-0.09	0.13	0.13	-0.32
foragerich	-1.13	1.28	1.11	-3.36
habitatrich	0.88	0.92	2.49	-0.73

Table 4.17. Logistic Regression nomadism composite model for South African birds located in wetland habitats. Aerial = aerial substrate, bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, ground = ground substrate, terrinverts = terrestrial invertebrate consumption.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
Intercept	-2.74	1.52	-0.21	-5.27
aerial	-0.05	0.12	0.15	-0.25
bodymass	1.04	0.35	1.62	0.46
edge	-0.03	0.06	0.07	-0.13
ground	-1	1.09	0.81	-2.82
terrinvets	1.14	0.65	2.22	0.06

DISCUSSION

Discontinuities in South African bird body mass distributions were discovered within each ecosystem/habitat, supporting the Textural Discontinuity Hypothesis. Patterns in body mass aggregations between data sets including and excluding aquatic species were similar; therefore I focus the rest of my discussion on analysis without aquatic species. The application of the Textural Discontinuity Hypothesis is traditionally used to examine species within large ecosystems (Allen et al. 1999; Allen et al. 2002). Applying the Textural Discontinuity Hypothesis to habitats may explain the weak inference achieved.

The ecosystems analyzed did not fare worse than habitats analyzed in terms of having more models in the confidence set explaining nomadism in South African bird species. There was not a correlation between the number of species and the number of plausible models within a habitat/ecosystem ($p = 0.347$). The percentage of models in each confidence set for each habitat/ecosystems ranged from 8% (woodland) to 65% (Namib). Many different species characteristics were included in the composite model sets for each habitat/ecosystem. Each set of composite models were unique to a particular habitat/ecosystem giving support to the idea that nomadism is a complex phenomena that incorporates many different species characteristics. Within the composite models forage rich species were nomadic in the savanna, grassland, and agricultural habitats, indicating that nomadic bird species utilize more foraging techniques than do their non-nomadic counterparts.

The composite models show that within agricultural habitats species located closer to the edges of body mass aggregations were nomadic, indicating that the Textural

Discontinuity Hypothesis plays a role in predicting nomadic bird species. Composition models of the savanna habitats revealed nomadic bird species to consume fruit. The consumption of fruit by nomadic birds may indicate that there is a changing temporal and spatial distribution of fruit which nomadic birds have exploited, and as a result move about in a fashion that reflects these changes. The savanna and woodland habitats, within the composite models show that nomadic bird species are less likely to be nectivorous. These data disagree with the results of Woinarski (2006), where he contended that nectivorous species tended to be nomadic. Woinarski's work involved birds from semi-arid southern Australia and not South Africa, so the exploitation of nectar by nomadic bird species may be geographically specific. The composite models also signify the exploitation of ground resources by nomadic bird species within the Karoo ecosystem, suggesting that ground is a preferred substrate. The body mass parameter in the agricultural habitat composite model indicated that these bird species tended to be larger than non-nomadic species.

Although the composite models often include zero in the confidence intervals model parameters alone in each habitat/ecosystem may indicate what type of parameters drive migratory behavior. The distance to the closest edge of a body mass aggregation was always negative, indicating that as a species approaches the edge of a body mass aggregation it has a tendency to be nomadic. This result is similar to the analyses by Allen and Saunders (2002 & 2006), where they concluded distance to closest edge of a body mass aggregation was predictive of nomadism. The granivory parameter was always negative, indicating that nomadic species do not consume seeds. Dean (1997), however, reported that granivorous species in the South African Karoo tended to be

nomadic. Aerial feeding was not useful for predicting nomadism. The parameters food richness, forage richness, habitat richness, body mass, and ground substrate are mixed in their results. In some habitat/ecosystems the parameters are positive and in others they are negative.

Plant part consumption and substrate richness may be an indicator for nomadic bird species of South Africa, both were always positive indicating that as a species increases its substrate utilization and consumed plant parts it has an increased tendency to be nomadic. Nomadic bird species may find it advantageous to utilize an assortment of different substrate allowing them to follow resources as they move throughout the landscape. This does not mean that the resources nomadic bird species utilize are diverse but instead the substrate they utilize is diverse. The consumption of terrestrial invertebrates was always positive when significant, indicating that nomadic bird species tend to use this resource frequently. As terrestrial invertebrate populations move throughout a landscape birds utilizing this resource may be forced to follow, catalyzing a nomadic response.

The data from this study agree with the some of the underlying ideas in the analyses performed by Allen and Saunders (2002 & 2006) where diet and proximity to the edge of a body mass aggregation aided in predicting nomadism in birds. The data as a whole suggest that to predict nomadism one needs to examine nomadic birds through many lenses. The prediction of nomadic birds is unlikely to be correctly accomplished with simple predictors such as Woinarski's suggestion of only using a species' dietary needs. The data suggest instead that primarily a mixture of dietary needs, foraging substrate, and proximity to the edge of a body mass aggregation are all predictors of

nomadism in South African bird species. Other factors may also play a role in predicting nomadism but more substantial data sets are needed to correctly indicate the roles they play. Nomadism is more than likely a complex phenomenon that should be viewed within the context of interacting bird species and their environment.

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CHAPTER V

A TEST OF ALTERNATIVE MODELS PREDICTING DECLINE IN SOUTH AFRICAN BIRDS

INTRODUCTION

Accurately predicting species decline has been the objective of many scientists. Resource managers, policy makers, and scientists could all benefit from predictions regarding decline. Scientists have developed competing hypotheses regarding the reasons for species decline. Species with larger body masses more frequently decline (Cardillo, et al., 2005; Fisher & Owens, 2004). Island species assemblages consist of a greater number of generalist species over time (Christian et al. 2009), so that specialist species have a tendency to decline. Scientists investigating species decline within the context of the Textural Discontinuity Hypothesis have discovered that, within their studied communities, body mass was not as significant of an indicator as was the location of species within a body mass distribution (Forys and Allen et al. 1990). The Textural Discontinuity Hypothesis suggests that spatial and temporal assemblages of resources discontinuously dispersed throughout landscapes forming aggregations of resources; and that each aggregation represents a different temporal and spatial scale (Figure 5.1) (Burrough, 1981; Holling, 1986; Holling, 1992).

These discontinuous aggregations of resources are the result of a small number of key processes occurring at different temporal and spatial scales (Carpenter & Leavitt, 1991; Holling et al. 1995). Animal species are limited in the resources they can utilize based on the species' perception of its environment (Peters, 1983; Milne et al. 1989; Holling, 1992). Smaller species utilize resources relative to the temporal and spatial scale in which they exist, and larger scales are perceived as a backdrop; larger species

behave likewise and utilize resources relative to their own scale, and smaller scales are not noticed (Peterson et al. 1998). This scale specific utilization of resources by species thus creates aggregations of species within a landscape that reflect resource aggregations (Figure 5.2).

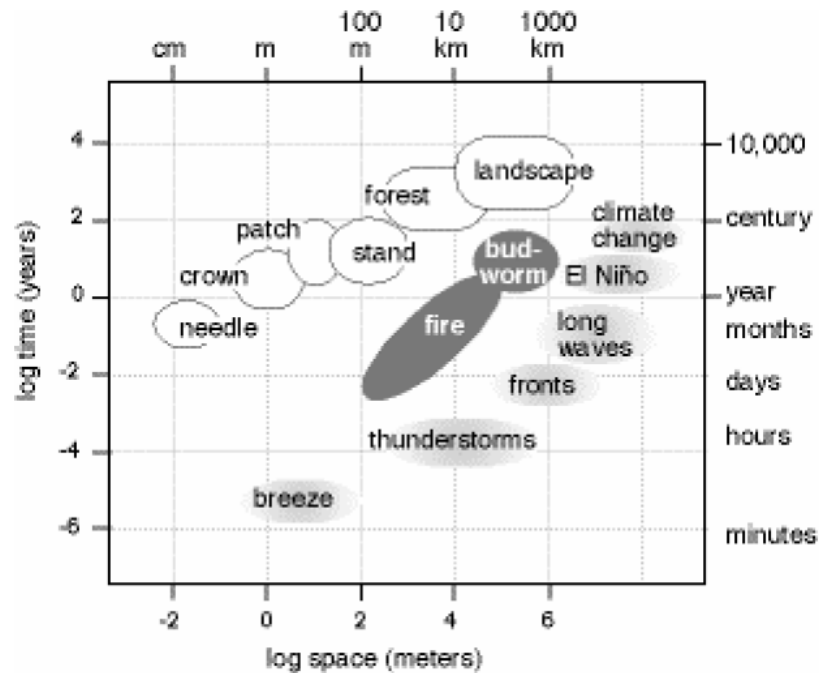


Figure 5.1 A representation of structures and processes within different spatial and temporal scales (Gunderson and Holling 2002). Events at a small temporal and spatial scale such as a thunderstorm, and events with large temporal and spatial scales such as climate change, represent different temporal and spatial scales in which resources may be located.

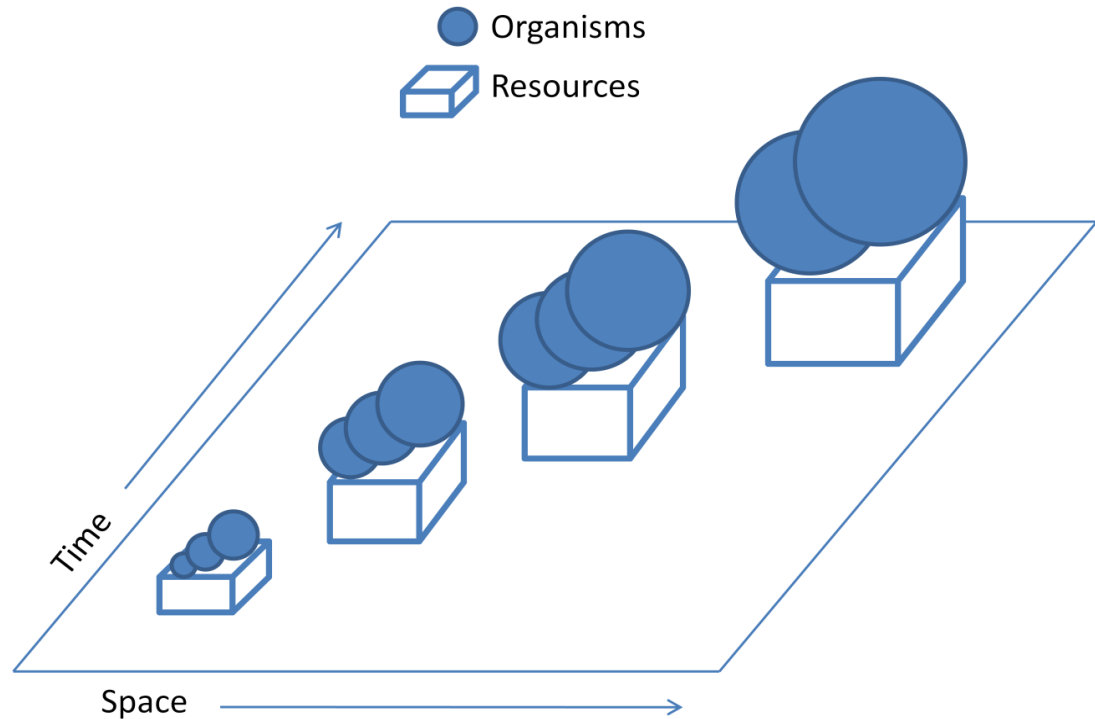


Figure 5.2 A hypothetical representation of organisms distributed throughout a discontinuous distribution of resources within and environment as predicted by the Textural Discontinuity Hypothesis. Organisms are represented by spheres, the diameter indicates body mass, and resources are represented by blocks. Each sphere and block set represents a different temporal spatial scale.

The Textural Discontinuity Hypothesis suggests that the body mass of a species reflects the temporal and spatial scale of resources the species utilize (Holling, 1992). An organism's body mass is allometric to metabolic rates, food consumption, and life expectancy, and is indicative of how the organism interacts with its environment (Peters, 1983). This tight relationship between a species body mass and its scale of resource utilization means that animal body mass distributions may reflect the discontinuous distribution of resources in a system. According to the Textural Discontinuity Hypothesis animal body mass distribution should be discontinuous. If species assemblages reflect aggregations of resources at different temporal and spatial scales,

then organisms located at the edges of organism aggregations may exhibit more variability in their life history because of the hypothetically transient and variable nature of the resources edge species utilize (Figure 3.3; Allen et al.1999; Allen & Saunders, 2002; Allen & Saunders, 2006). That is, species located at the edges of aggregations may be prone migration because the resources they depend on are highly variable in their availability (Figure 5.3). To test these hypotheses I conducted identical analyses using two data sets, one excluding aquatic species and one including aquatic species.

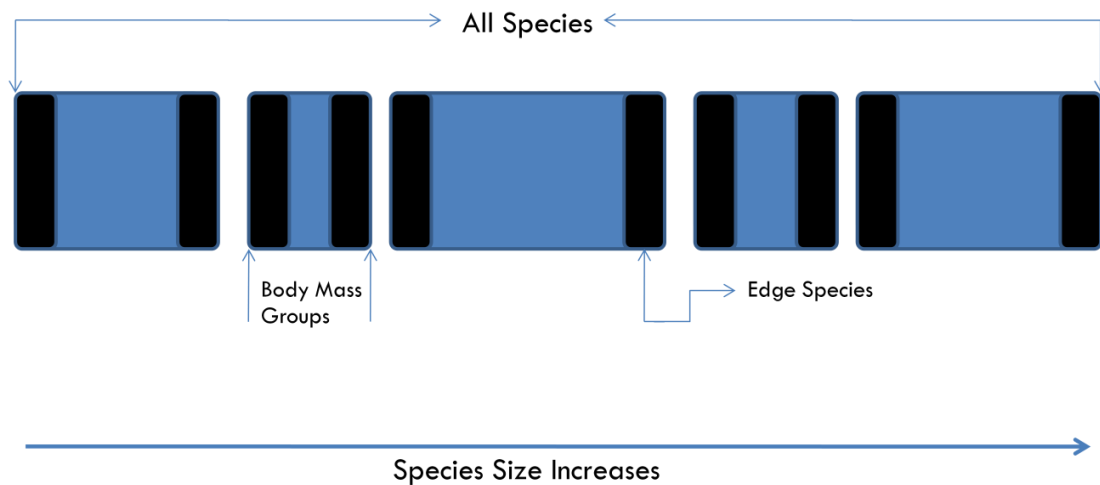


Figure 5.3 A representation of potential aggregations within a body mass distribution of a taxon of vertebrates from an ecosystem. Grey bars represent individual aggregations of species with similar body size and black bars within grey bars represent edge species.

METHODS

The data were independently collected by Austin Roberts from the Percy Fitzpatrick Institute in Cape Town, and donated for this study by Graeme Cumming also from the Percy Fitzpatrick Institute in Cape Town. A series of *a priori* models were constructed to predict species decline, each derived from theoretically suggested characteristics of declining species. I conducted identical analyses using two data sets, with and without aquatic species. Aquatic species food webs are compartmentalized, meaning they might have little influence in the composition of terrestrial food webs (Pimm & Lawton, 1980). Thus, aquatic species may have little influence in the distribution of terrestrial body masses (Allen et al. 1999). Aquatic species were identified by the usage of freshwater invertebrates as a main or secondary food sources and the usage of aquatic substrate.

South African bird species lacking sufficient observational data for the analysis were removed from the Robert's dataset ($n = 10$). Birds were grouped into habitat specific assemblages. The Robert's dataset provides four categories to describe a bird's habitat use: main, secondary, occasional use, and not used. In building habitat specific assemblages I included as "present" in a habitat species categorized by Roberts as "main" or "secondary" users of that habitat. The habitats analyzed were agricultural, Fynbos, grassland, Karoo, lagoon, savanna, wetland, and woodland.

Body masses of species were ordered from smallest to largest within each habitat and log transformed. I used Bayesian Classification And Regression Tree (BCART) analysis to test for and then calculate aggregations of species body masses within each

habitat. BCART examines numerical data for aggregations by creating combinations of observations in order to calculate the largest log integrated likelihood for all combinations of data entered into the software (Chipman et al. 1998). One million iterations of BCART were performed for each habitat to calculate aggregations of species.

Plausible models for each habitat were created and relative fit of models were analyzed (SAS Institute, 1985). Models with a weight of 10% of the highest ranked model were considered to be plausible models for explaining nomadism (Royall, 1997). AIC_c was used to account for bias in small sample sizes i.e. the ratio of observations to parameters used was less than 40 (Turkheimer et al. 2003). A test for linearity was performed for each model; none were determined to have linear model parameters. The models considered were (a) decline = body mass, (b) decline = DTCE (distance to the closest edge of a body mass aggregation), (c) decline = DTCE bodymass, (d) decline = DTCE foodrich, (e) decline = DTCE foragerich, (f) decline = DTCE habitatrich, (g) decline = DTCE habitatrich foodrich foragerich substratumrich bodymass, (h) decline = DTCE substratumrich, (i) decline = foodrich, (j) decline = foragerich, (k) decline = habitatrich, and (l) decline = substratumrich.

Foodrich, foragerich, habitatrich, and substratumrich tested for a link between generalism and species decline. Species exhibiting specialist characteristics have been hypothesized to decline more frequently over time (Christian et al. 2009). The bodymass parameter is included because size affects the scale of resources used and has been suggested as a predictor of decline (Cardillo, et al., 2005; Fisher & Owens, 2004). The distance to the closest edge of a body mass parameter describes a species location relative

to the edges of a body mass aggregation. It has been hypothesized that species located near body mass aggregation edges are frequently exposed to highly variable resource availability and thus tend to decline (Allen et al. 1999). Because the distance to the closest edge of a body mass aggregation may indicate highly variable resource availability (Allen et al. 1999) the parameter was included with other parameters to determine if a combination of resource variability and specializing or generalizing regarding resource utilization explains species decline. The distance to closest edge is determined by calculating the difference between each species in a species aggregation and the edge defining species of the aggregation.

RESULTS

Discontinuous distributions of body masses were identified for each South African habitat/ecosystem type (Table 5.1). The number of aggregations present with aquatic species excluded from analysis ranged from 4 to 12. The number of aggregations present with aquatic species included from analysis ranged from 5 to 12. Five habitats/ecosystems contained aquatic species. The percentage of aquatic species removed from each of these five habitats/ecosystems ranged from 1.4% (n = 1 Karoo) to 52% (n = 33 Lagoon). The differences in patterns among body mass distributions with aquatic and non-aquatic species was minimal. Even when 50% of the species are aquatic, and thus removed (Lagoon) for analysis, there was at most one fewer aggregation present. Thus, for the remainder of the results section I will only discuss the results of analysis with aquatic species removed.

Declining species were a minor component in most habitats: 3% (n = 2 Karoo), 5% (n = 7 agricultural), 12% (n = 13 grassland), 13% (n = 2 lagoon), 10% (n = 11 wetland), 6% (n = 16 woodland), and 6% (n = 13 savanna) for each habitat/ecosystem. There was generally a weak inference amongst logistic regression models in most habitats/ecosystems (Tables 5.2 – 5.8). Because of weak inference amongst models, model averaging was performed for each habitat's set of plausible model parameters (Table 5.9 – 5.15).

Within the top 10% of models associated with species decline was habitat richness and body mass. Within the composite models these parameters were also associated with species decline. All other parameters that were in the top 10% of ranked models had mixed results. The parameters substratumrich, edge, foodrich, and foragerich

had both negative and positive estimates associated with them throughout each habitat/ecosystem.

Table 5.1. The number of body mass aggregations and species per habitat within South African bird species, including and excluding aquatic species. The data are the result of Bayesian classification and regression tree analysis of South African bird species.

Habitat Type	Number of Aggregations Including Aquatic Species	Number of Species Including Aquatic Species	Number of Aggregations Excluding Aquatic Species	Number of Species Excluding Aquatic Species
Agricultural	10	152	10	145
Grassland	9	106	9	106
Karoo	7	70	7	69
Lagoon	5	33	4	16
Savanna	12	214	12	214
Wetland	9	177	8	108
Woodland	11	254	12	251

Table 5.2. Grassland Logistic Regression model results of South African bird species. The percentage of declining species is 12%. Models a value of 10% the highest ranked model (bold) are considered plausible explanatory models for decline within South African bird species. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.24	79.01	intercept only	-1.98	0.3
			-0.57	0.33
0.19	79.49	habitatrich		
0.12	80.35	bodymass	0.62	0.36
0.1	80.82	substratumrich	1.37	1.07
0.07	81.36	edge	-0.04	0.08
		habitatrich	-0.55	0.33
0.05	82	edge	-0.05	0.08
		bodymass	0.61	0.36
0.05	82.29	edge	-0.07	0.08
		substratumrich	1.41	1.07
0.05	82.25	foodrich	-0.37	0.41
0.04	82.56	edge	-0.06	0.08
0.03	83	foragerich	-0.23	0.65
0.02	84.09	edge	-0.04	0.08
		foragerich	-0.25	0.7
		foodrich	-0.25	0.42
		habitatrich	-0.54	0.36
		substratumrich	1.29	1.1
		bodymass	0.65	0.41
0.02	84.55	edge	-0.06	0.08
		foragerich	-0.25	0.63
0.01	84.87	edge	-0.05	0.08
		foodrich	-0.32	0.42

Table 5.3. Woodland Logistic Regression model results of South African bird species. The percentage of declining species is 6%. Models a value of 10% the highest ranked model (bold) are considered plausible explanatory models for decline within South African bird species. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.69	107.8	bodymass	1.37	0.35
0.27	109.69	edge	-0.03	0.07
		bodymass	1.38	0.35
0.03	113.89	edge	-0.02	0.08
		foragerich	0.91	0.46
		foodrich	-0.05	0.29
		habitatrich	-0.24	0.42
		substratumrich	0.75	0.68
		bodymass	1.31	0.37
0.01	117.35	foragerich	0.95	0.37
0	119.1	intercept only	-2.69	0.26
0	119.41	edge	0.0	0.08
		foragerich	0.95	0.37
0	121.91	foodrich	0.3	0.26
0	123.06	substratumrich	0.16	0.56
0	123.14	habitatrich	0.02	0.3
0	123.15	edge	0.0	0.08
0	123.97	edge	-0.01	0.08
		foodrich	0.3	0.26
0	125.12	edge	0.0	0.08
		substratumrich	0.16	0.56
0	125.21	edge	0.0	0.08
		habitatrich	0.02	0.3

Table 5.4. Wetland Logistic Regression model results of South African bird species. The percentage of declining species is 10%. Models a value of 10% the highest ranked model (bold) are considered plausible explanatory models for decline within South African bird species. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.28	70.56	bodymass	0.84	0.38
0.22	71.02	edge	-0.09	0.07
		bodymass	0.88	0.4
0.21	71.09	intercept only	-2.18	0.32
0.06	73.57	edge	-0.1	0.08
0.04	74.6	foragerich	0.55	0.63
0.03	74.78	edge	-0.1	0.08
		foragerich	0.66	0.66
0.03	74.92	substratumrich	-0.41	0.66
0.03	75.23	foodrich	0.11	0.35
0.03	75.26	habitatrich	0.07	0.3
0.02	75.48	edge	-0.1	0.08
		substratumrich	-0.33	0.67
0.02	75.64	edge	-0.1	0.08
		foodrich	0.1	0.35
0.02	75.72	edge	-0.1	0.08
		habitatrich	0.03	0.3
0	78.83	edge	-0.1	0.08
		foragerich	0.14	0.79
		foodrich	-0.44	0.42
		habitatrich	0.19	0.35
		substratumrich	0.11	0.75
		bodymass	1.16	0.52

Table 5.5. Agricultural Logistic Regression model results of South African bird species. The percentage of declining species is 5%. Models a value of 10% the highest ranked model (bold) are considered plausible explanatory models for decline within South African bird species. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.29	56.17	intercept only	-2.98	0.39
0.17	57.28	foodrich	-0.93	0.63
0.1	58.33	edge	0.09	0.09
		foodrich	-0.9	0.63
0.08	58.82	bodymass	0.62	0.5
0.07	59.13	foragerich	-0.94	1.03
0.07	59.14	edge	0.1	0.09
0.06	59.4	habitatrich	-0.4	0.45
0.04	60.03	edge	0.1	0.09
		foragerich	-0.96	1.01
0.04	60.18	substratumrich	-0.21	0.78
0.04	60.33	edge	0.07	0.09
		bodymass	0.52	0.53
0.03	60.54	edge	0.09	0.09
		habitatrich	-0.37	0.46
0.02	61.15	edge	0.1	0.09
		substratumrich	-0.26	0.79
0.01	64.18	edge	0.07	0.09
		foragerich	-1.1	1.07
		foodrich	-0.79	0.61
		habitatrich	-0.15	0.49
		substratumrich	-0.64	0.86
		bodymass	0.66	0.59

Table 5.6. Lagoon Logistic Regression model results of South African bird species. The percentage of declining species is 13%. Models a value of 10% the highest ranked model (bold) are considered plausible explanatory models for decline within South African bird species. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.59	12.98	intercept only	-1.94	0.75
0.08	16.87	substratumrich	1.79	1.61
0.08	17.06	foodrich	-0.71	0.77
0.05	17.95	foragerich	-0.41	1.32
0.05	17.98	habitatrich	-0.31	1.16
0.05	18	edge	-0.03	0.13
0.05	18.06	bodymass	-0.05	1.14
0.01	20.33	edge substratumrich	-0.06 1.93	0.15 1.68
0.01	20.6	edge bodymass	-0.04 -0.22	0.14 1.26
0.01	20.7	edge foodrich	-0.01 -0.69	0.14 0.83
0.01	21.51	edge habitatrich	-0.04 -0.4	0.13 1.16
0.01	21.56	edge foragerich	-0.02 -0.36	0.13 1.36
0	43.75	edge foragerich foodrich habitatrich substratumrich bodymass	-0.22 2.35 -1.37 1.13 3.5 -2.15	0.33 3.25 1.67 2.02 3.31 3.1

Table 5.7. Karoo Logistic Regression model results of South African bird species. The percentage of declining species is 3%. Models a value of 10% the highest ranked model (bold) are considered plausible explanatory models for decline within South African bird species. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.43	18.29	intercept only	-3.51	0.72
0.09	21.39	habitatrich	-0.74	0.81
0.07	21.77	foragerich	-1.48	1.96
0.07	21.77	substratumrich	-1.24	1.44
0.07	22.03	foodrich	0.33	0.46
0.06	22.23	edge	-0.07	0.15
0.06	22.24	bodymass	0.44	0.88
0.04	23.21	edge habitatrich	-0.1 -0.83	0.16 0.86
0.03	23.37	edge substratumrich	-0.15 -1.76	0.21 1.68
0.03	23.72	edge foragerich	-0.08 -1.54	0.16 1.99
0.03	23.86	edge foodrich	-0.1 0.47	0.16 0.58
0.02	24.2	edge bodymass	-0.07 0.49	0.14 0.89
0	28.98	edge foragerich foodrich habitatrich substratumrich bodymass	-0.2 -2.7 0.91 -1.5 -2.32 0.08	0.2 3.84 1.02 1.34 1.77 1.53

Table 5.8. Savanna Logistic Regression model results of South African bird species. The percentage of declining species is 6%. Models a value of 10% the highest ranked model (bold) are considered plausible explanatory models for decline within South African bird species. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness.

AIC _w	AIC _c	Model	Estimate	Standard Error
0.73	65.19	bodymass	2.53	0.54
0.26	67.25	edge	0.01	0.08
		bodymass	2.52	0.55
0.01	73.18	edge	0.01	0.08
		foragerich	0.63	0.47
		foodrich	-0.26	0.32
		habitatrich	-0.14	0.44
		substratumrich	-0.14	0.83
		bodymass	2.52	0.56
0	96.44	edge	0.13	0.08
		foragerich	0.88	0.36
0	96.77	foragerich	0.9	0.36
0	98.08	intercept only	-2.74	0.29
0	99.53	edge	0.13	0.08
0	100.62	edge	0.14	0.08
		foodrich	0.26	0.25
0	101.49	edge	0.13	0.08
		habitatrich	-0.1	0.31
0	101.56	edge	0.13	0.08
		substratumrich	0.14	0.62
0	101.52	foodrich	0.2	0.24
0	101.79	habitatrich	-0.17	0.3
0	102.11	substratumrich	0.09	0.62

Table 5.9. Logistic Regression composite decline model for South African birds located in grassland habitats. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, habitatrich = habitat richness, substratumrich = substrate richness.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
intercept	-2.14	1.35	0.1	-4.38
bodymass	0.62	0.37	1.23	0.01
edge	-0.05	0.08	0.08	-0.19
foodrich	-0.34	0.42	0.35	-1.03
habitatrich	-0.56	0.33	-0.01	-1.11
substratumrich	1.38	1.07	3.16	-0.4

Table 5.10. Logistic Regression composite decline model for South African birds located in woodland habitats. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
intercept	-5.4	0.93	-3.86	-6.94
bodymass	1.37	0.35	1.96	0.79
edge	-0.03	0.08	0.09	-0.16

Table 5.11. Logistic Regression composite decline model for South African birds located in wetland habitats. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
intercept	-2.84	1.11	-1	-4.68
bodymass	0.86	0.39	1.51	0.22
edge	-0.1	0.08	0.03	-0.22
foodrich	0.06	0.38	0.69	-0.56
foragerich	0.58	0.66	1.68	-0.52
habitatrich	0.07	0.31	0.58	-0.45
substratumrich	-0.34	0.68	0.79	-1.47

Table 5.12. Logistic Regression composite decline model for South African birds located in agricultural habitats. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
intercept	-2.6	1.23	-0.58	-4.63
bodymass	0.59	0.52	1.45	-0.26
edge	0.09	0.09	0.24	-0.06
foodrich	-0.91	0.63	0.13	-1.95
foragerich	-0.96	1.02	0.73	-2.65
habitatrich	-0.38	0.46	0.38	-1.13
substratumrich	-0.26	0.8	1.05	-1.58

Table 5.13. Logistic Regression composite decline model for South African birds located in lagoon habitats. Foodrich = food richness, foragerich = forage richness, substratumrich = substrate richness.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
intercept	-1.95	1.47	0.63	-4.53
foodrich	-0.71	0.78	0.66	-2.08
substratumrich	1.81	1.62	4.65	-1.02

Table 5.14. Logistic Regression composite decline model for South African birds located in the Karoo ecosystem. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation, foodrich = food richness, foragerich = forage richness, habitatrich = habitat richness, substratumrich = substrate richness.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
intercept	-2.88	1.75	0.04	-5.8
bodymass	0.44	0.9	1.94	-1.05
edge	-0.1	0.17	0.19	-0.38
foodrich	0.38	0.51	1.23	-0.47
foragerich	-1.52	2.01	1.83	-4.87
habitatrich	-0.78	0.84	0.62	-2.18
substratumrich	-1.42	1.54	1.16	-4

Table 5.15. Logistic Regression composite decline model for South African birds located in savanna habitats. Bodymass = species body mass, edge = distance to the closest edge of a body mass aggregation.

Parameter	Estimate	SE	Upper 90% CI	Lower 90% CI
intercept	-9.11	1.65	-6.39	-11.83
bodymass	2.53	0.54	3.42	1.64
edge	0.01	0.08	0.14	-0.12

DISCUSSION

Discontinuities within body mass axes were discovered within each ecosystem/habitat, reinforcing the ideas behind the Textural Discontinuity Hypothesis. Patterns of body mass aggregations among data sets including and excluding aquatic species were similar, suggesting that aquatic species have little influence on the body mass assemblages of terrestrial species and reinforcing the findings of Pimm & Lawton (1980) suggesting aquatic species food webs are compartmentalized.

There was little consistency among models in the confidence sets across habitats. Weights were generally low and confidence sets were large, yielding only weak inference. The application of the Textural Discontinuity Hypothesis is traditionally used to examine communities within ecosystems (Allen et al. 1999; Allen et al. 2002), applying the hypothesis to habitats may explain the weak inference. The percentage of plausible models for each habitat/ecosystems ranged from 15% ($n = 2$ savanna and woodland) to 85% ($n = 11$ agricultural). There did not exist a correlation between the number of species and the number of plausible models in the set of confidence set for the habitat/ecosystems ($p = 0.42$).

Among the set of composite models most confidence intervals included zero, giving little indication as to the actual response of those parameters in relation to species decline. Only two parameters, body mass and habitat richness, were repeatedly within confidence intervals above or below zero. Within the grassland, woodland, wetland, and savanna habitats the body mass of declining species were larger than their non-declining counterparts. The hypothesis that larger species are more likely to decline has been tested multiple times and the results of this analysis support such claims (Cardillo, et al., 2005; Fisher & Owens, 2004).

The grassland habitat composite model also indicates that non-habitat rich species tend to decline. A species that uses a greater diversity of habitats may decrease its likelihood of declining. These results may explain why island species assemblages consist of a greater number of generalist species over time (Christian et al. 2009). Generalists would have a greater capacity to utilize many different habitats and thus outcompete other animal species confined to a finite number of habitats.

Within the confidence set of models the parameters body mass and habitat rich are always positive and negative respectively. Four other model parameters substratum rich, edge, food rich, and forage rich are within the confidence set of models. These four parameters vary based on the habitat they are applied to, and thus yield little information as to a general set of species characteristics that predict species decline. These results do not necessarily indicate that the parameters are a poor predictor of species decline though. The amount of power in these analyses is poor due to the small amount of actual declining species, thus they likely contributed to the conflicting results.

The set of species characteristics that predict decline may be location specific. Within the models in each confidence set parameters were either negative or positive, and never both. For example within the Karoo ecosystem and grassland, woodland, and wetland habitats the edge parameter is within the confidence set and negative; indicating that species near the edges of body mass aggregations tend to decline. These results are countered within the agricultural and savanna habitats though. The results from these habitats suggest that species toward the center of body mass aggregations tend to decline. Nonetheless overall trends among the confidence set of models are difficult to assess with much certainty.

Multiple species characteristics appear to contribute to species decline. The data may indicate that predicting species decline is dependent on species location, and that a general “formula” for declining species is not necessarily possible. The data also indicate that species decline is primarily the result of increased body mass and a low capacity to utilize a diverse set of habitats.

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CHAPTER VI

SUMMARY

Discontinuities within body mass axes were discovered within each ecosystem/habitat; these results support the results of other studies (Allen et al. 1999; Havlicek & Carpenter, 2001; Allen et al. 2002). Body mass aggregations between data sets including and excluding aquatic species were similar, suggesting that aquatic species have little influence on the body mass assemblages of terrestrial species and reinforcing the findings of Pimm & Lawton (1980) suggesting aquatic species food webs are compartmentalized from terrestrial food webs.

My first analysis examined the underlying structure within species body mass aggregations. I hypothesized that species within a body mass aggregation would more evenly distribute themselves within a body mass aggregation due to morphological overdispersion, that is, I expected species within a given size class to have similar variance in the distance separating species in terms of body mass. The data suggested the opposite of my hypothesis; the data suggested there was more variance among species within body mass aggregations than one would expect by chance. It is clear that species are discontinuously dispersed into body mass aggregations, but how the interactions between species affect within aggregation distributions, if at all, is unknown. Based on the data morphological overdispersion is an unlikely candidate for the explanation of species distributions within body mass aggregations; species are not evenly spread out through body mass aggregations.

My second analysis examined migratory bird species within the framework of the Textural Discontinuity Hypothesis. The causes of migration are not well known and are debated (Rappole et al. 2003). Some scientists hypothesize that Neotropical forest birds

are mainly frugivorous/insectivorous (Levey & Stiles, 1992). Other scientists hypothesize that it is not a specific resource utilized by migratory bird species that tend to make them migratory, but a dependency on resources with increased scarcity (Boyle & Conway, 2007).

Only weak inference was possible in the analysis of predictors of migration, although the data did disagree with the findings of Levey & Stiles (1992) regarding fruit and nectar consumption of migratory birds. The distance to the closest edge of a body mass aggregation parameter was often negative indicating that it may play some part in predicting migration in bird species. The data support the initial hypothesis, that species near the edges of body mass aggregations will exhibit migratory tendencies.

The composite models for migration indicate that in the savanna habitat migratory species tend to be at the edges of body mass aggregations. Savanna migratory bird species also tended not to aerial feed as indicated by the composite models. In woodland habitats and the Karoo ecosystem more habitat rich species tended to be migratory; perhaps these results indicate that migratory bird species have a large capacity to utilize a wider array of habitats than do non-migratory species. In the savanna habitats migratory species tended not to utilize more substrate than their non-migratory counterparts; utilizing fewer substrates may lead birds to migrate and find usable substrate.

Also in the composite models the consumption of grain was positively associated with migration in the Fynbos ecosystem and woodland habitat. The consumption of grains by migratory birds may be the result of compensating for fluctuations in fat storage (Levey & Stiles 1992). In the composite models of the Karoo ecosystem migratory

species did not tend to utilize fruit which is contrary to the work of Levey and Stiles (1992) that suggest migratory bird species tend to utilize fruit.

My third analysis investigated nomadic bird species and their locations within body mass distributions. I hypothesized that nomadic bird species would be located more frequently at the edges of species aggregations, because they may utilize highly variable resources. Literature suggested that resources utilized by nomadic species are highly variable (Sinclair, 1984). If species near the edges of body mass aggregations were utilizing highly variable resources (Allen et al. 1999) then one would expect to observe nomadic species in close proximity to the edges of body mass aggregations.

Some of the data supported the initial hypothesis. The distance to the closest edge of a body mass aggregation was always negative, that is near the edges of body mass aggregations species tended to be nomadic. The data did not agree with the results from previous studies suggesting that granivory was an indicator of nomadism among South African bird species (Dean, 1997).

Within the composite models forage rich species were nomadic in the savanna, grassland, and agricultural habitats, indicating that nomadic bird species utilize more foraging techniques than do their non-nomadic counterparts. The composite models show that within agricultural habitats species located closer to the edges of body mass aggregations were nomadic, indicating that the Textural Discontinuity Hypothesis plays a role in predicting nomadic bird species. Composition models of the savanna habitats reviled nomadic bird species to consume fruit. The consumption of fruit by nomadic birds may indicate that there is a changing temporal and spatial distribution of fruit which nomadic birds have exploited, and as a result move about in a fashion that reflects these

changes. The savanna and woodland habitats, within the composite models show that nomadic bird species are less likely to be nectivorous. These data disagree with the results of Woinarski (2006), where he contended that nectivorous species tended to be nomadic. Woinarski's work involved birds from semi-arid southern Australia and not South Africa, so the exploitation of nectar by nomadic bird species may be geographically specific. The body mass parameter in the agricultural habitat composite model indicated that these bird species tended to be larger than non-nomadic species.

My final analysis investigated the phenomenon of species decline within the context of the Textural Discontinuity Hypothesis. I had hypothesized that highly variable resource availability reduces the probability of species located closer to the edges of species aggregations to avoid species decline. Other literature suggests that species with larger average body masses and specialist species have a tendency to decline over time (Cardillo, et al., 2005; Fisher & Owens, 2004; Christian et al. 2009).

The parameters habitatrich and body mass were negative and positive respectively, indicating that declining species were larger, which agrees with current literature (Cardillo, et al., 2005; Fisher & Owens, 2004), and utilized fewer habitats. The distance to the closest edge of a body mass aggregation was both positive and negative within different habitats, suggesting that body mass aggregations may be exhibiting different characteristics within different environments, or that the proximity to the edge of an aggregation is not an accurate predictor of species decline, or that there simply were not enough declining species to capture real differences among species.

Among the set of composite models most confidence intervals included zero, giving little indication as to the actual response of those parameters in relation to species

decline. Only two parameters, body mass and habitat richness, were repeatedly within confidence intervals above or below zero. Within the grassland, woodland, wetland, and savanna habitats the body mass of declining species were larger than their non-declining counterparts. The hypothesis that larger species are more likely to decline has been tested multiple times and the results of this analysis support such claims (Cardillo, et al., 2005; Fisher & Owens, 2004).

The grassland habitat composite model also indicates that non-habitat rich species tend to decline. A species that uses a greater diversity of habitats may decrease its likelihood of declining. These results may explain why island species assemblages consist of a greater number of generalist species over time (Christian et al. 2009). Generalists would have a greater capacity to utilize many different habitats and thus outcompete other animal species confined to a finite number of habitats.

Within the confidence set of models the parameters body mass and habitat rich are always positive and negative respectively. Four other model parameters substratum rich, edge, food rich, and forage rich are within the confidence set of models. These four parameters vary based on the habitat they are applied to, and thus yield little information as to a general set of species characteristics that predict species decline. These results do not necessarily indicate that the parameters are a poor predictor of species decline though. The amount of power in these analyses is poor because of a small amount of actual declining species, thus they likely contributed to the conflicting results.

Morphological overdispersion is an unlikely predictor of species spacing within body mass aggregations, although smaller species did tend to space themselves out more variably within body mass aggregations. Overall the data suggest that a combination of

species characteristics and species preferred habitat/ecosystems may describe different species phenomena. Generally birds seemed to be migratory or nomadic as a result of following resources throughout the landscape as the resources shift temporally and spatially. Also, the application of the Textural Discontinuity Hypothesis did assist in predicting migratory and nomadic bird species within composite models. There were no models that contained most of the weight excluding other potential models. It is likely that the species characteristics scientists observe are complex, and to assume there is a single observation to explain these characteristics may be an incorrect way of approaching the problem. Perhaps the conflicts between scientists and their explanations of species phenomena can be explained by acknowledging that a combination of scientific hypotheses may be correct, and that these species characteristics are context specific.

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