BOREAL BEAVERS (*CASTOR CANADENSIS*): HOME RANGE, TERRITORIALITY, FOOD HABITS AND GENETICS OF A MID-CONTINENT POPULATION

BY

MICHELLE WHEATLEY

A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

Department of Zoology
University of Manitoba
Winnipeg, Manitoba

(c) April, 1994

National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

THE AUTHOR HAS GRANTED AN IRREVOCABLE NON-EXCLUSIVE LICENCE ALLOWING THE NATIONAL LIBRARY OF CANADA TO REPRODUCE, LOAN, DISTRIBUTE OR SELL COPIES OF HIS/HER THESIS BY ANY MEANS AND IN ANY FORM OR FORMAT, MAKING THIS THESIS AVAILABLE TO INTERESTED PERSONS.

L'AUTEUR A ACCORDE UNE LICENCE IRREVOCABLE ET NON EXCLUSIVE PERMETTANT A LA BIBLIOTHEQUE NATIONALE DU CANADA DE REPRODUIRE, PRETER, DISTRIBUER OU VENDRE DES COPIES DE SA THESE DE QUELQUE MANIERE ET SOUS QUELQUE FORME QUE CE SOIT POUR METTRE DES EXEMPLAIRES DE CETTE THESE A LA DISPOSITION DES PERSONNE INTERESSEES.

THE AUTHOR RETAINS OWNERSHIP OF THE COPYRIGHT IN HIS/HER THESIS. NEITHER THE THESIS NOR SUBSTANTIAL EXTRACTS FROM IT MAY BE PRINTED OR OTHERWISE REPRODUCED WITHOUT HIS/HER PERMISSION.

L'AUTEUR CONSERVE LA PROPRIETE DU DROIT D'AUTEUR QUI PROTEGE SA THESE. NI LA THESE NI DES EXTRAITS SUBSTANTIELS DE CELLE-CI NE DOIVENT ETRE IMPRIMES OU AUTREMENT REPRODUITS SANS SON AUTORISATION.

ISBN 0-315-99007-4

Canada

Name Michelle Wheatley

Dissertation Abstracts International is arranged by broad, general subject categories. Please select the one subject which most nearly describes the content of your dissertation. Enter the corresponding four-digit code in the spaces provided.

Zoology
SUBJECT TERM

0472
SUBJECT CODE

UMI

Subject Categories

THE HUMANITIES AND SOCIAL SCIENCES

COMMUNICATIONS AND THE ARTS
Architecture 0729
Art History 0377
Cinema 0900
Dance 0378
Fine Arts 0357
Information Science 0723
Journalism 0391
Library Science 0399
Mass Communications 0708
Music 0413
Speech Communication 0459
Theater 0465

EDUCATION
General 0515
Administration 0514
Adult and Continuing 0516
Agricultural 0517
Art 0273
Bilingual and Multicultural 0282
Business 0688
Community College 0275
Curriculum and Instruction 0727
Early Childhood 0518
Elementary 0524
Finance 0277
Guidance and Counseling 0519
Health 0680
Higher 0745
History of 0520
Home Economics 0278
Industrial 0521
Language and Literature 0279
Mathematics 0280
Music 0522
Philosophy of 0998
Physical 0523
Psychology 0525
Reading 0535
Religious 0527
Sciences 0714
Secondary 0533
Social Sciences 0534
Sociology of 0340
Special 0529
Teacher Training 0530
Technology 0710
Tests and Measurements 0288
Vocational 0747

LANGUAGE, LITERATURE AND LINGUISTICS
Language
- General 0679
- Ancient 0289
- Linguistics 0290
- Modern 0291

Literature
- General 0401
- Classical 0294
- Comparative 0295
- Medieval 0297
- Modern 0298
- African 0316
- American 0591
- Asian 0305
- Canadian (English) 0352
- Canadian (French) 0355
- English 0593
- Germanic 0311
- Latin American 0312
- Middle Eastern 0315
- Romance 0313
- Slavic and East European 0314

PHILOSOPHY, RELIGION AND THEOLOGY
Philosophy 0422
Religion
- General 0318
- Biblical Studies 0321
- Clergy 0319
- History of 0320
- Philosophy of 0322

Theology 0469

SOCIAL SCIENCES
American Studies 0323
Anthropology
- Archaeology 0324
- Cultural 0326
- Physical 0327

Business Administration
- General 0310
- Accounting 0272
- Banking 0770
- Management 0454
- Marketing 0338

Canadian Studies 0385
Economics
- General 0501
- Agricultural 0503
- Commerce-Business 0505
- Finance 0508
- History 0509
- Labor 0510
- Theory 0511

Folklore 0358
Geography 0366
Gerontology 0351
History
- General 0578
- Ancient 0579
- Medieval 0581
- Modern 0582
- Black 0328
- African 0331
- Asia, Australia and Oceania 0332
- Canadian 0334
- European 0335
- Latin American 0336
- Middle Eastern 0333
- United States 0337

History of Science 0585
Law 0398
Political Science
- General 0615
- International Law and Relations 0616
- Public Administration 0617

Recreation 0814
Social Work 0452
Sociology
- General 0626
- Criminology and Penology 0627
- Demography 0938
- Ethnic and Racial Studies 0631
- Individual and Family Studies 0628
- Industrial and Labor Relations 0629
- Public and Social Welfare 0630
- Social Structure and Development 0700
- Theory and Methods 0344

Transportation 0709
Urban and Regional Planning 0999
Women's Studies 0453

THE SCIENCES AND ENGINEERING

BIOLOGICAL SCIENCES
Agriculture
- General 0473
- Agronomy 0285
- Animal Culture and Nutrition 0475
- Animal Pathology 0476
- Food Science and Technology 0359
- Forestry and Wildlife 0478
- Plant Culture 0479
- Plant Pathology 0480
- Plant Physiology 0817
- Range Management 0777
- Wood Technology 0746

Biology
- General 0306
- Anatomy 0287
- Biostatistics 0308
- Botany 0309
- Cell 0379
- Ecology 0329
- Entomology 0353
- Genetics 0369
- Limnology 0793
- Microbiology 0410
- Molecular 0307
- Neuroscience 0317
- Oceanography 0416
- Physiology 0433
- Radiation 0821
- Veterinary Science 0778
- Zoology 0472

Biophysics
- General 0786
- Medical 0760

EARTH SCIENCES
Biogeochemistry 0425
Geochemistry 0996
Geodesy 0370
Geology 0372
Geophysics 0373
Hydrology 0388
Mineralogy 0411
Paleobotany 0345
Paleoecology 0426
Paleontology 0418
Paleozoology 0985
Palynology 0427
Physical Geography 0368
Physical Oceanography 0415

HEALTH AND ENVIRONMENTAL SCIENCES
Environmental Sciences 0768
Health Sciences
- General 0566
- Audiology 0300
- Chemotherapy 0992
- Dentistry 0567
- Education 0350
- Hospital Management 0769
- Human Development 0758
- Immunology 0982
- Medicine and Surgery 0564
- Mental Health 0347
- Nursing 0569
- Nutrition 0570
- Obstetrics and Gynecology 0380
- Occupational Health and Therapy 0354
- Ophthalmology 0381
- Pathology 0571
- Pharmacology 0419
- Pharmacy 0572
- Physical Therapy 0382
- Public Health 0573
- Radiology 0574
- Recreation 0575
- Speech Pathology 0460
- Toxicology 0383

Home Economics 0386

PHYSICAL SCIENCES
Pure Sciences
Chemistry
- General 0485
- Agricultural 0749
- Analytical 0486
- Biochemistry 0487
- Inorganic 0488
- Nuclear 0738
- Organic 0490
- Pharmaceutical 0491
- Physical 0494
- Polymer 0495
- Radiation 0754

Mathematics 0405
Physics
- General 0605
- Acoustics 0986
- Astronomy and Astrophysics 0606
- Atmospheric Science 0608
- Atomic 0748
- Electronics and Electricity 0607
- Elementary Particles and High Energy 0798
- Fluid and Plasma 0759
- Molecular 0609
- Nuclear 0610
- Optics 0752
- Radiation 0756
- Solid State 0611

Statistics 0463

Applied Sciences
Applied Mechanics 0346
Computer Science 0984
Engineering
- General 0537
- Aerospace 0538
- Agricultural 0539
- Automotive 0540
- Biomedical 0541
- Chemical 0542
- Civil 0543
- Electronics and Electrical 0544
- Heat and Thermodynamics 0348
- Hydraulic 0545
- Industrial 0546
- Marine 0547
- Materials Science 0794
- Mechanical 0548
- Metallurgy 0743
- Mining 0551
- Nuclear 0552
- Packaging 0549
- Petroleum 0765
- Sanitary and Municipal 0554
- System Science 0790

Geotechnology 0428
Operations Research 0796
Plastics Technology 0795
Textile Technology 0994

PSYCHOLOGY
General 0621
Behavioral 0384
Clinical 0622
Developmental 0620
Experimental 0623
Industrial 0624
Personality 0625
Physiological 0989
Psychobiology 0349
Psychometrics 0632
Social 0451

Nom _____

Dissertation Abstracts International est organisé en catégories de sujets. Veuillez s.v.p. choisir le sujet qui décrit le mieux votre thèse et inscrivez le code numérique approprié dans l'espace réservé ci-dessous.

_____ ☐☐☐ U·M·I

SUJET — CODE DE SUJET

Catégories par sujets

HUMANITÉS ET SCIENCES SOCIALES

COMMUNICATIONS ET LES ARTS
Architecture 0729
Beaux-arts 0357
Bibliothéconomie 0399
Cinéma 0900
Communication verbale 0459
Communications 0708
Danse 0378
Histoire de l'art 0377
Journalisme 0391
Musique 0413
Sciences de l'information 0723
Théâtre 0465

ÉDUCATION
Généralités 515
Administration 0514
Art 0273
Collèges communautaires 0275
Commerce 0688
Économie domestique 0278
Éducation permanente 0516
Éducation préscolaire 0518
Éducation sanitaire 0680
Enseignement agricole 0517
Enseignement bilingue et multiculturel 0282
Enseignement industriel 0521
Enseignement primaire. 0524
Enseignement professionnel 0747
Enseignement religieux 0527
Enseignement secondaire 0533
Enseignement spécial 0529
Enseignement supérieur 0745
Évaluation 0288
Finances 0277
Formation des enseignants 0530
Histoire de l'éducation 0520
Langues et littérature 0279
Lecture 0535
Mathématiques 0280
Musique 0522
Orientation et consultation 0519
Philosophie de l'éducation 0998
Physique 0523
Programmes d'études et enseignement 0727
Psychologie 0525
Sciences 0714
Sciences sociales 0534
Sociologie de l'éducation 0340
Technologie 0710

LANGUE, LITTÉRATURE ET LINGUISTIQUE
Langues
- Généralités 0679
- Anciennes 0289
- Linguistique 0290
- Modernes 0291

Littérature
- Généralités 0401
- Anciennes 0294
- Comparée 0295
- Médiévale 0297
- Moderne 0298
- Africaine 0316
- Américaine 0591
- Anglaise 0593
- Asiatique 0305
- Canadienne (Anglaise) 0352
- Canadienne (Française) 0355
- Germanique 0311
- Latino-américaine 0312
- Moyen-orientale 0315
- Romane 0313
- Slave et est-européenne 0314

PHILOSOPHIE, RELIGION ET THÉOLOGIE
Philosophie 0422
Religion
- Généralités 0318
- Clergé 0319
- Études bibliques 0321
- Histoire des religions 0320
- Philosophie de la religion 0322

Théologie 0469

SCIENCES SOCIALES
Anthropologie
- Archéologie 0324
- Culturelle 0326
- Physique 0327

Droit 0398
Économie
- Généralités 0501
- Commerce-Affaires 0505
- Économie agricole 0503
- Économie du travail 0510
- Finances 0508
- Histoire 0509
- Théorie 0511

Études américaines 0323
Études canadiennes 0385
Études féministes 0453
Folklore 0358
Géographie 0366
Gérontologie 0351
Gestion des affaires
- Généralités 0310
- Administration 0454
- Banques 0770
- Comptabilité 0272
- Marketing 0338

Histoire
- Histoire générale 0578
- Ancienne 0579
- Médiévale 0581
- Moderne 0582
- Histoire des noirs 0328
- Africaine 0331
- Canadienne 0334
- États-Unis 0337
- Européenne 0335
- Moyen-orientale 0333
- Latino-américaine 0336
- Asie, Australie et Océanie 0332

Histoire des sciences 0585
Loisirs 0814
Planification urbaine et régionale 0999
Science politique
- Généralités 0615
- Administration publique 0617
- Droit et relations internationales 0616

Sociologie
- Généralités 0626
- Aide et bien-être social 0630
- Criminologie et établissements pénitentiaires 0627
- Démographie 0938
- Études de l' individu et de la famille 0628
- Études des relations interethniques et des relations raciales 0631
- Structure et développement social 0700
- Théorie et méthodes. 0344
- Travail et relations industrielles 0629

Transports 0709
Travail social 0452

SCIENCES ET INGÉNIERIE

SCIENCES BIOLOGIQUES
Agriculture
- Généralités 0473
- Agronomie. 0285
- Alimentation et technologie alimentaire 0359
- Culture 0479
- Élevage et alimentation 0475
- Exploitation des pâturages 0777
- Pathologie animale 0476
- Pathologie végétale 0480
- Physiologie végétale 0817
- Sylviculture et faune 0478
- Technologie du bois 0746

Biologie
- Généralités 0306
- Anatomie 0287
- Biologie (Statistiques) 0308
- Biologie moléculaire 0307
- Botanique 0309
- Cellule 0379
- Écologie 0329
- Entomologie 0353
- Génétique 0369
- Limnologie 0793
- Microbiologie 0410
- Neurologie 0317
- Océanographie 0416
- Physiologie 0433
- Radiation 0821
- Science vétérinaire 0778
- Zoologie 0472

Biophysique
- Généralités 0786
- Medicale 0760

SCIENCES DE LA TERRE
Biogéochimie 0425
Géochimie 0996
Géodésie 0370
Géographie physique 0368
Géologie 0372
Géophysique 0373
Hydrologie 0388
Minéralogie 0411
Océanographie physique 0415
Paléobotanique 0345
Paléoécologie 0426
Paléontologie 0418
Paléozoologie 0985
Palynologie 0427

SCIENCES DE LA SANTÉ ET DE L'ENVIRONNEMENT
Économie domestique 0386
Sciences de l'environnement 0768
Sciences de la santé
- Généralités 0566
- Administration des hôpitaux 0769
- Alimentation et nutrition 0570
- Audiologie 0300
- Chimiothérapie 0992
- Dentisterie 0567
- Développement humain 0758
- Enseignement 0350
- Immunologie 0982
- Loisirs 0575
- Médecine du travail et thérapie 0354
- Médecine et chirurgie 0564
- Obstétrique et gynécologie 0380
- Ophtalmologie 0381
- Orthophonie 0460
- Pathologie 0571
- Pharmacie 0572
- Pharmacologie 0419
- Physiothérapie 0382
- Radiologie 0574
- Santé mentale 0347
- Santé publique 0573
- Soins infirmiers 0569
- Toxicologie 0383

SCIENCES PHYSIQUES
Sciences Pures
Chimie
- Généralités 0485
- Biochimie 487
- Chimie agricole 0749
- Chimie analytique 0486
- Chimie minérale 0488
- Chimie nucléaire 0738
- Chimie organique 0490
- Chimie pharmaceutique 0491
- Physique 0494
- PolymÈres 0495
- Radiation 0754

Mathématiques 0405
Physique
- Généralités 0605
- Acoustique 0986
- Astronomie et astrophysique 0606
- Électronique et électricité 0607
- Fluides et plasma 0759
- Météorologie 0608
- Optique 0752
- Particules (Physique nucléaire) 0798
- Physique atomique 0748
- Physique de l'état solide 0611
- Physique moléculaire 0609
- Physique nucléaire 0610
- Radiation 0756

Statistiques 0463

Sciences Appliqués Et Technologie
Informatique 0984
Ingénierie
- Généralités 0537
- Agricole 0539
- Automobile 0540
- Biomédicale 0541
- Chaleur et thermodynamique 0348
- Conditionnement (Emballage) 0549
- Génie aérospatial 0538
- Génie chimique 0542
- Génie civil 0543
- Génie électronique et électrique 0544
- Génie industriel 0546
- Génie mécanique 0548
- Génie nucléaire 0552
- Ingénierie des systèmes 0790
- Mécanique navale 0547
- Métallurgie 0743
- Science des matériaux 0794
- Technique du pétrole 0765
- Technique minière 0551
- Techniques sanitaires et municipales 0554
- Technologie hydraulique 0545

Mécanique appliquée 0346
Géotechnologie 0428
Matières plastiques (Technologie) 0795
Recherche opérationnelle 0796
Textiles et tissus (Technologie) 0794

PSYCHOLOGIE
Généralités 0621
Personnalité 0625
Psychobiologie 0349
Psychologie clinique 0622
Psychologie du comportement 0384
Psychologie du développement 0620
Psychologie expérimentale 0623
Psychologie industrielle 0624
Psychologie physiologique 0989
Psychologie sociale 0451
Psychométrie 0632

BOREAL BEAVER (*CASTOR CANADENSIS*):HOME RANGE, TERRITORIALITY, FOOD HABITS AND GENETICS OF A MID-CONTINENT POPULATION

BY

MICHELLE WHEATLEY

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

© 1994

Permission has been granted to the LIBRARY OF THE UNIVERSITY OF MANITOBA to lend or sell copies of this thesis, to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film, and UNIVERSITY MICROFILMS to publish an abstract of this thesis.

The author reserves other publications rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's permission.

MICHELLE WHEATLEY

BOREAL BEAVERS (*CASTOR CANADENSIS*): HOME RANGE, TERRITORIALITY, FOOD HABITS AND GENETICS OF A MID-CONTINENT POPULATION

ABSTRACT

I studied beavers (*Castor canadensis*) in the boreal forest of eastern Manitoba from 1986 to 1992. I captured and ear tagged 60 different beavers, and outfitted 42 of these animals with transmitters. I collected sufficient data to determine summer home range size for 34 beavers and to determine fall home range size for 27 beavers. I examined: methods of delineating beaver home range; the effects of season, habitat, sex and age class on home range size; whether beavers were territorial; food selection by beavers; and genetic relatedness within the beaver population in my study area.

I compared estimates of beaver home range size and shape using four different methods: grid; minimum convex polygon (MCP); modified minimum area (MMA); and the Jennrich-Turner ellipse. The grid gives the smallest estimate most often and the ellipse or minimum convex polygon give the largest. The ellipse works best for home ranges with only one area of concentrated use near the centre. The MCP and MMA work best when the distribution of observations is a regular shape, with no protruding arms. The grid method is most suitable for animals with irregularly shaped home ranges or home ranges with several areas of concentrated use, and appears best suited for use with beavers.

Summer home range areas average 10.34 ha and fall averaged 3.07 ha. Thirty-seven of 38 beavers had core areas in summer, and 21 of 27 had core areas in fall. Home range size and core size were positively correlated in both summer and fall. Summer home ranges were significantly larger than fall home ranges, with fall home ranges being

centred closer to the lodge than summer ranges. Winter home ranges were restricted to less than 0.25 ha around the lodge.

Summer home range size was positively correlated with fall home range size, and summer and fall core sizes were also positively correlated. Percent of area in the core and percent of activity in the core were similar for all habitats and sex and age classes in summer.

Beavers living in river habitat had the largest summer and fall home ranges. Those living in pond habitats had the smallest summer home ranges but did not differ from lake beavers in the fall. Adult males usually had the largest home ranges, and adult females the smallest in both seasons. Adult females usually had home ranges centred closer to the lodge, and adult males farther from the lodge, than other family members.

In 6 years and over 600 days of observing beavers, I never observed any evidence of aggressive behaviour among beavers. Some overlap of home ranges occurred, especially on the river, but most home ranges were almost exclusive to a family group. I found no evidence that scent mounds delineated territory and no evidence to prove the presence of territories. I hypothesize that mutual avoidance is more likely than territorialism.

Beavers in the taiga show a preference for *Populus tremuloides* as a primary food in both spring and summer. In spring *Pinus banksiana* is also consumed. *P. tremuloides* leaves are the preferred summer food and *P. tremuloides* bark and *P. banksiana* growing tips are preferred in spring. Beaver food choices appear to maximize protein intake and minimize potassium to sodium ratio. This strategy may serve to foster growth during the relatively short period of high protein availability.

DNA fingerprinting studies of 60 beavers showed a mean band sharing coefficient (BSC) among unrelated beavers of 0.36 ± 0.087, and among known first order relatives of 0.62 ± 0.099. Beavers of unknown relationship in the population had a mean BSC of 0.40 ± 0.107,

significantly smaller than known first order relatives, but significantly larger than the value for unrelated animals. Further study is needed to determine what role the relatedness plays in limiting territorial behaviour.

ACKNOWLEDGEMENTS

My supervisor, Dr. W.O. Pruitt, Jr. initiated this project. I thank him for his encouragement, patience and enthusiasm as this venture took shape and reached completion. I also thank him and his wife Erna for their hospitality during my trips to Winnipeg over my five years living at Taiga Biological Station. My parents Drs. Brian and Margaret Wheatley provided encouragement and financial support. This thesis would never have reached completion without their support. I thank them for everything.

Bill Conley provided companionship in the field and many tips on repairing snowmobiles and boat motors. He also entertained with many a fine meal and drink of rum and numerous interesting tales of the past. I thank both Bill and his sister Nell for their kindness and hospitality. Ed Engen of Manitoba Department of Natural Resources supplied the station with a snowmobile and provided many great meals and care packages. The people of Bissett welcomed me into their community. I thank them for their hospitality and friendship.

Numerous volunteers and summer assistants helped with bushwhacking, boat driving and surgery. The many people are too numerous to mention, but their efforts are much appreciated.

The Statistical Advisory Service, and especially Llewellyn Armstrong provided statistical advice and expertise in determining the centroids of activity for beavers.

I am grateful for the financial support provided by the Murphy Foundation; Taiga Biological Station Research Trust; Wildlife Branch, Manitoba Natural Resources; Manitoba Wildlife Foundation; Manitoba Chapter, The Wildlife Society; and Sigma Xi.

The Department of Zoology secretaries, Urmilla Deonauth, Madeleine Harris, Judy Johnson and Irene Labrosse typed many a grant or

scholarship application on short notice and provided cheerful greetings on my trips to Winnipeg.

My advisory committee has changed over the years, but I thank the present and past members: Dr. C. Jay, Dr. J. Gee, Dr. K.W. Stewart and Dr. R.R. Riewe. Their advice over the years has improved this thesis and guided my research. In addition, Dr. S.H. Jenkins from the University of Nevada - Reno served as my external examiner and provided many useful comments and criticisms of this manuscript.

TABLE OF CONTENTS

ABSTRACT ii

ACKNOWLEDGEMENTS v

TABLE OF CONTENTS vii

LIST OF TABLES xii

LIST OF FIGURES xiv

CHAPTER 1. INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION 1

LITERATURE REVIEW 3

FOOD 3

MOVEMENTS AND HOME RANGE 4

Dispersal 4

Home Range 5

WINTER ACTIVITIES 5

BEHAVIOUR 6

REPRODUCTION AND SURVIVORSHIP 6

TECHNIQUES 7

OBJECTIVES 8

STUDY AREA 9

LITERATURE CITED 11

CHAPTER 2. AN ANALYSIS OF FOUR TECHNIQUES OF ESTIMATING HOME RANGE SIZES USING FIELD DATA

ABSTRACT 17

INTRODUCTION 18

METHODS 20

RESULTS 23

DISCUSSION 42

APPLICATION OF METHODS TO ESTIMATE HOME RANGE SIZE 43

CONCLUSIONS 46

LITERATURE CITED 47

CHAPTER 3. HOME RANGE SIZES OF BEAVER IN SUMMER

ABSTRACT 49

INTRODUCTION 50

METHODS 52

RADIOTELEMETRY 52

TERMS AND DEFINITIONS 54

ANALYSIS 55

RESULTS 56

HABITAT 59

Pond 59

Lake 60

River 60

FAMILY 60

Centroids 62

DISCUSSION 70

HOME RANGE SIZE AND SHAPE 70

CORE AREAS 71

HABITAT 72

FAMILY 73

CONCLUSIONS 75

LITERATURE CITED 76

CHAPTER 4. HOME RANGE SIZES OF BEAVER IN FALL

ABSTRACT 78

INTRODUCTION 79

METHODS 80

RADIOTELEMETRY 80

TERMS AND DEFINITIONS 82

ANALYSIS 83

RESULTS 84

HABITAT 87

Pond 87

Lake 87
River 88
FAMILY 88
Centroids 91
DISCUSSION 97
HOME RANGE SIZE AND USE 97
CONCLUSIONS 100
LITERATURE CITED 101
CHAPTER 5. SEASONAL VARIATION IN HOME RANGE SIZES OF BEAVER
ABSTRACT 103
INTRODUCTION 104
METHODS 106
RADIOTELEMETRY 106
TERMS AND DEFINITIONS 108
ANALYSIS 109
RESULTS 110
HABITAT 115
Pond 115
Lake 115
River 116
CENTROIDS 116
DISCUSSION 122
HOME RANGE SIZE AND USE 122
Core Areas 123
CORRELATIONS 124
CENTROIDS 124
CONCLUSIONS 125
LITERATURE CITED 126
CHAPTER 6. ARE BEAVERS TERRITORIAL?
ABSTRACT 128
INTRODUCTION 129

METHODS 130
RESULTS 132
DISCUSSION 141
Scent Mounds 141
Mutual Avoidance 142
CONCLUSIONS 145
LITERATURE CITED 146
CHAPTER 7. SEASONAL VARIATION IN FOOD PREFERENCES OF BEAVERS
ABSTRACT 148
INTRODUCTION 149
METHODS 151
RESULTS 152
SPECIES PREFERENCES 152
NUTRIENT CONTENT 152
Protein 154
Macroelements 154
Trace elements 162
DISCUSSION 168
SEASONAL PREFERENCES 168
NUTRIENTS 170
Protein 170
Macroelements 171
Trace Elements 172
Energy and other aspects 172
CONCLUSIONS 175
LITERATURE CITED 176
CHAPTER 8. DNA FINGERPRINTING OF BEAVERS: AN ASSESSMENT OF RELATEDNESS
ABSTRACT 179
INTRODUCTION 180
METHODS 182

COLLECTION OF SAMPLES 182
DNA FINGERPRINTING 182
STATISTICAL ANALYSIS 185
RESULTS 186
FAMILY 186
DISCUSSION 190
CONCLUSIONS 194
LITERATURE CITED 195
CHAPTER 9. SUMMARY
SUMMARY 197
LITERATURE CITED 200
APPENDIX 1. HOME RANGE MAPS 211
APPENDIX 2. HOME RANGE USE GRAPHS 285
APPENDIX 3. KOLMOGOROV-SMIRNOV VALUES 330
APPENDIX 4. CENTROID MAPS 334
APPENDIX 5. DNA AUTORADIOGRAPHS 343

LIST OF TABLES

CHAPTER 2

Table 1. Home range sizes, as determined by grid cell method, minimum convex polygon method (MCP), modified minimum area method (MMA) and Jennrich Turner ellipse method (JT ellipse). 24

Table 2. Home range estimate values using different methods of estimatation for examples where JT ellipse, MCP or Grid give the largest estimates and for cases where JT ellipse, MMA or Grid give the smallest estimates. Grid = grid cell method, MCP = minimum convex polygon method, MMA = modified minimum area method, JT ellipse = Jennrich Turner ellipse method. 33

CHAPTER 6

Table 1. Overlap values (S) for beavers with overlapping home ranges in 1987, 1989 and 1990.

$$S_{12} = \frac{A}{A_1} \quad \text{and} \quad S_{21} = \frac{A}{A_2}$$

where: A_1 = home range area of beaver 1
A_2 = home range area of beaver 2
A = area of overlap of beavers 1 and 2
S_{12} = proportion of home range of beaver 1 overlapped by beaver 2
S_{21} = proportion of home range of beaver 2 overlapped by beaver 1 139

CHAPTER 7

Table 1. Summary of vegetation samples used for nutrient testing. Code numbers correlate with codes in Figures 1 to 12. 153

CHAPTER 8

Table 1. Literature values for mean band sharing coefficients for known first order relatives for several bird and mammal species. 191

Table 2. Literature values for mean band sharing coefficients for unrelated members of several bird and mammal species. 192

APPENDIX 3

Table 1. Values of K (Kolmogorov-Smirnov Statistic) for summer home ranges, p value <0.05 indicates presence of core area.
† 1987, ‡ 1988, ¶ 1989, § 1990, # 1991, * Overnights . . 330

Table 2. Values of K (Kolmogorov-Smirnov Statistic) for fall home ranges, p value <0.05 indicates presence of core area. † 1987, ‡ 1988, ¶ 1989, § 1990, # 1991, * Overnights . . 332

Table 3. Values of K (Kolmogorov-Smirnov Statistic) for spring, late spring and late summer home ranges, p value <0.05 indicates presence of core area. † 1987, ‡ 1988, ¶ 1989, § 1990, # 1991, * Overnights . . 333

APPENDIX 5

Table 1. Summary of composition of families groups in DNA study. Refer to Figure 1 in Chapter 8 for geographic location of families. 343

LIST OF FIGURES

CHAPTER 1

Figure 1. Location of study area in Manitoba and detail of study area. 10

CHAPTER 2

Figure 1. Correlation between home range area estimates using JT ellipse method and grid method. 27

Figure 2. Correlation between home range area estimates using JT ellipse method and MCP method. 28

Figure 3. Correlation between home range area estimates using JT ellipse method and MMA method. 29

Figure 4. Correlation between home range area estimates using MCP method and grid method. 30

Figure 5. Correlation between home range area estimates using MCP method and MMA method. 31

Figure 6. Correlation between home range area estimates using MMA method and grid method. 32

Figure 7. Comparisons of home range outlines for 4 home range estimation methods, for the case with the largest difference between the estimates, BR1848. Squares = grid method;——— = JT ellipse;——— = minimum convex polygon; and- - - - = modified minimum area. Ellipse method largest, grid smallest. 35

Figure 8. Comparisons of home range outlines for 4 home range estimation methods, for the case with the most similar estimates, GP1611. Squares = grid method;——— = JT ellipse;——— = minimum convex polygon; and- - - - = modified minimum area. Grid largest, MMA smallest. 36

Figure 9. Comparisons of home range outlines for 4 home range estimation methods, JRB1649. Squares = grid method;——— = JT ellipse;——— = minimum convex polygon; and- - - - = modified minimum area. Ellipse largest, grid smallest. 37

Figure 10. Comparisons of home range outlines for 4 home range estimation methods, BR1603. Squares = grid method;——— = JT ellipse;——— = minimum convex polygon; and- - - - = modified minimum area. MCP largest, grid smallest. 38

Figure 11. Comparisons of home range outlines for 4 home range estimation methods, IP403. Squares = grid method;——— = JT ellipse;——— = minimum convex polygon; and- - - - = modified minimum area. MCP largest, MMA smallest. 39

Figure 12. Comparisons of home range outlines for 4 home range estimation methods, TB1510. Squares = grid method;——— = JT ellipse;——— = minimum convex polygon; and– – – – = modified minimum area. MCP largest, ellipse smallest. 40

CHAPTER 3

Figure 1. Summer home range area size (open symbols) and core area size (closed symbols) (hectares) for all beavers combined and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range. 57

Figure 2. Summer core size as percent of total home range size (open symbols) and percent of all activity in core area (closed symbols) for all beavers combined and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range. 58

Figure 3. Summer home range area size (open symbols) and core area size (closed symbols) (hectares) for beavers living in family groups, by sex and age class. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range. 61

Figure 4. Summer core size as percent of total home range size (open symbols) and percent of all activity in core area (closed symbols) for beavers living in family groups, by sex and age class. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range. 63

Figure 5. Centroids of activity for Implant Pond Family, Summer, 1989. Centroids are shown ± 2 standard errors in both the X and Y directions. Adult Male = IP491, Adult Female = IP414, Yearling Male = IP433, Juvenile Female = IP403. 64

Figure 6. Centroids of activity for Twin Bays Family, Summer, 1991. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = TB1510, Adult Female = TB1508, Yearling Male = TB1528, Yearling Female = TB1502. 65

Figure 7. Centroids of activity for JRB Bay Family, Summer, 1990. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = JRB1617, Adult Female = JRB1629, Yearling Male (Triangle Down) = JRB1641, Yearling Male (Triangle Up) = JRB1649. 66

Figure 8. Centroids of activity for Gatlan Ponds Family, Summer, 1990. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = GP1611, Adult Female GP1676, Yearling Male = GP1684, Yearling Female = GP1623. 67

Figure 9. Centroids of activity for Gatlan Ponds Family, Summer, 1991. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = GP1611, Adult Female = GP1676, Yearling Female = GP1526. 68

CHAPTER 4

Figure 1. Fall home range area size (open symbols) and core area size (closed symbols) (hectares) for all beavers combined and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range. 85

Figure 2. Fall core size as percent of total home range size (open symbols) and percent of all activity in core area (closed symbols) for all beavers combined and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range. 86

Figure 3. Fall home range area size (open symbols) and core area size (closed symbols) (hectares) for beavers living in family groups, by sex and age class. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range. 89

Figure 4. Fall core size as percent of total home range size (open symbols) and percent of all activity in core area (closed symbols) for beavers living in family groups, by sex and age class. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range. 90

Figure 5. Centroids of activity for Implant Pond Family, Fall, 1989. Centroids are shown ± 2 standard errors in both the X and Y directions. Adult Male = IP491, Adult Female = IP414, Yearling Male = IP433, Juvenile Female = IP403. 92

Figure 6. Centroids of activity for Twin Bays Family, Fall, 1991. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = TB1510, Adult Female = TB1508, Yearling Male = TB1528, Yearling Female = TB1502, Kits = TB1518, TB1520, TB1522. 93

Figure 7. Centroids of activity for JRB Bay Family, Fall, 1990. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = JRB1617, Adult Female = JRB1629, Yearling Male (Triangle Down) = JRB1641, Yearling Male (Triangle Up) = JRB1649. 94

Figure 8. Centroids of activity for Gatlan Ponds Family, Fall, 1990. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = GP1611, Adult Female GP1676, Yearling Male = GP1684. 95

Figure 9. Centroids of activity for Gatlan Ponds Family, Fall, 1991. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = GP1611, Yearling Female = GP1526. 96

CHAPTER 5

Figure 1. Home range size (hectares) for summer (closed symbols) and fall (open symbols) for all beavers combined, and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range. 111

Figure 2. Core area size (hectares) for summer (closed symbols) and fall (open symbols) for all beavers combined, and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range. 112

Figure 3. Core area size as percent of total home range size for summer (closed symbols) and fall (open symbols) for all beavers combined, and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range. 113

Figure 4. Activity in the core area as percent of all activity for summer (closed symbols) and fall (open symbols) for all beavers combined, and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range. 114

Figure 5. Centroids of activity for Implant Pond Family, Summer and Fall, 1989. Centroids are shown ± 2 standard errors in both the X and Y directions. Adult Male = IP491, Adult Female = IP414, Yearling Male = IP433, Juvenile Female = IP403. 117

Figure 6. Centroids of activity for Twin Bays Family, Summer, Late Summer and Fall, 1991. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = TB1510, Adult Female = 1508, Yearling Male = TB1528, Yearling Female = TB 1502, Kits = TB1518, TB1520, TB1522. 118

Figure 7. Centroids of activity for JRB Bay Family, Summer and Fall, 1990. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = JRB1617, Adult Female = JRB1629, Yearling Male (Triangle Down) = JRB1641, Yearling Male (Triangle Up) = JRB1649. 119

Figure 8. Centroids of activity for Gatlan Ponds Family, Summer and Fall, 1990. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = GP1611, Adult Female GP1676, Yearling Male = GP1684, Yearling Female = GP1623. 120

Figure 9. Centroids of activity for Gatlan Ponds Family, Summer and Fall, 1991. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = GP1611, Adult Female = GP1676, Yearling Female = GP1526. 121

CHAPTER 6

Figure 1. Map of home range for beaver in 1986 (fall only). Known individual home range = ▓ ; ● = other adult female captures; ◆ = other juvenile, undetermined sex, captures. 133

Figure 2. Map of home ranges for beavers in 1987. Known individual home ranges = ▓ ; approximate individual home ranges = ⣿ ; ● = other adult female captures; ▼ = other juvenile male captures; ◆ = other juvenile, undetermined sex, captures. 134

Figure 3. Map of home ranges for beavers in 1988. Known individual home ranges = ▓ ; approximate individual home ranges = ⣿ ; ▼ = other juvenile male captures; ▲ = other juvenile female captures; ◆ = other juvenile, undetermined sex, captures. 135

Figure 4. Map of home ranges for beavers in 1989. Known family home ranges = \\ ; known individual home ranges = ▓ ; approximate individual home ranges = ⣿ ; ● = other adult female captures; ▼ = other juvenile male captures; ▲ = other juvenile female captures; ◆ = other juvenile, undetermined sex, captures. 136

Figure 5. Map of home ranges for beavers in 1990. Known family home ranges = \\ ; known individual home ranges = ▓ ; approximate individual home ranges = ⣿ ; ● = other adult female captures; ▼ = other juvenile male captures; ▲ = other juvenile female captures. 137

Figure 6. Map of home ranges for beavers in 1991. Known family home ranges = \\ ; known individual home ranges = ▓ ; approximate individual home ranges = ⣿ ; ▼ = other juvenile male captures; ▲ = other juvenile female captures. 138

CHAPTER 7

Figure 1. Protein content (percent of dry matter) in vegetation samples. See Table 1 for codes. 155

Figure 2. Sodium content (percent of dry matter) in vegetation samples. See Table 1 for codes. ND = not discernible. 156

Figure 3. Potassium content (percent of dry matter) in vegetation samples. See Table 1 for codes. 157

Figure 4. Potassium to sodium ratio in vegetation samples. See Table 1 for codes. ND = not discernible due to sodium level not being discernible. 158

Figure 5. Calcium content (percent of dry matter) in vegetation samples. See Table 1 for codes. 159

Figure 6. Magnesium content (percent of dry matter) in vegetation samples. See Table 1 for codes. 160

Figure 7. Phosphorus content (percent of dry matter) in vegetation samples. See Table 1 for codes. 161

Figure 8. Sulfur content (percent of dry matter) in vegetation samples. See Table 1 for codes. 163

Figure 9. Copper content (parts per million) in vegetation samples. See Table 1 for codes. 164

Figure 10. Iron content (parts per million) in vegetation samples. See Table 1 for codes. 165

Figure 11. Manganese content (parts per million) in vegetation samples. See Table 1 for codes. 166

Figure 12. Zinc content (parts per million) in vegetation samples. See Table 1 for codes. 167

CHAPTER 8

Figure 1. Map showing location of capture sites of beavers used for DNA fingerprinting. Numbers refer to family numbers used in coding the samples (See Appendix 5). 183

Figure 2. Histogram of frequency of occurrence of band sharing coefficient values for all beavers, known first order relatives, known non-first order relatives ("unrelated"), unknown same lodge residents, and all other comparisons between beavers of unknown relatedness. 187

Figure 3. Histogram of frequency of occurrence of band sharing coefficient values for beavers living in common lodges: father-offspring; mother-offspring; same year class siblings; and different year class siblings. 188

APPENDIX 1

Figure 1. Maps of home range area for beavers in the Implant Pond Family for summer and fall, 1989. L indicates location of the lodge. 211

Figure 2. Maps of home range area for beavers in the Twin Bays Family for summer and fall, 1991. L indicates location of the lodge. 218

Figure 3. Maps of home range area for beavers in the JRB Family for summer and fall, 1990. L indicates location of the lodge. 233

Figure 4. Maps of home range area for beavers in the Gatlan Pond Family for summer and fall, 1990. L indicates location of the lodge. 241

Figure 5. Maps of home range area for beavers in the Gatlan Pond Family for summer and fall, 1991. L indicates location of the lodge. 248

Figure 6. Maps of home range area for beaver BR1848 for 1987, 1988 and 1989. L indicates the location of the lodge. 253

Figure 7. Maps of home range area for beaver BR1844 for summer and fall, 1987. L indicates location of the lodge. 265

Figure 8. Maps of home range area for beaver BR1830 for fall, 1986 and summer, 1989. L indicates location of the lodge. 267

Figure 9. Maps of home range area for beaver HB481 for summer and fall, 1989. L indicates location of the lodge. 269

Figure 10. Maps of home range area for beavers BR1534 and BR1524 for summer and late fall, 1991. L indicates location of the lodges. 271

Figure 11. Maps of home range area for beavers BR1603 for summer and fall, 1990. L indicates location of the lodge. 273

Figure 12. Maps of home range area for beaver BR1834 for summer and fall, 1987 and 1988. L indicates location of the lodge. 275

Figure 13. Maps of home range area for beaver GP286 for overnights in summer, 1988, and summer 1989. L indicates location of the lodge. 279

Figure 14. Maps of home range area for beavers SL109, summer, 1989 and SL1686 and SL1682, summer, 1990. L indicates known lodges. 282

APPENDIX 2

Figure 1. Graphs of cumulative percent of home range area versus cumulative percent of activity for beavers in the Implant Pond Family for summer and fall, 1989. 285

Figure 2. Graphs of cumulative percent of home range area versus cumulative percent of activity for beavers in the Twin Bays Family for summer and fall, 1991. 289

Figure 3. Graphs of cumulative percent of home range area versus cumulative percent of activity for beavers in the JRB Family for summer and fall, 1990. 296

Figure 4. Graphs of cumulative percent of home range area versus cumulative percent of activity for beavers in the Gatlan Pond Family for summer and fall, 1990. 300

Figure 5. Graphs of cumulative percent of home range area versus cumulative percent of activity for beavers in the Gatlan Pond Family for summer and fall, 1991. 304

Figure 6. Graphs of cumulative percent of home range area versus cumulative percent of activity for beaver BR1848 for 1987, 1988 and 1989. 307

Figure 7. Graphs of cumulative percent of home range area versus cumulative percent of activity for beaver BR1844 for summer and fall, 1987. 315

Figure 8. Graphs of cumulative percent of home range area versus cumulative percent of activity for beaver BR1830 for fall, 1986 and summer, 1989. 316

Figure 9. Graphs of cumulative percent of home range area versus cumulative percent of activity for beaver HB481 for summer and fall, 1989. 318

Figure 10. Graphs of cumulative percent of home range area versus cumulative percent of activity for beavers BR1534 and BR1524 for summer and late fall, 1991. 319

Figure 11. Graphs of cumulative percent of home range area versus cumulative percent of activity for beaver BR1603 for summer and fall, 1990. 321

Figure 12. Graphs of cumulative percent of home range area versus cumulative percent of activity for beaver BR1834 for summer and fall, 1987 and 1988. 322

Figure 13. Graphs of cumulative percent of home range area versus cumulative percent of activity for beaver GP286 for overnights in summer, 1988, and summer 1989. 324

Figure 14. Graphs of cumulative percent of home range area versus cumulative percent of activity for beavers SL109, summer, 1989 and SL1686 and SL1682, summer, 1990. 327

APPENDIX 4

Figure 1. Centroids of activity for beavers living on the Blind River and North Wallace Lake, Summer, Late Summer and Fall, 1987. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = BR1844, Juvenile Female 1 = BR1834, Juvenile Female 2 = BR1848. 334

Figure 2. Centroids of activity for beavers living on the Blind River and North Wallace Lake, Spring, Late Spring, Summer and Fall, and Summer Overnights, 1988. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Female 1 = BR1848, Adult Female 2 = BR1834. 335

Figure 3. Centroids of activity for beavers living on the Blind River and North Wallace Lake, Summer and Fall, 1989. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male 1 = BR1830, Adult Female = BR1848, Adult Male 2 = HB481. 336

Figure 4. Centroids of activity for beavers living on the Blind River and North Wallace Lake, Summer and Late Summer, 1991. Centroids are shown ± 2 standard errors in both X and Y directions. Yearling Male 1 = BR1534, Yearling Male 2 = BR1524. 337

Figure 5. Centroids of activity for beaver BR1603 living on the Blind River, Summer and Fall, 1990. Centroids are shown ± 2 standard errors in both X and Y directions. 338

Figure 6. Centroids of activity for beaver BR1848 living on the Blind River and Wallace Lake, Summer and Fall, 1987, 1988, and 1989. Centroids are shown ± 2 standard errors in both X and Y directions. 339

Figure 7. Centroids of activity for beaver BR1834 living on the Blind River, Summer and Fall, 1987 and 1988. Centroids are shown ± 2 standard errors in both X and Y directions. 340

Figure 8. Centroids of activity for beaver GP286, living in Lower Gatlan Pond, Summer (Overnights) 1988 and Summer, 1989. Centroids are shown ± 2 standard errors in both X and Y directions. 341

Figure 9. Centroids of activity for beavers living in the vicinity of Salt Lick Pond and Salt Lick Bay. Centroids are shown ± 2 standard errors in both X and Y directions. Yearling Male = SL109, Juvenile Female 1 = SL1686, Juvenile Female 2 = SL1682. 342

APPENDIX 5

Figure 1. Autoradiograph of DNA samples from beavers from families 1, 2, 6, 26, 27 and 28. See Table 1 for summary of family composition, and Figure 1 in Chapter 8 for geographic location of families. V = visual control, M = molecular weight sizing standard, H = human control, square = adult male, circle = adult female, triangle up = yearling or two-year old female, triangle down = yearling or two-year old male, diamond = kit. 344

Figure 2. Autoradiograph of DNA samples from beavers from families 7 and 8. See Table 1 for summary of family composition, and Figure 1 in Chapter 8 for geographic location of families. V = visual control, M = molecular weight sizing standard, triangle up = yearling or two-year old female, triangle down = yearling or two-year old male, diamond = kit. 345

Figure 3. Autoradiograph of DNA samples from beavers from families 3, 4, 5, 10 and 29. See Table 1 for summary of family composition, and Figure 1 in Chapter 8 for geographic location of families. M = molecular weight sizing standard, H = human control, square = adult male, circle = adult female, triangle up = yearling or two-year old female, triangle down = yearling or two-year old male, diamond = kit, small open circles = fetuses. 346

Figure 4. Autoradiograph of DNA samples from beavers from families 11 and 12. See Table 1 for summary of family composition, and Figure 1 in Chapter 8 for geographic location of families. V = visual control, M = molecular weight sizing standard, H = human control, square = adult male, circle = adult female, diamond = kit, small open circles = fetuses. 347

Figure 5. Autoradiograph of DNA samples from beavers from families 13, 15, 16 and 17. See Table 1 for summary of family composition, and Figure 1 in Chapter 8 for geographic location of families. M = molecular weight sizing standard, H = human control, square = adult male, circle = adult female, triangle up = yearling or two-year old female, triangle down = yearling or two-year old male. 348

Figure 6. Autoradiograph of DNA samples from beavers from families 9 and 18. See Table 1 for summary of family composition, and Figure 1 in Chapter 8 for geographic location of families. V = visual control, M = molecular weight sizing standard, H = human control, square = adult male, circle = adult female, triangle up = yearling or two-year old female, triangle down = yearling or two-year old male, diamond = kit. 349

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Seton (1909:478) wrote: "There can be no doubt that the beaver did more to open up Canada than any other creature or product". The search for furs led traders to move farther and farther west as beaver were extirpated from one region after another. Explorers were fascinated by nature's "furry engineer", and gave much credit to the beaver for extreme intelligence, planning, organizational skills and foresight. Many of the early writings on beaver are purely anecdotal and anthropomorphic. Samuel Hearne (1795, in Morgan 1986) criticized and questioned many of the attributes given to beavers. The first major study and report on beavers was done by Morgan in 1868 (Morgan 1986). He reports in detail on their morphology, their constructions and methods of capturing them. Seton (1909) and Warren (1927) present similar reviews.

Seton (1909) estimated that the original population of beavers in Canada probably exceeded 10 million animals. By the beginning of the twentieth century, they had been extirpated from many regions of North America and numbers may have been as low as 500,000 (Seton, 1909). Much of the literature on beavers from the first half of the Twentieth Century pertains to management issues concerning the reintroduction of beavers to areas from which they had been extirpated (Atwood 1938; Atwater 1940; Cook 1943; Patric and Webb 1953). More recently the literature has turned to studies of natural movements, feeding habits and general ecology of the beaver and techniques for use in these studies. The importance of the beaver in establishing and maintaining habitat for other wildlife has also been recognized (Hall 1972). The beaver is a nocturnal, semi-aquatic mammal. Until the advent of radio-telemetry, studies of movements and habits were difficult.

Although there is an abundance of literature on beavers, much of it is anecdotal, and often of dubious basis in fact (Bradt 1938). Most

of the scientific literature is the result of research in the United States. However research on beaver ecology in Canada has been done in Newfoundland (Northcott 1971; Bergerud and Miller 1977; Payne 1981; 1982; 1984), Quebec (Potvin and Bovet 1975; Patenaude and Bovet 1983; 1984; Courcelles and Nault 1983), Ontario (Stephenson 1969; Gillespie 1977; Novak 1977; Ingle-Sidorowicz 1982), Manitoba (Green 1936; Nash 1951; Wheatley 1989; 1993; Dyck 1991), Alberta (Novakowski 1967; Bovet and Oertli 1974) and the Mackenzie Delta region of the Northwest Territories (Aleksiuk 1968; 1970; Aleksiuk and Cowan 1969a; 1969b).

The boreal forest or taiga constitutes a large proportion of the range of beavers. Forest fires have "always been an integral part of the boreal forest" (Rowe and Scotter 1973:446). One of the frequent colonizing tree species after fire is *Populus tremuloides* (Rowe and Scotter 1973) which has a very similar distribution to that of beaver (Hall 1960). *P. tremuloides* is a common food of beavers throughout their range, and frequently the one preferred over all others. The boreal forest may therefore be an important part of the range of beavers. However, the amount of research on beavers in the boreal forest is minimal when compared to that for other regions of North America. Even small differences in habitat may result in changes in characteristic behaviours (Green 1936). Information from other regions of North America, and especially those regions with much shorter periods of ice cover, may have restricted application in the boreal forest.

LITERATURE REVIEW

FOOD

The most studied area of beaver ecology in recent literature has been food selection and preferences. Beaver food preferences differ geographically, seasonally and yearly (Aleksiuk 1977; Jenkins 1979; Svendsen 1980). Authors generally agree on the preference of beavers for aspen (*P. tremuloides*) when it is available (Aldous 1938; Bradt 1938; Gese and Shadle 1943; Shadle 1943 *et al.*; Tevis 1950; Hall 1960; Brenner 1962; Northcott 1971; Jenkins 1981; Pinkowski 1983; Basey *et al.* 1988). However, beavers are choosy generalist herbivores (Aleksiuk 1977; Jenkins and Busher 1979) which eat a wide variety of plants including willow (*Salix* spp.) (Aldous 1938; Bradt 1938; Townsend 1953; Hall 1960; Aleksiuk 1970; Jenkins 1981), maple (*Acer saccharum*) (Bradt 1938; Belovsky 1984), birch (*Betula alleghaniensis*) (Aldous 1938; Belovsky 1984), alder (*Alnus crispa* and *Alnus rugosa*) (Aldous 1938; Northcott 1971), and even corn from farmers' fields (Atwood 1938). Aquatic plants are also frequently part of the beaver diet in summer (Townsend 1953; Brenner 1962; Northcott 1971; Gillespie 1977; Svendsen 1980; Jenkins 1981).

Recently, there has been an abundance of literature on tree size preferences of beaver. Smaller trees appear to be preferred at increasing distance from the water's edge (Jenkins 1980; 1981; Pinkowski 1983; Belovsky 1984; Basey *et al.* 1988), while for saplings, larger diameter stems are preferred with increasing distance from the shore (McGinley and Whitham 1985; Fryxell and Doucet 1991; Fryxell 1992). Secondary juvenile growth of *P. tremuloides* after cutting by beavers may be avoided due to the presence of a phenolic compound which appears to serve as a deterrent to beaver cutting (Basey *et al.* 1988; 1990).

Brenner (1962) speculated that nutrient content of *P. tremuloides* may be important in its selection by beavers. Jenkins (1978) recorded beavers sampling trees by removing a small piece of bark and theorized that this may serve to assess the nutritional level of different trees. Chabreck (1958) also reported sampling behaviour among beavers.

MOVEMENTS AND HOME RANGE

Studies of beaver movements have been of two types. Many early studies examined dispersal distances from release points for reintroduced beaver. More recent studies have focused on natural movements, both in the form of dispersal from the natal colony and movements within the home range.

Dispersal

Beavers generally follow water courses when dispersing, but may travel overland (Bradt 1938; Knudsen and Hale 1965; Leege 1968; Wheatley 1989). Two-year-old beaver appear to have an innate tendency to disperse and do not appear to be driven out by their parents (Leege 1968; Brady and Svendsen 1981). Beer (1955) described little movement (dispersal) by adults, while yearlings moved distances up to 82 km. Libby (1957) recorded only one beaver dispersing more than 10 km, but the exception travelled over 240 km. Leege (1968) reported a mean dispersal distance of 8.5 km, and a maximum distance of 18 km. For transplanted beavers, dispersal distances of up to 237 km have been recorded (Hibbard 1958), but usually distances are much less, with beavers transplanted to streams moving greater distances than those transplanted to lakes (Knudsen and Hale 1965).

Home Range

Several authors have studied the day to day movement patterns of beavers within their home ranges (Aleksiuk 1968; Busher 1975; Gillespie 1977; Busher *et al.* 1983; Davis 1984; Wheatley 1989). Davis (1984) found the greatest amount of movement took place in fall and winter, and least in summer, with correspondingly greater distances between extreme points of the home range in fall and winter than in summer. Only Gillespie (1977) has delineated actual home range size, with beavers residing in ponds having an average home range size of 0.38 ha and those residing on lakes an average size of 7.25 ha.

Busher *et al.* (1983) reported intercolony movement among beavers living in areas of high beaver density, but no intercolony movements for beavers living in areas of low beaver density. Davis (1984) also noted home range overlap between stream and lake colonies. Several authors have considered beavers territorial, and have regarded scent mounds as territorial markers (Bradt 1938; Brenner 1964; Aleksiuk 1968; Bergerud and Miller 1977). However, more recent studies of scent mounds and their role in beaver communication have found no support for the function of scent mounds in territorial maintenance, and have hypothesized that they actually play a role in communicating sexual information (Butler and Butler 1979; Walro 1980).

WINTER ACTIVITIES

Winter activities differ with differing climatic constraints. In areas with little or no ice cover, winter activities may be similar to those at other times of the year, although food choice and feeding sites may differ (Brenner 1962; Davis 1984). In areas with extended periods of ice cover, above-ice activity usually only occurs at warmer temperatures (Lancia 1979; Lancia *et al.* 1982; Wheatley 1989). When

beavers remain under the ice, they generally exhibit a free-running circadian rhythm (Potvin and Bovet 1975; Lancia *et al.* 1982). Lodge temperatures in winter remain fairly constant, and the walls and snow provide sufficient insulation from outside temperatures (Stephenson 1969; Buech *et al.* 1989). Novakowski (1967) demonstrated that the energy supply available from the food pile was insufficient to meet the beavers' requirements for the winter at his study site in the Northwest Territories. Beavers may also be stressed if water levels vary more than 0.7 m in winter (Smith and Peterson 1991).

BEHAVIOUR

Behavioural studies have encompassed many aspects of beaver biology. Patenaude and Bovet (1983; 1984) examined parturition and related behaviours and grooming habits of beavers. Hodgdon and Larson (1973) considered sexual differences in behaviour and colony organization. Brady and Svendsen (1981) investigated the social behaviour and social interactions of a family of beavers. Svendsen (1989) studied the duration of pair bonds and determined that no beaver stayed with the same mate throughout life.

REPRODUCTION AND SURVIVORSHIP

In conjunction with interest in beaver management and increasing beaver numbers, several studies have examined age structures and sexual maturity within beaver populations. Boyce (1981) determined that human exploitation (trapping) resulted in a decrease in adult survivorship and increased the immediate survival of pre-reproductive animals. However, this in turn led to higher mortality of the younger animals which reproduced earlier and therefore did not attain full normal adult size.

Sexual maturity occurs at about 2 years of age, and females may carry 1 to 9 embryos ($\bar{X}$ = 5.5) (Brenner 1964). Dieter (1992) found a sex ratio of 1:1 in South Dakota; while Leege and Williams (1967) found a 1.13:1 male to female ratio in Idaho.

TECHNIQUES

The development of techniques of trapping, marking, censusing, and ageing beavers has been the focus of much literature. Buech (1983) describes a modification of the Bailey live-trap to ensure greater success with captures. A variety of methods of marking beavers have been described including web punching on the feet (Aldous 1940); coloured plastic ear markers (Miller 1964); and a night identification collar (Brooks and Dodge 1978). The reliability of aerial surveys of beaver lodges or food caches has been the focus of studies by Payne (1981), Brown and Parsons (1982) and Swenson *et al.* (1983). Patric and Webb (1960) investigated weight, tail dimensions and zygomatic breadth as methods of ageing beavers. Van Nostrand and Stephenson (1964) and Larson and Van Nostrand (1968) describe a technique for ageing beavers by tooth development. Hartman (1992) has modified the latter technique for use on live beavers by using dental x-rays to examine tooth development. With the advent of radiotelemetry, methods of anaesthetizing (Lancia *et al.* 1978) and attaching radiotransmitters have been described (Busher 1975; Lancia 1979; Davis 1984; Davis *et al.* 1984; Guynn *et al.* 1987; Wheatley 1989).

OBJECTIVES

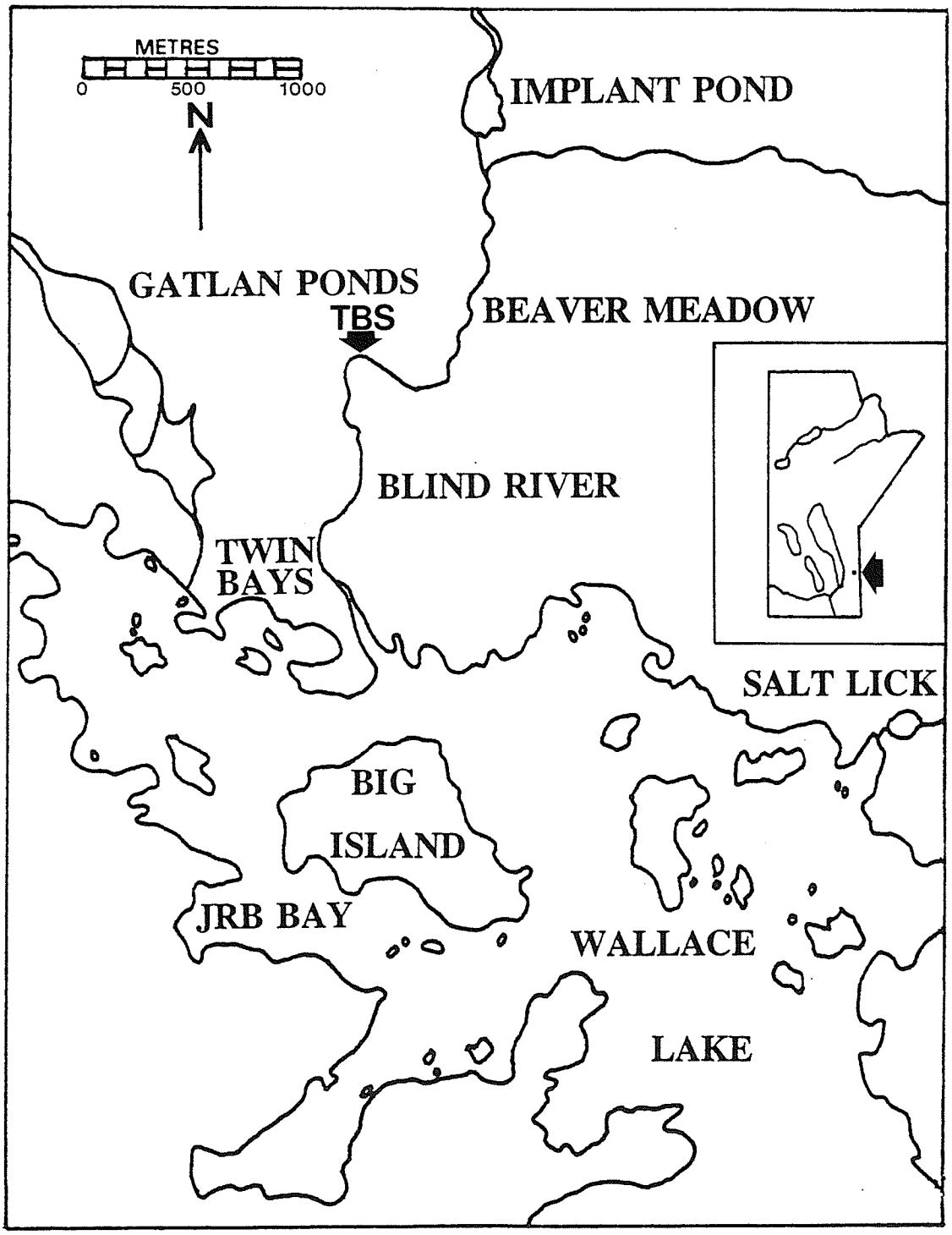
In this study my objectives are: 1. To identify a suitable method of delineating home ranges for beavers; 2. To determine home range sizes for beavers living in a mid-continent, boreal environment; 3. To determine habitat, sex, age class, and seasonal differences in home range size for beavers in a mid-continent, boreal environment; 4. To assess whether territories are present in this beaver population; 5. To determine feeding habits of beavers in this area; 6. To determine any seasonal variation in these feeding habits and possible reasons for variation; 7. To assess relatedness among the beaver in this population using DNA fingerprinting and determine if relatedness and territoriality are correlated.

STUDY AREA

This study was based at Taiga Biological Station (TBS), 51°02'40" N, 95°20'40" W, 250 km northeast of Winnipeg, Manitoba (Figure 1). The study took place on Wallace Lake, the Blind River which enters Wallace Lake from the north, and Implant and Gatlan Ponds. The area was burnt in the 1980 Wallace Lake fire. The river and ponds are bordered primarily by burnt bogs with a few burnt ridges. The lake is bordered primarily by burnt ridges. There are irregular patches of unburnt land in the area, some bordering the river and lake. To the east of TBS, the Blind River traverses and all but disappears in a large boggy area known as the Beaver Meadow (Figure 1). It is the result of numerous changes of river flow caused by beavers damming the river at various times in the past. The bogs, and also some ridges where erosion has not been too extensive, support a good growth of *Populus tremuloides*, *Alnus crispa*, *Picea mariana* and *Pinus banksiana*.

This area has a climate which is typical for mid-continent boreal forest. Temperatures range from -40°C in winter to +35°C in summer. Freeze-up occurs in late October or very early November and breakup in late April or early May. Ice cover is continuous throughout the period except for occasional areas around rapids or fast flowing water. February ice thicknesses range from 50 cm to 100 cm depending upon snow cover and air temperatures.

Figure 1. Location of study area in Manitoba and detail of study area.


METRES
0
500
1000
N
IMPLANT POND
GATLAN PONDS
TBS
BEAVER MEADOW
BLIND RIVER
TWIN
BAYS
SALT LICK
BIG
ISLAND
JRB BAY
WALLACE
LAKE

LITERATURE CITED

Aldous, S.E. 1938. Beaver food utilization studies. Journal of Wildlife Management 2:215-222.

Aleksiuk, M. 1968. Scent-mound communication, territoriality, and population regulation in beaver (*Castor canadensis* Kuhl). Journal of Mammalogy 49:759-762.

Aleksiuk, M. 1970. The seasonal food regime of arctic beavers. Ecology 51:264-270.

Aleksiuk, M. 1977. Diets (natural and synthetic): Castoridae. In M. Recheigl, Jr. (Ed.) Diets for Mammals, Vol. 1, CRC Press, Cleveland, pp.89-92.

Aleksiuk, M. and I.McT. Cowan. 1969a. Aspects of seasonal energy expenditure in the beaver (*Castor canadensis* Kuhl) at the northern limit of its distribution. Canadian Journal of Zoology 47:471-481.

Aleksiuk, M. and I.McT. Cowan. 1969b. The winter metabolic depression in Arctic beavers (*Castor canadensis* Kuhl) with comparisons to California beavers. Canadian Journal of Zoology 47:965-979.

Atwater, M.M. 1940. South Fork (Montana) beaver survey:1939. Journal of Wildlife Management 4:100-103.

Atwood, E.L., Jr. 1938. Some observations on adaptability of Michigan beavers released in Missouri. Journal of Wildlife Management 2:165-166.

Basey, J.M., S.H. Jenkins and P.E. Busher. 1988. Optimal central-place foraging by beavers: Tree-size selection in relation to defensive chemicals of quaking aspen. Oecologia 76:278-282.

Basey, J.M., S.H. Jenkins and G.C. Miller. 1990. Food selection by beavers in relation to inducible defenses of *Populus tremuloides*. Oikos 59:57-62.

Beer, J.R. 1955. Movements of tagged beaver. Journal of Wildlife Management 19:492-493.

Belovsky, G.E. 1984. Summer diet optimization by beaver. American Midland Naturalist 111:209-222.

Bergerud, A.T. and D.R. Miller. 1977. Population dynamics of Newfoundland beaver. Canadian Journal of Zoology 55:1480-1492.

Bovet, J. and E.F. Oertli. 1974. Free-running circadian activity rhythms in free-living beavers (*Castor canadensis*). Journal of Comparative Physiology 94:1-10.

Boyce, M.S. 1981. Beaver life-history responses to exploitation. Journal of Applied Ecology 18:749-753.

Bradt, G.W. 1938. A study of beaver colonies in Michigan. Journal of Mammalogy 19:139-162.

Brady, C.A. and G.E. Svendsen. 1981. Social behaviour in a family of beaver, *Castor canadensis*. Biology of Behaviour 6:99-114.

Brenner, F.J. 1962. Foods consumed by beavers in Crawford County, Pennsylvania. Journal of Wildlife Management 26:104-107.

Brenner, F.J. 1964. Reproduction of the beaver in Crawford County, Pennsylvania. Journal of Wildlife Management 28:743-747.

Brooks, R.P. and W.E. Dodge. 1978. A night identification collar for beavers. Journal of Wildlife Management 42:448-452.

Brown, M.K. and G.R. Parsons. 1982. Reliability of fall aerial censuses for locating active beaver colonies in northern New York. New York Fish and Game Journal 29:204-206.

Buech, R.R. 1983. Modification of the Bailey live trap for beaver. Wildlife Society Bulletin 11:66-68.

Buech, R.R., D.J. Rugg and N.L. Miller. 1989. Temperature in beaver lodges and bank dens in a near-boreal environment. Canadian Journal of Zoology 67:1061-1066.

Busher, P.E. 1975. Movements and activities of beavers, *Castor canadensis*, on Sagehen Creek, California. M.A. Thesis, San Francisco State University, California, 86 pp.

Busher, P.E., R.J. Warner and S.H. Jenkins. 1983. Population density, colony composition, and local movements in two Sierra Nevadan beaver populations. Journal of Mammalogy 64:314-318.

Butler, R.G. and L.A. Butler. 1979. Toward a functional interpretation of scent marking in beaver (*Castor canadensis*). Behavioral and Neural Biology 26:442-454.

Chabreck, R.H. 1958. Beaver-forest relationships in St. Tammany Parish, Louisiana. Journal of Wildlife Management 22:179-183.

Cook, D.B. 1943. History of a beaver colony. Journal of Mammalogy 24:12-18.

Courcelles, R. and R. Nault. 1983. Beaver programs in the James Bay area, Quebec, Canada. Acta Zoologica Fennica 174:129-131.

Davis, J.R. 1984. Movement and Behavior Patterns of Beaver in the Piedmont of South Carolina. M.Sc. Thesis, Clemson University, Clemson, South Carolina, 83pp.

Davis, J.R., A.F. Von Recum, D.D. Smith and D.C. Guynn, Jr. 1984. Implantable telemetry in beaver. Wildlife Society Bulletin 12:322-324.

Dieter, C.D. and T.R. McCabe. 1989. Factors influencing beaver lodge-site selection on a prairie river. American Midland Naturalist 122:408-411.

Dyck, A.P. 1991. Bioenergetics and thermoregulation of beavers (*Castor canadensis*). M.Sc. Thesis, University of Manitoba, Winnipeg, Manitoba, 79 pp.

Fryxell, J.M. 1992. Space use by beavers in relation to resource abundance. Oikos 64:474-478.

Fryxell, J.M. and C.M. Doucet. 1991. Provisioning time and central-place foraging in beavers. Canadian Journal of Zoology 69:1308-1313.

Gese, E.C. and A.R. Shadle. 1943. Reforestation of aspen after complete cutting by beavers. Journal of Wildlife Management 7:223-228.

Gillespie, P.S. 1977. Summer Activities, Home Range and Habitat Use of Beaver. M.Sc. Thesis, University of Toronto, Toronto, Ontario, 149 pp.

Green, H.U. 1936. The beaver of the Riding Mountain, Manitoba: An ecological study and commentary. Canadian Field-Naturalist 50:1-8, 21-23, 36-50, 61-67, 85-92.

Guynn, D.C., J.R. Davis and A.F. Von Recum. 1987. Pathological potential of intraperitoneal transmitter implants in beavers. Journal of Wildlife Management 51:605-606.

Hall, A.M. 1972. Beaver and the beaver eaters. Ontario Naturalist 10:14-18.

Hall, J.G. 1960. Willow and aspen in the ecology of beaver on Sagehen Creek, California. Ecology 41:484-494.

Hartman, G. 1992. Age determination of live beaver by dental x-ray. Wildlife Society Bulletin 20:216-220.

Hibbard, E.A. 1958. Movements of beaver transplanted in North Dakota. Journal of Wildlife Management 22:209-211.

Hodgdon, H.E. and J.S. Larson. 1973. Some sexual differences in behaviour within a colony of marked beavers (*Castor canadensis*). Animal Behaviour 21:147-152.

Ingle-Sidorowicz, H.M. 1982. Beaver increase in Ontario. Result of changing environment. Mammalia 46:167-175.

Jenkins, S.H. 1978. Food selection by beavers: sampling behavior. Breviora 447:1-8.

Jenkins, S.H. 1979. Seasonal and year-to-year differences in food selection by beavers. Oecologia 44:112-116.

Jenkins, S.H. 1980. A size-distance relation in food selection by beavers. Ecology 61:740-746.

Jenkins, S.H. 1981. Problems, progress, and prospects in studies of food selection by beavers. Proceedings of the Worldwide Furbearer Conference 1:559-579.

Jenkins, S.H. and P.E. Busher. 1979. *Castor canadensis*. Mammalian Species 120:1-8.

Knudsen, G.J. and J.B. Hale. 1965. Movements of transplanted beavers in Wisconsin. Journal of Wildlife Management 29:685-688.

Lancia, R.A. 1979. Year-long activity patterns of radio-marked beaver (*Castor canadensis*). Ph.D. Dissertation, University of Massachusetts, Amherst, Massachusetts, 146 pp.

Lancia, R.A., R.P. Brooks and M.W. Fleming. 1978. Ketamine hydrochloride as an immobilant and anesthetic for beaver. Journal of Wildlife Management 42:946-948.

Lancia, R.A., W.E. Dodge and J.S. Larson. 1982. Winter activity patterns of two radio-marked beaver colonies. Journal of Mammalogy 63:598-606.

Larson, J.S. and F.C. Van Nostrand. 1968. An evaluation of beaver aging techniques. Journal of Wildlife Management 32:99-103.

Leege, T.A. 1968. Natural movements of beavers in southeastern Idaho. Journal of Wildlife Management 32:973-976.

Leege, T.A. and R.M. Williams. 1967. Beaver productivity in Idaho. Journal of Wildlife Management 31:326-332.

Libby, W.L. 1957. Observations on beaver movements in Alaska. Journal of Mammalogy 38:269.

McGinley, M.A. and T.G. Whitham. 1985. Central place foraging by beavers (*Castor canadensis*): a test of foraging predictions and the impact of selective feeding on the growth form of cottonwoods (*Populus fremontii*). Oecologia 66:558-562.

Miller, D.R. 1964. Colored plastic ear markers for beavers. Journal of Wildlife Management 28:859-861.

Morgan, L.H. 1986. The American Beaver: A Classic of Natural History and Ecology. Dover Publications Inc., New York.

Nash, J.B. 1951. An Investigation of Some Problems of Ecology of the Beaver *Castor canadensis canadensis* Kuhl, in Northern Manitoba. M.Sc. Thesis, University of Manitoba, Winnipeg, Manitoba, 74 pp.

Northcott, T.H. 1971. Feeding habits of beaver in Newfoundland. Oikos 22:407-410.

Novak, M. 1977. Determining the average size and composition of beaver families. Journal of Wildlife Management 41:751-754.

Novakowski, N.S. 1967. The winter bioenergetics of a beaver population in northern latitudes. Canadian Journal of Zoology 45:1107-1118.

Patenaude, F. and J. Bovet. 1983. Parturition and related behavior in wild American beavers (*Castor canadensis*). Zeitschrift fur Säugetierkunde 48:136-145.

Patenaude, F. and J. Bovet. 1984. Self-grooming and social grooming in the North American beaver, *Castor canadensis*. Canadian Journal of Zoology 62:1872-1878.

Patric, E.F. and W.L. Webb. 1960. An evaluation of three age determination criteria in live beavers. Journal of Wildlife Management 24:37-44.

Patric, E.F. and W.L. Webb. 1953. A preliminary report on intensive beaver management. Eighteenth North American Wildlife Conference, pp.533-539.

Payne, N.F. 1981. Accuracy of aerial censusing for beaver colonies in Newfoundland. Journal of Wildlife Management 45:1014-1016.

Payne, N.F. 1982. Colony size, age, and sex structure of Newfoundland beaver. Journal of Wildlife Management 46:655-661.

Payne, N.F. 1984. Mortality rates of beaver in Newfoundland. Journal of Wildlife Management 48:117-126.

Pinkowski, B. 1983. Foraging behavior of beavers (*Castor canadensis*) in North Dakota. Journal of Mammalogy 64:312-314.

Potvin, C.L. and J. Bovet. 1975. Annual cycle of patterns of activity rhythms in beaver colonies (*Castor canadensis*). Journal of Comparative Physiology A 93:243-256.

Rowe, J.S. and G.W. Scotter. 1973. Fire in the boreal forest. Quaternary Research 3:444-464.

Seton, E.T. 1909. Life Histories of Northern Animals. Charles Scribner's Sons, New York.

Shadle, A.R., A.M. Nauth, E.C. Gese and T.S. Austin. 1943. Comparison of tree cuttings of six beaver colonies in Allegany State Park, New York. Journal of Mammalogy 24:32-39.

Smith, D.W. and R.O. Peterson. 1991. Behavior of beaver in lakes with varying water levels in northern Minnesota. Environmental Management 15:395-401.

Stephenson, A.B. 1969. Temperatures within a beaver lodge in winter. Journal of Mammalogy 50:134-136.

Svendsen, G.E. 1980. Seasonal change in feeding patterns of beaver in southeastern Ohio. Journal of Wildlife Management 44:285-290.

Svendsen, G.E. 1989. Pair formation, duration of pair-bonds, and mate replacement in a population of beavers (*Castor canadensis*). Canadian Journal of Zoology 67:336-340.

Swenson, J.E., S.J. Knapp, P.R. Martin and T.C. Hinz. 1983. Reliability of aerial cache surveys to monitor beaver population trends on prairie rivers in Montana. Journal of Wildlife Management 47:697-703.

Tevis, L., Jr. 1950. Summer behavior of a family of beavers in New York State. Journal of Mammalogy 31:40-65.

Townsend, J.E. 1953. Beaver ecology in western Montana with special reference to movements. Journal of Mammalogy 34:459-479.

Van Nostrand, F.C. and A.B. Stephenson. 1964. Age determination for beavers by tooth development. Journal of Wildlife Management 28:430-434.

Walro, J.M. 1980. Castor and anal glands of North American beaver (*Castor canadensis*): Histology and communicatory functions of secretions. Ph.D. Thesis, Ohio University.

Warren, E.R. 1927. The Beaver Its Works and Its Ways. American Society of Mammalogists Monographs 2, Baltimore, The Williams and Wilkins Company.

Wheatley, M. 1989. Ecology of Beaver (*Castor canadensis*) in the Taiga of Southeastern Manitoba. M.Sc. Thesis, University of Manitoba, Winnipeg, Manitoba, 167 pp.

Wheatley, M. 1993. Report on two pregnant beavers, *Castor canadensis*, at one beaver lodge. Canadian Field-Naturalist 107:103.

CHAPTER 2

AN ANALYSIS OF FOUR TECHNIQUES OF ESTIMATING HOME RANGE SIZE USING FIELD DATA

ABSTRACT

I compared estimates of beaver home range size and shape using four different methods: grid; minimum convex polygon (MCP); modified minimum area (MMA); and the Jennrich-Turner ellipse. The grid gives the smallest estimate most often and the ellipse or minimum convex polygon gives the largest. The ellipse works best for home ranges with only one area of concentrated use near the centre. The MCP and MMA work best when the distribution of observations is a regular shape, with no protruding arms. The grid method is most suitable for animals with irregularly shaped home ranges or home ranges with several areas of concentrated use.

INTRODUCTION

Home range is "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943:351) or "the area in which an animal normally lives exclusive of migrations, emigrations or unusual erratic wanderings" (Brown and Orians 1970:240). The home range may vary with season, sex, age and population density of a species (Burt 1943).

Many methods of determining the size of an animal's home range have been developed (Mohr 1947; Harvey and Barbour 1965; Jennrich and Turner 1969; Van Winkle *et al.* 1973; Dixon and Chapman 1980; Schoener 1981; Anderson 1982; Don and Rennolls 1983; Samuel and Garton 1985; Hutton 1989). Metzgar (1973), however, noted that much of this literature on home range was developed in the absence of accurate information on either actual shapes of home ranges or the way activity is distributed within them. Jennrich and Turner (1969), Ford and Krumme (1979), Macdonald *et al.* (1979), Schoener (1981), Samuel and Garton (1985) and White and Garrott (1990) have reviewed and compared the various methods, usually using a few field examples. No comparison of these methods has been made using a large number of field examples. No method will be suitable in every situation (Anderson 1982), and there has been no agreement on which techniques yield the most valuable results for field ecologists (Don and Rennolls 1983). In addition, all the commonly used methods have problems with biological assumptions, sample size bias and sensitivities to extreme locations (Samuel and Garton 1985).

The purpose of this paper is to compare the 4 most common and simple methods of home range estimation: the minimum convex polygon or minimum area method; the modified minimum area method; the Jennrich-Turner ellipse method; and the grid method. The data I use are the result of 6 years of tracking and observing beavers (*Castor canadensis*).

Here I compare the home range sizes estimated by the different methods, and examine the apparent home range delineated by each method, to determine if certain patterns of use of the home range differentially affect the ability of the various methods to delineate the home range accurately.

These home range methods are frequently applied without evaluating the fit of the assumed probability distribution to the observed data, and the data frequently violate the assumed probability distributions (Samuel *et al.* 1985; White and Garrott 1990). I also did not test the fit of my data to the probability distribution, since the purpose of this paper is to assess how well each of these methods fits for different patterns of home range use.

METHODS

I live-trapped beavers and attached uniquely numbered and coloured ear tags (Monel, Number 3) to both ears (Miller 1964) to allow for visual identification of individuals. I also attached tail collar radio transmitters or implanted radio transmitters in 29 of the 32 beavers discussed in this study (Wheatley 1989). For tracking beavers I used an H-shaped antenna and 24 channel receiver (Wildlife Materials Inc.). For beavers residing on the river or lake, I generally tracked and observed from a 6.5 m freighter canoe. When observing at ponds, I chose a high ridge or similar good vantage point from which to make observations. In general, I used telemetry to locate a beaver and then, as much as possible, continued with visual observations of activities and movements. At night I could track beaver movements using telemetry, sound and by observing water ripples.

I recorded information about the location, time, type of activity and any movement to another location during the period of observation. Observation periods varied in length from 5 minutes to 13 hours, depending upon weather conditions and the number of beavers being observed in one night. Because beaver home ranges are extremely small and restricted in winter under ice (Wheatley 1989) (Chapter 5), the data I present here are for open water seasons only. Most observations were made between 1800 and 2400 h. I recorded data directly into a field book or on cassette audio tape for later transcription into the field book. I later transferred the data onto forms for each beaver. I considered one minute as one observation. While this does not allow for true independence of observations (Swihart and Slade 1985a; 1985b), the beavers move throughout their home range too much to be able to reflect accurately their home range use by 1 observation per night. Although independence of observations is desirable, successive locations are

essential in order to describe space use patterns (Ford and Krumme 1979).

I drew maps of appropriate size and scale to encompass the home range of each beaver or group of beavers. For the purpose of this paper, I have analyzed the data by 4 different methods: grid, minimum convex polygon (MCP); modified minimum area (MMA); and Jennrich-Turner 95 % ellipse (JT ellipse). For the grid method (Adams and Davis 1967; Whitten 1982; Samuel *et al.* 1985) I used a grid equivalent to 50 by 50 m on the ground (0.25 ha). I chose this size of grid because 50 m is approximately the distance a beaver can swim in one minute, the period I considered as one observation.

For the minimum convex polygon method I connected the outermost points of location for each individual in each season (Mohr 1947; Harvey and Barbour 1965). The modified minimum area method similarly connects the outermost points, but limits the length of the line segment connecting any two points to one quarter of the distance between the two most extreme points (Harvey and Barbour 1965). Any point greater than one quarter of the distance is connected to the nearest point by a straight line. No biological justification is given for this limit of one quarter of the home range length. For the JT ellipse, I used SAS (SAS Institute Inc. 1988) to calculate the geometric centre of all observations for an individual in a season and used the formulas given by Jennrich and Turner (1969) and White and Garrott (1990) to calculate the 95 % confidence ellipse for each case.

I classified beavers as pond, lake or river residents based on the location of their primary residence (lodge or bank burrow). Total numbers of observations on which each of the estimates are based range from 45 to 2934 ($\bar{X}$ = 486 ± 69.1 ($\bar{X}$ ± 2SE)). Size estimates are given as $\bar{X}$ ± 2SE. I used simple correlations and regression to compare the home range estimates produced by the different methods. I examined the estimates and grouped them by which methods gave the largest or smallest

estimate. For each group, I compared the estimates by each method with estimates by the same method for all other groups using a t-test. I also made a visual examination of the distribution of observations to identify any shape patterns associated with the different groups.

RESULTS

Home range size estimates using the grid method averaged 7.73 ± 1.63 ha (range 1 - 42.75 ha, N=69); using the MCP method the values averaged 19.38 ± 7.77 ha (range 0.91 - 223.9 ha, N=69); using the MMA method, values averaged 13.62 ± 5.88 ha (range 0.80 - 175.5 ha, N=69); and using the JT ellipse method the values averaged 27.04 ± 12.9 ha (range 0.404 - 383.8 ha, N=69) (Table 1). The estimates using the four different methods were all significantly positively correlated ($p<0.01$, N=69) (Figures 1 to 6). The JT ellipse and MMA methods, JT ellipse and MCP methods and MCP and MMA methods are all related in direct linear fashion. The JT ellipse and grid, MMA and grid and the MCP and grid methods are related by second order regression.

The grid method gave the largest estimate in 2 cases (both fall) (1 pond, 1 lake), and the smallest in 50 cases (31 summer, 6 late summer, 11 fall, 1 spring, 1 late spring) (13 pond, 20 lake, 17 river). The MCP method gave the largest estimate in 31 cases (11 summer, 3 late summer 17 fall) (10 pond, 15 lake, 6 river) and the smallest in none, and usually included area not used by the beaver. The MMA method gave the largest estimate in none of the cases and the smallest estimate in 5 cases (1 summer, 4 fall) (5 pond). The JT ellipse method gave the largest estimate in 36 cases (23 summer, 3 late summer, 8 fall, 1 spring, 1 late spring) (10 pond, 12 lake, 14 river) and the smallest in 14 cases (2 summer, 12 fall) (3 pond, 8 lake, 3 river). The JT ellipse usually included area not used, and excluded some areas that were used.

Home range estimates using all methods were significantly larger (t-test, $p<0.05$ to $p<0.005$, df=67) for cases in which the JT ellipse gave the largest estimate than for cases in which the MCP gave the largest estimate (Table 2). Home range sizes for the 2 cases in which the grid gave the largest estimate were smaller than those with the JT

Table 1. Home range sizes, as determined by grid cell method, minimum convex polygon method (MCP), modified minimum area method (MMA) and Jennrich Turner ellipse method (JT ellipse).

BEAVER	YEAR	SEASON	HOME RANGE ESTIMATE (HA)			
			GRID	MCP	MMA	ELLIPSE
IP403	1989	SUMMER	6.50	9.38	7.63	12.56
IP414	1989	SUMMER	4.75	6.00	4.55	7.92
IP433	1989	SUMMER	7.25	10.63	8.88	14.86
IP491	1989	SUMMER	7.50	10.88	9.00	14.75
IP403	1989	FALL	5.25	7.68	5.10	6.66
IP414	1989	FALL	2.00	2.50	2.15	2.53
IP491	1989	FALL	4.25	6.30	4.15	6.98
GP286	1989	SUMMER	8.00	11.75	10.75	17.06
GP1611	1990	SUMMER	5.25	7.00	6.00	6.53
GP1623	1990	SUMMER	5.75	8.63	7.25	7.70
GP1676	1990	SUMMER	4.00	5.13	4.75	4.33
GP1684	1990	SUMMER	6.75	9.88	8.50	8.36
GP1611	1990	FALL	2.50	3.13	2.88	2.83
GP1676	1990	FALL	2.50	3.50	2.88	2.14
GP1684	1990	FALL	3.00	4.25	3.63	2.68
GP1526	1991	SUMMER	8.25	12.88	12.00	22.46
GP1611	1991	SUMMER	7.75	11.75	10.88	16.55
GP1676	1991	SUMMER	2.50	2.75	2.50	2.03
GP1526	1991	FALL	1.00	0.94	0.82	1.02
GP1611	1991	FALL	1.00	0.95	0.85	0.85
TB1502	1991	SUMMER	4.25	5.75	5.25	4.37
TB1508	1991	SUMMER	2.75	4.00	3.38	3.06
TB1510	1991	SUMMER	6.00	9.75	7.75	10.32
TB1528	1991	SUMMER	5.75	10.38	7.75	11.81
TB1502	1991	L.SUM.	6.75	13.25	9.63	9.09
TB1508	1991	L.SUM.	5.50	11.00	8.31	16.70
TB1510	1991	L.SUM.	6.00	11.38	8.88	10.95
TB1528	1991	L.SUM.	7.00	13.88	10.63	9.67
TB1502	1991	FALL	1.50	1.75	1.50	1.16
TB1508	1991	FALL	1.00	0.91	0.80	0.48
TB1510	1991	FALL	2.75	3.10	2.45	1.69
TB1518	1991	FALL	1.50	1.88	1.50	0.67

BEAVER	YEAR	SEASON	HOME RANGE ESTIMATE (HA)			
			GRID	MCP	MMA	ELLIPSE
TB1520	1991	FALL	1.25	1.75	1.25	0.40
TB1522	1991	FALL	1.50	1.88	1.50	0.62
TB1528	1991	FALL	2.50	3.50	2.88	2.13
SL109	1989	SUMMER	4.75	5.75	5.25	5.24
SL1682	1990	SUMMER	14.50	36.88	23.38	59.71
SL1686	1990	SUMMER	12.50	29.50	20.00	35.42
JRB1617	1990	SUMMER	13.25	31.38	19.25	37.81
JRB1629	1990	SUMMER	5.00	8.75	6.38	13.25
JRB1641	1990	SUMMER	9.75	17.25	12.75	19.81
JRB1649	1990	SUMMER	11.75	30.13	19.63	33.72
JRB1617	1990	FALL	2.75	3.38	3.13	3.11
JRB1629	1990	FALL	1.25	1.75	1.25	1.10
JRB1641	1990	FALL	3.75	5.25	4.63	4.42
JRB1649	1990	FALL	3.25	4.50	3.75	4.02
BR1830	1986	FALL	8.00	14.75	11.00	16.16
BR1834	1987	SUMMER	8.25	28.63	12.00	59.90
BR1844	1987	SUMMER	13.75	52.00	33.50	109.39
BR1848	1987	SUMMER	42.75	223.88	175.50	383.85
BR1848	1987	L.SUM.	13.25	35.88	23.00	51.31
BR1834	1987	FALL	2.75	3.88	3.25	1.72
BR1844	1987	FALL	2.75	5.13	4.13	2.50
BR1848	1987	FALL	5.00	8.38	7.13	10.46
BR1834	1988	SUMMER	2.25	3.38	3.00	2.01
BR1848	1988	SUMMER	26.75	110.25	97.88	47.24
BR1834	1988	FALL	2.75	2.90	2.50	3.46
BR1848	1988	FALL	6.75	14.25	8.88	23.01
BR1848	1988	SPRING	11.25	32.38	19.63	48.53
BR1848	1988	L.SPR.	12.00	50.63	18.50	107.02
HB481	1989	SUMMER	20.50	55.50	34.25	128.83
BR1830	1989	SUMMER	16.00	54.50	28.75	54.71
BR1848	1989	SUMMER	9.50	23.25	17.50	29.59
HB481	1989	FALL	6.50	11.00	9.00	15.70

BEAVER	YEAR	SEASON	HOME RANGE ESTIMATE (HA)			
			GRID	MCP	MMA	ELLIPSE
BR1603	1990	SUMMER	12.50	37.38	22.25	37.04
BR1603	1990	FALL	4.25	5.00	4.65	5.06
BR1524	1991	SUMMER	14.00	43.75	27.50	101.82
BR1534	1991	SUMMER	20.75	89.50	53.88	137.83
BR1534	1991	L.SUM.	5.75	26.38	13.88	26.54

Figure 1. Correlation between home range area estimates using JT ellipse method and grid method.

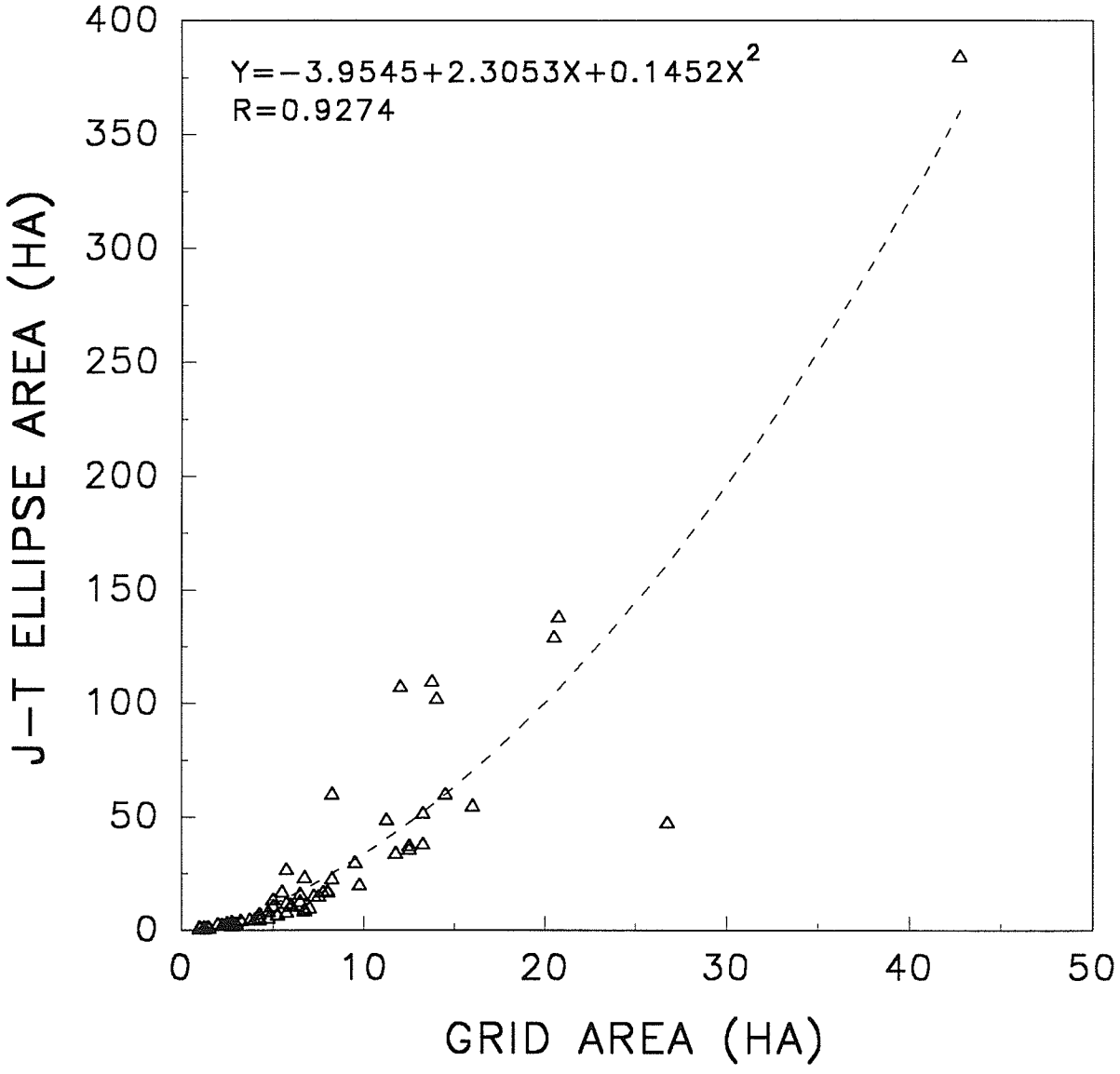

Y=−3.9545+2.3053X+0.1452X²
R=0.9274
J−T ELLIPSE AREA (HA)
GRID AREA (HA)
0
50
100
150
200
250
300
350
400
0
10
20
30
40
50

Figure 2. Correlation between home range area estimates using JT ellipse method and MCP method.

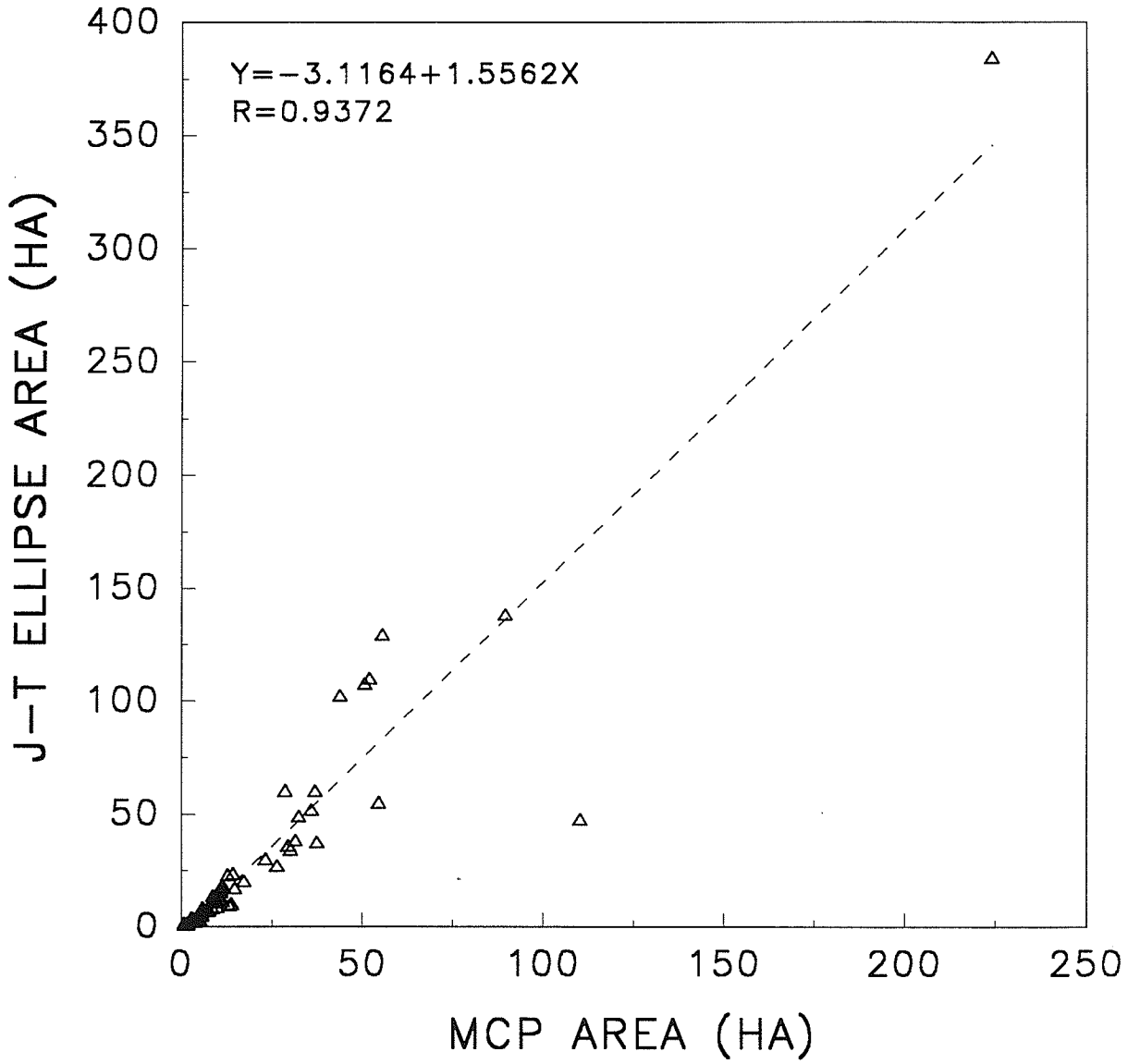

Y=-3.1164+1.5562X
R=0.9372
J-T ELLIPSE AREA (HA)
MCP AREA (HA)
0
50
100
150
200
250
300
350
400

Figure 3. Correlation between home range area estimates using JT ellipse method and MMA method.

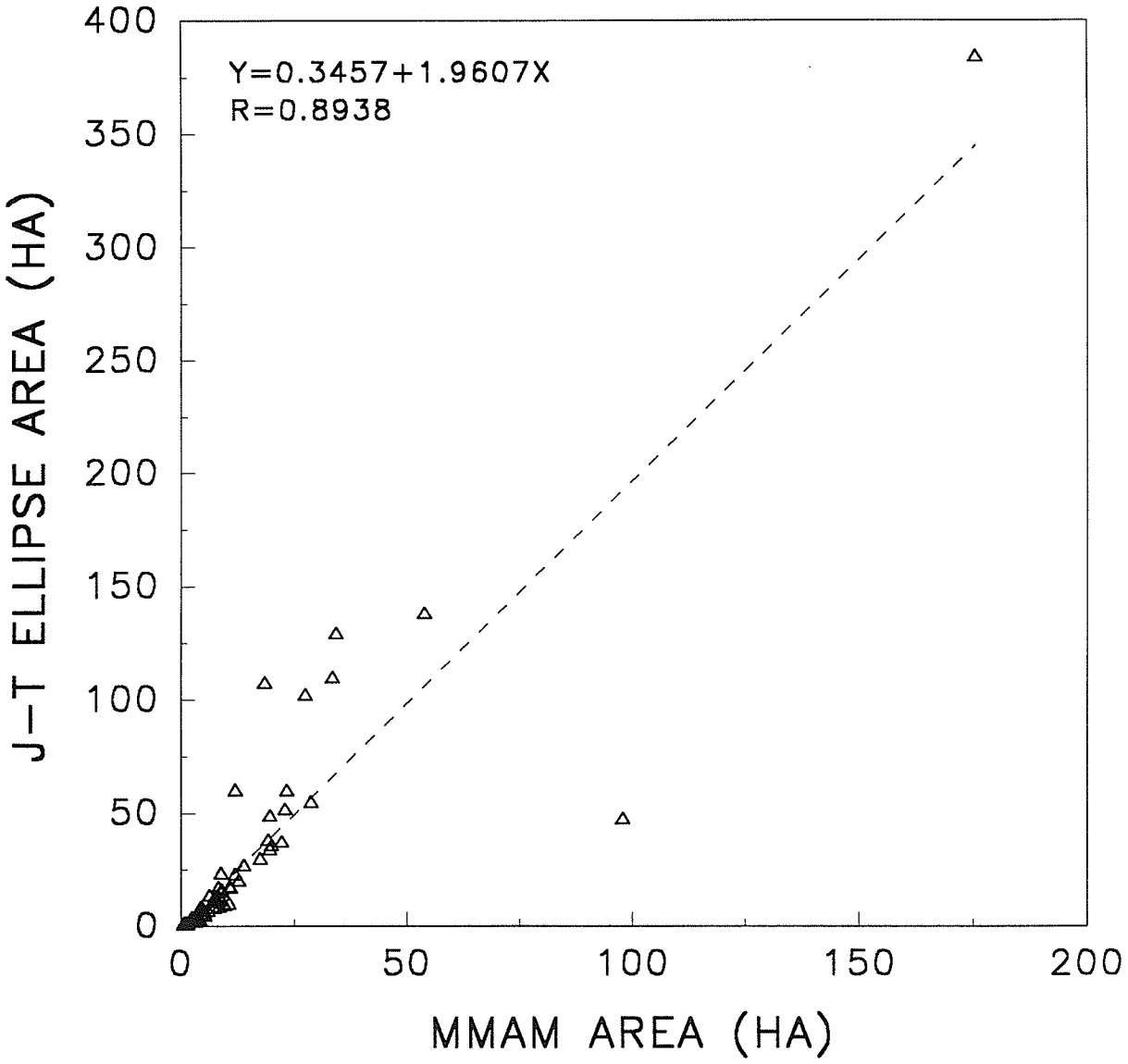

Y=0.3457+1.9607X
R=0.8938
J-T ELLIPSE AREA (HA)
MMAM AREA (HA)
0
50
100
150
200
250
300
350
400

Figure 4. Correlation between home range area estimates using MCP method and grid method.

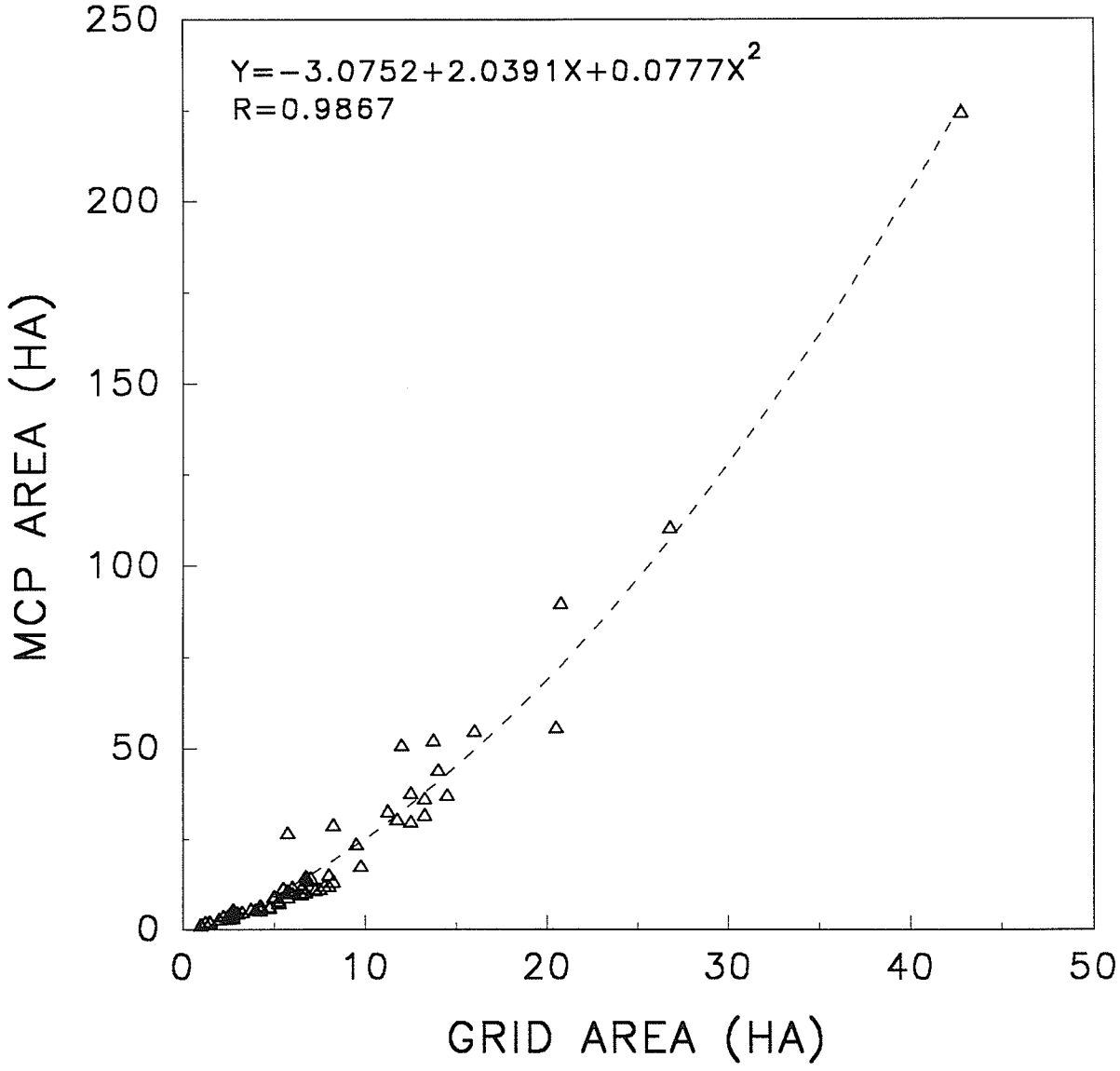

Y=−3.0752+2.0391X+0.0777X2
R=0.9867
MCP AREA (HA)
GRID AREA (HA)
0
50
100
150
200
250
0
10
20
30
40
50

Figure 5. Correlation between home range area estimates using MCP method and MMA method.

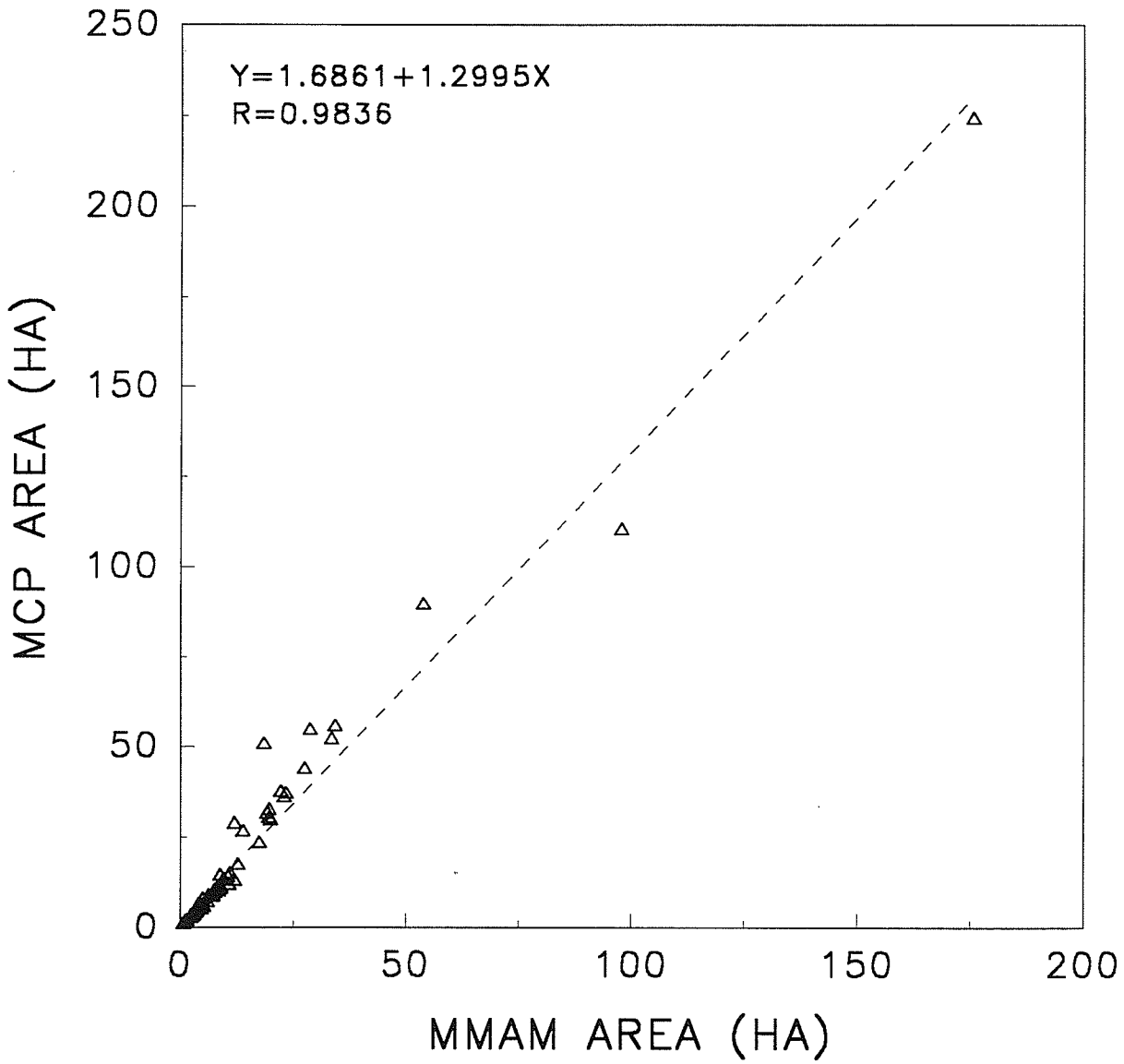

Y=1.6861+1.2995X
R=0.9836
MCP AREA (HA)
MMAM AREA (HA)
0
50
100
150
200
250

Figure 6. Correlation between home range area estimates using MMA method and grid method.

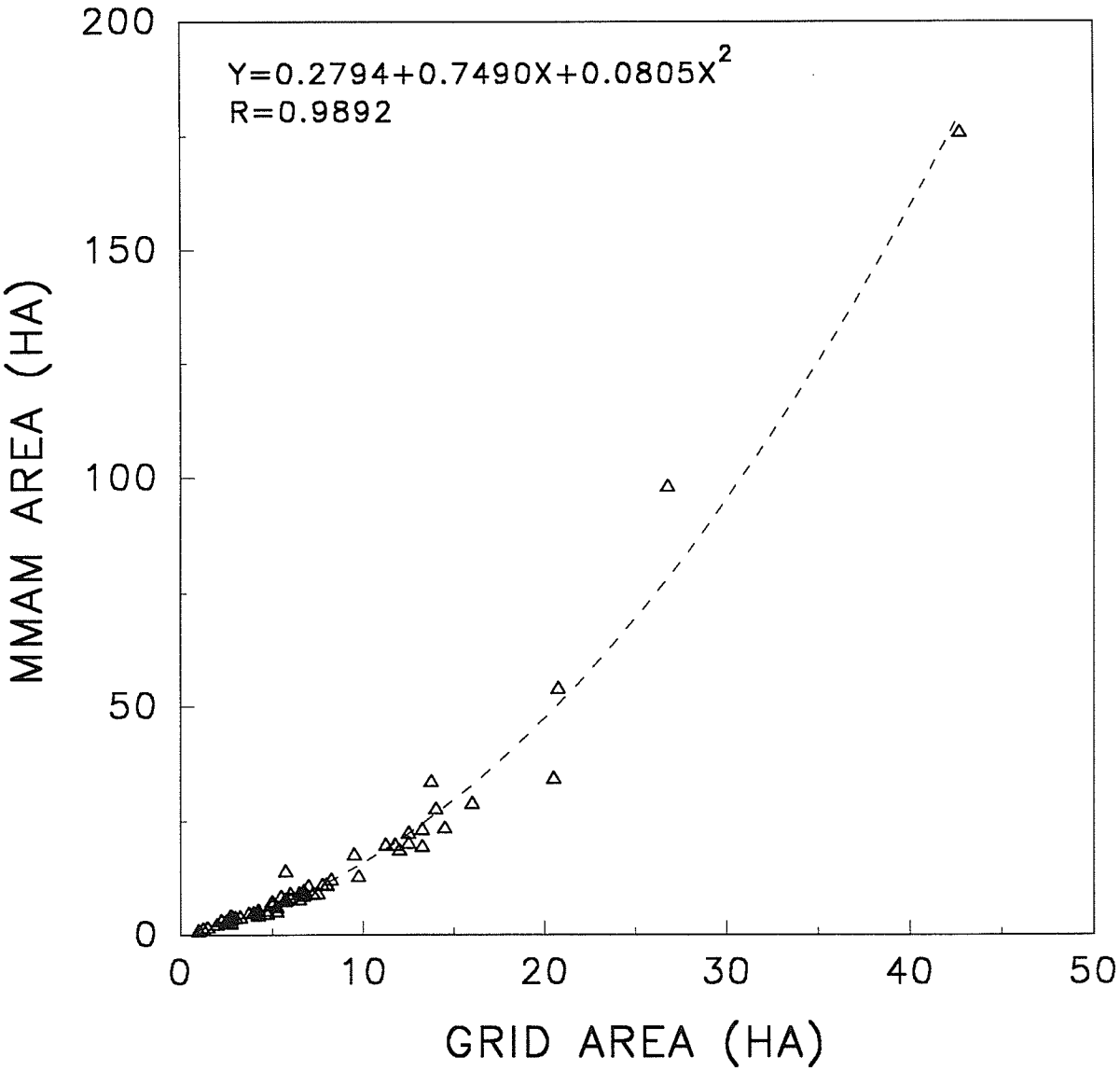

Y=0.2794+0.7490X+0.0805X2
R=0.9892
MMAM AREA (HA)
GRID AREA (HA)
0
50
100
150
200
0
10
20
30
40
50

Table 2. Home range estimate values using different methods of estimation for examples where JT ellipse, MCP or Grid give the largest estimates and for cases where JT ellipse, MMA or Grid give the smallest estimates. Grid = grid cell method, MCP = minimum convex polygon method, MMA = modified minimum area method, JT ellipse = Jennrich Turner ellipse method.

LARGEST ESTIMATES

LARGEST METHOD	GRID		MCP		MMA		JT ELLIPSE		N
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	
JT ELLIPSE	9.99	7.27	28.82	38.60	19.29	28.87	46.26	68.51	36
MCP	4.54	4.74	9.61	19.82	7.87	17.19	6.42	10.03	31
GRID	1.00	0.0	0.93	0.03	0.83	0.04	0.67	0.26	2

SMALLEST ESTIMATES

SMALLEST METHOD	GRID		MCP		MMA		JT ELLIPSE		N
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	
JT ELLIPSE	2.07	0.69	2.78	1.19	2.29	1.01	1.52	0.77	14
MMA	3.25	2.08	4.37	3.19	3.09	2.09	4.69	3.45	5
GRID	9.14	7.06	25.53	36.10	17.85	27.58	36.42	60.46	50

ellipse largest or MCP largest for all methods except the JT ellipse (Table 2).

Home range estimates using all methods were significantly smaller (t-test, $p<0.005$, df=64) for cases in which the JT ellipse gave the smallest estimate, than for cases in which the grid gave the smallest estimate. Estimates were only significantly smaller for the JT ellipse (t-test, $p<0.05$, df=19) when compared to those cases in which the MMA gave the smallest estimate. Mean home range sizes were significantly smaller (t-test, $p<0.005$, df=55) by all methods for cases in which the MMA method gave the smallest home range estimate as compared to cases in which the grid method gave the smallest estimate.

The largest difference between estimates was for beaver BR1848 in summer 1987, when the largest estimate (JT ellipse) was 8.98 times the smallest estimate (grid) (Figure 7). The most similar estimates were for beaver GP1611 in fall 1991 when the largest estimate (grid) was 1.176 times the smallest estimate (MMA) (Figure 8).

Neither of the 2 cases where the grid gave the largest home range estimate had any areas of concentrated use; both were small and somewhat circular (Figure 8). Forty-six of the cases where the grid estimate was smallest had 2 or more separate areas of concentrated use (Figure 7, 9 and 10); 3 had no areas of concentrated use; and 1 had 1 area of concentrated use. These home ranges tended to be irregular in shape, with several arms of activity.

Sixteen of the cases where MCP gave the largest estimate had 2 or more separate areas of concentrated use, usually at least one of these areas was at one edge or end of the home range (Figure 10); 12 cases had only one area of concentrated use, usually elongate through the home range (Figures 11 and 12); and 2 had no areas of concentrated use. Many of these home ranges included irregular protrusions of areas of non-concentrated use at one side or end of the home range (Figures 10, 11, 12).

Figure 7. Comparisons of home range outlines for 4 home range estimation methods, for the case with the largest difference between the estimates, BR1848. Squares = grid method;——— = JT ellipse;—— = minimum convex polygon; and- - - -= modified minimum area. Ellipse method largest, grid smallest.

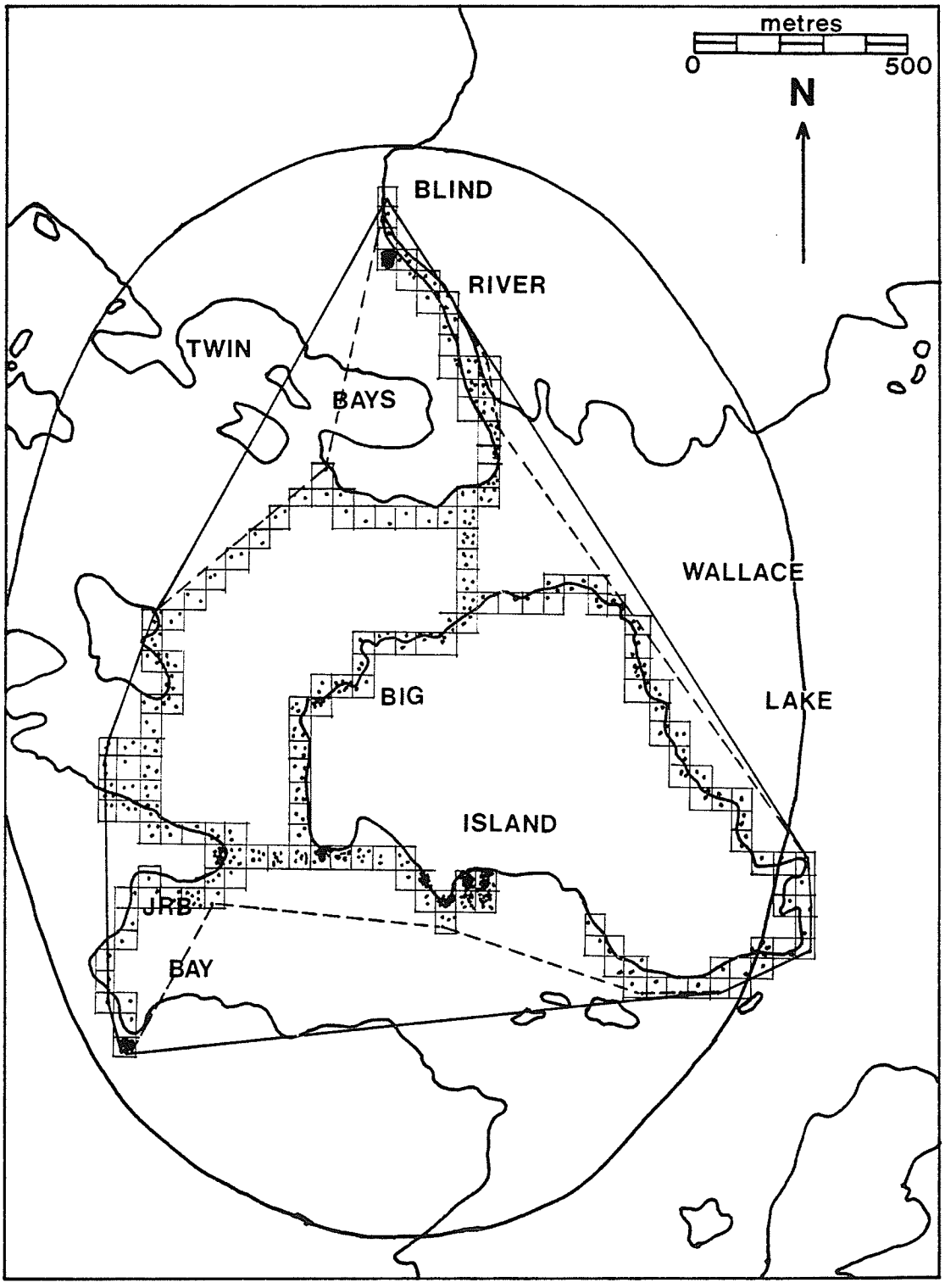

metres
0
500
N
BLIND
RIVER
TWIN
BAYS
WALLACE
BIG
LAKE
ISLAND
JRB
BAY

Figure 8. Comparisons of home range outlines for 4 home range estimation methods, for the case with the most similar estimates, GP1611. Squares = grid method; ——— = JT ellipse; —— = minimum convex polygon; and - - - = modified minimum area. Grid largest, MMA smallest.

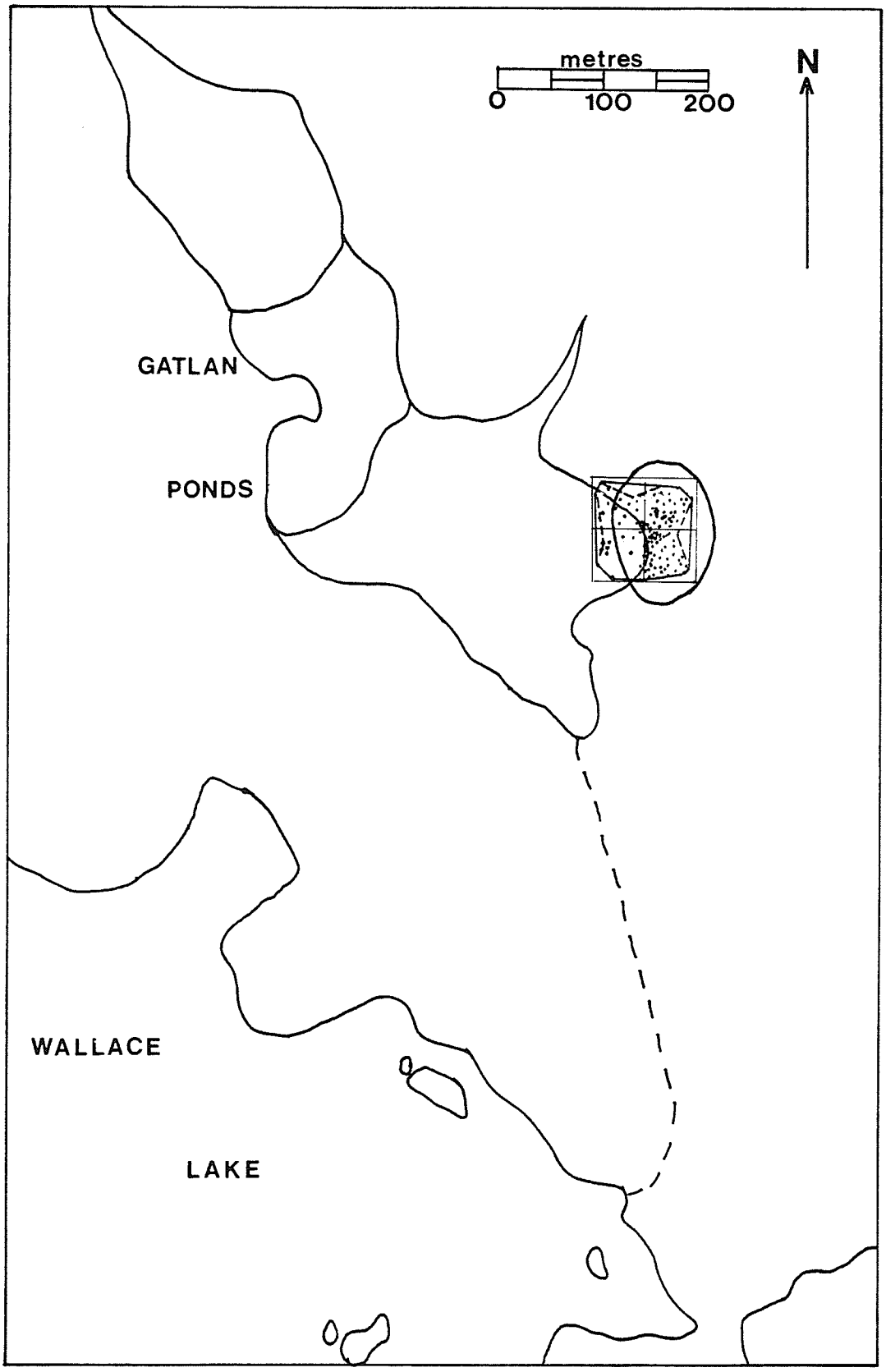

metres
0
100
200
N
GATLAN
PONDS
WALLACE
LAKE

Figure 9. Comparisons of home range outlines for 4 home range estimation methods, JRB1649. Squares = grid method; ▬▬ = JT ellipse; —— = minimum convex polygon; and - - - = modified minimum area. Ellipse largest, grid smallest.

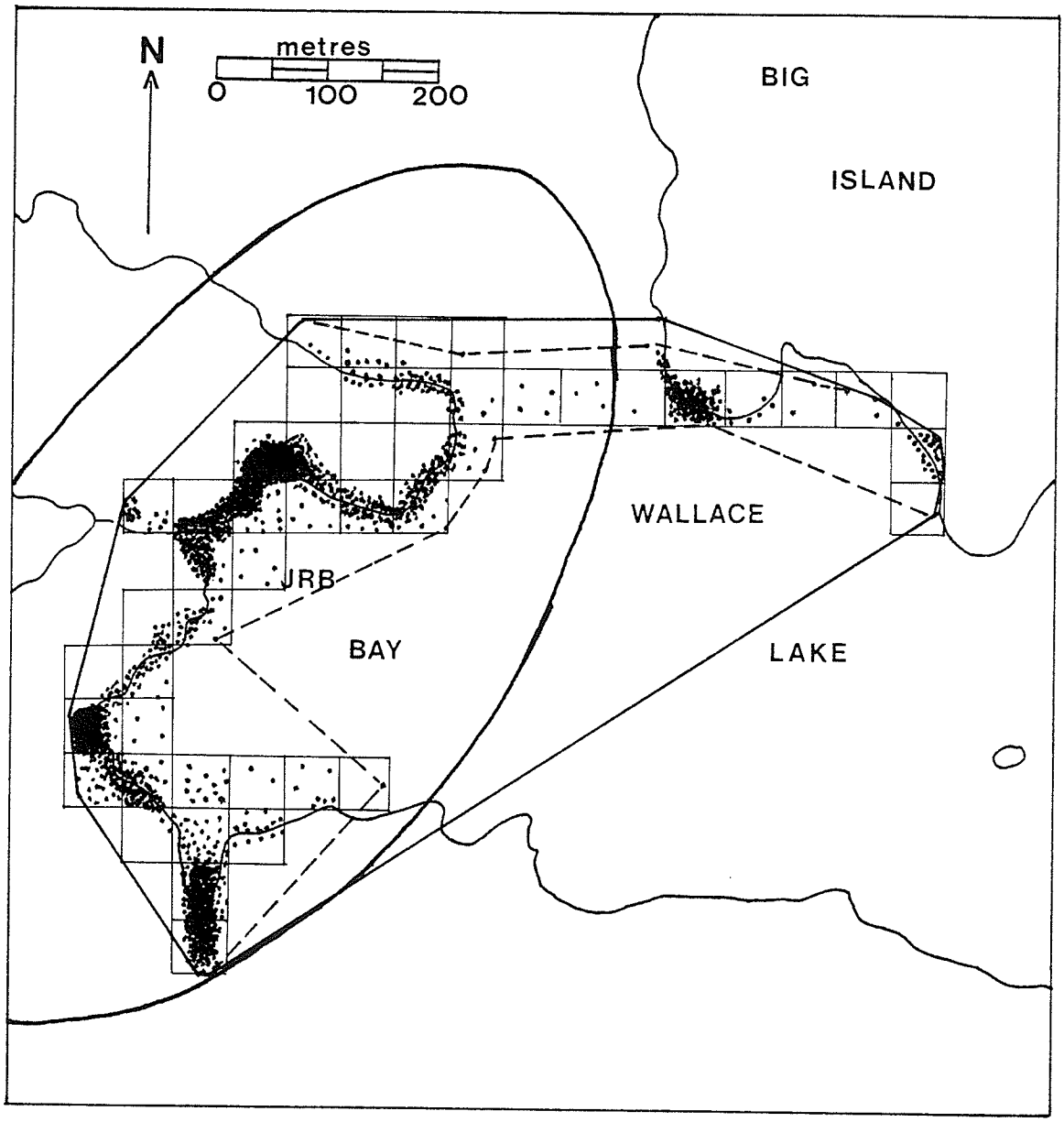

N
metres
0
100
200
BIG
ISLAND
WALLACE
JRB
BAY
LAKE

Figure 10. Comparisons of home range outlines for 4 home range estimation methods, BR1603. Squares = grid method; ——— = JT ellipse; ——— = minimum convex polygon; and — — — = modified minimum area. MCP largest, grid smallest.

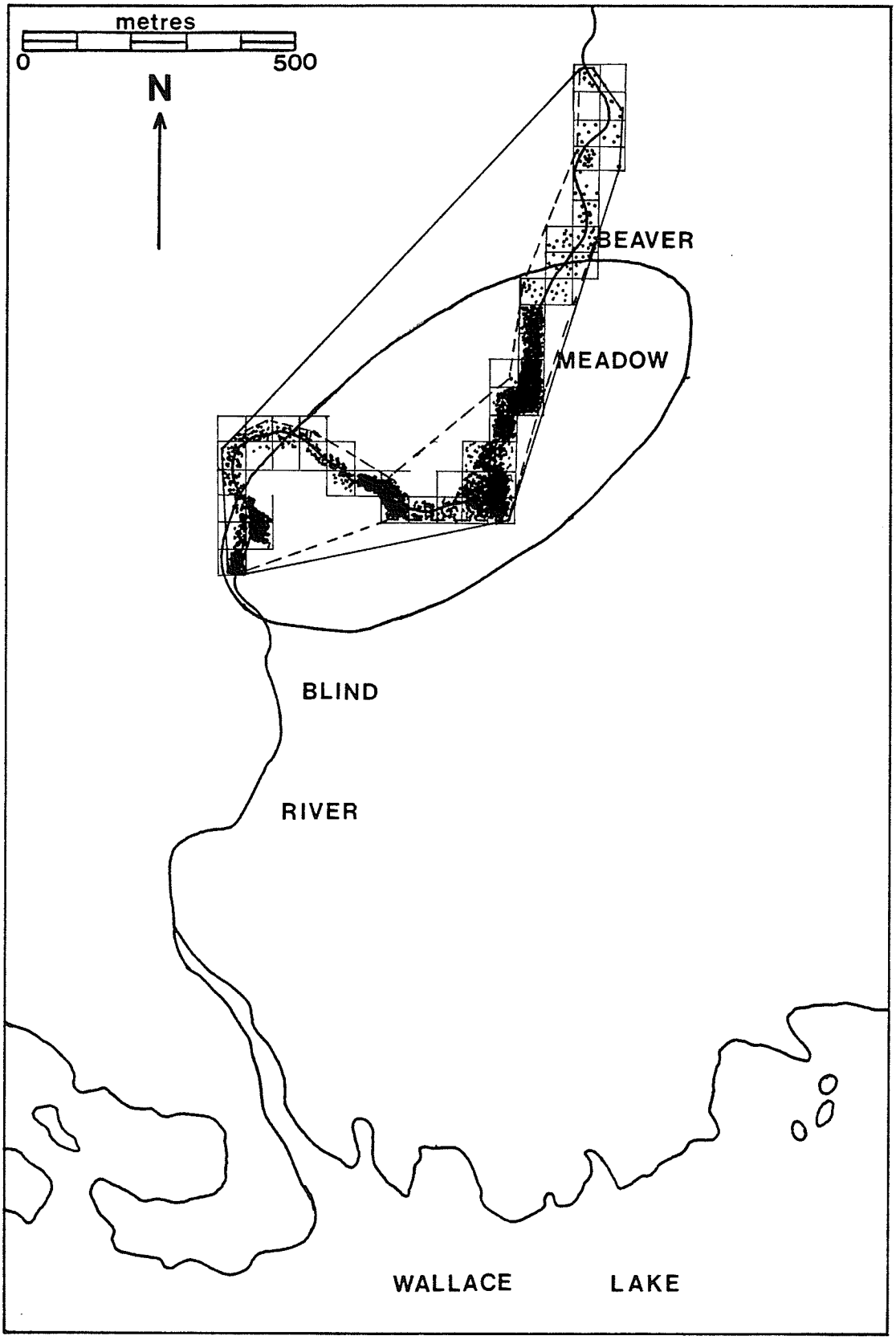

metres
0
500
N
BEAVER
MEADOW
BLIND
RIVER
WALLACE
LAKE

Figure 11. Comparisons of home range outlines for 4 home range estimation methods, IP403. Squares = grid method;——— = JT ellipse;——— = minimum convex polygon; and— — — = modified minimum area. MCP largest, MMA smallest.

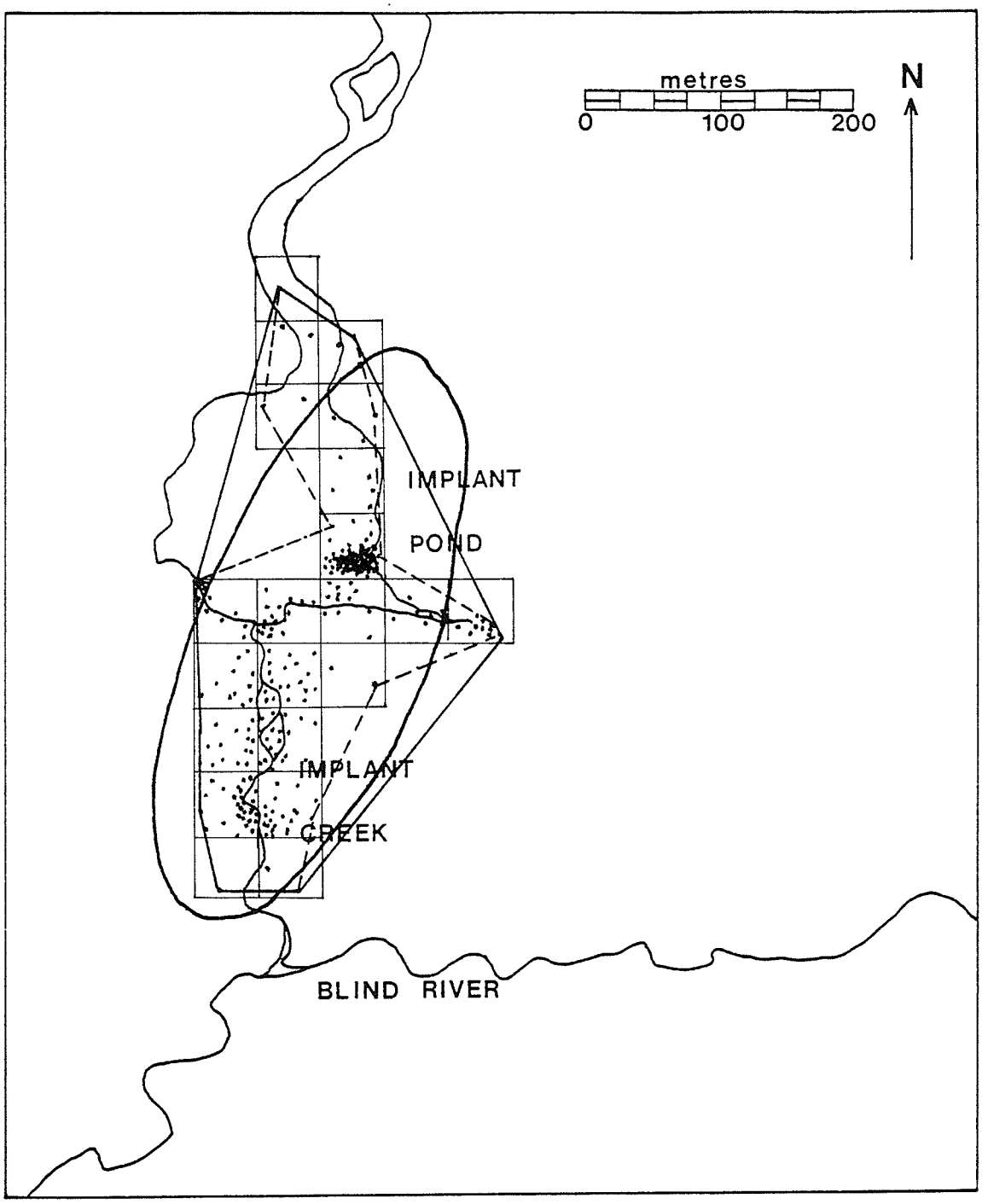
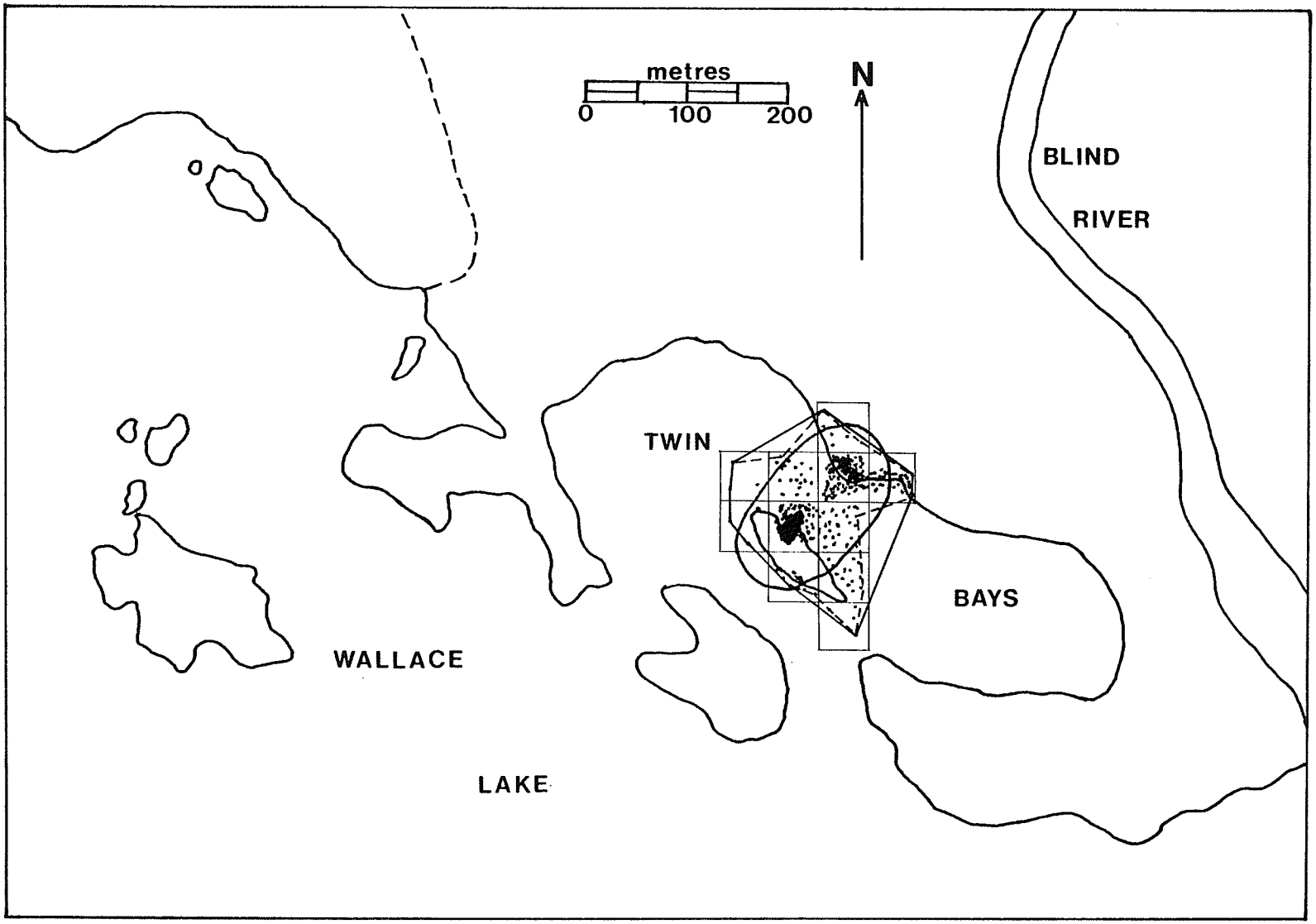

metres
0
100
200
N
IMPLANT
POND
IMPLANT
CREEK
BLIND RIVER

Figure 12. Comparisons of home range outlines for 4 home range estimation methods, TB1510. Squares = grid method;——— = JT ellipse;—— = minimum convex polygon; and—·—·= modified minimum area. MCP largest, ellipse smallest.


metres
0
100
200
N
BLIND
RIVER
TWIN
BAYS
WALLACE
LAKE

Of the 5 cases where the MMA gave the smallest estimate: 2 had only 1 area of concentrated use (Figure 11); 2 had no areas of concentrated use (Figure 8); and 1 had 2 separate areas of concentrated use. Four of these 5 home ranges were somewhat circular in shape.

Thirty-two of the 36 cases where the JT ellipse gave the largest method had home ranges with more than one area of concentrated use, usually towards the ends of the home range (Figures 7 and 9). One case had only one area of concentrated use but this area was elongate throughout the home range, and the remaining 3 cases had no areas of concentrated use. Ten of the 14 cases where the JT ellipse gave the smallest estimate had only one area of concentrated use, usually towards the centre of the home range (Figure 12); 3 cases had no areas of concentrated use; and 1 case had 2 areas of concentrated use, both close to the centre of the home range.

DISCUSSION

In general, the grid method gives the smallest estimate for larger home ranges, especially those of irregular shape, while the MCP gives the largest estimates for smaller to mid-size home ranges when there are several protruding arms, often with low use values. The JT ellipse gives the largest estimates for larger home ranges and smallest estimates for smaller home ranges with concentrated use near the centre of the home range. The MCP estimates will always be the same or larger than the MMA estimate, and may be significantly larger (Craig and Keller 1986). Galbraith *et al.* (1987) found that with turtles, the MCP generally gave the largest home range estimate and the MMA the smallest in 5 of 7 cases, with the grid giving intermediate values. However, Galbraith *et al.* (1987) used the MMA method to determine which grid squares to include in the home range estimate.

The grid method can be very useful, but depends somewhat on the grid size chosen (Macdonald *et al.* 1979). The grid has an assumption of homogeneity of use within each grid square. However, so long as the grid cell size has some biological basis, it should never give an estimate that is substantially larger than the MCP or MMA estimates. If there are several observations that are only just within grid squares, then the grid may overestimate the home range. If the number of observations are adequate, then the grid method should not underestimate the home range drastically. Macdonald *et al.* (1979) argue that the grid method does not give any measure of the distribution of fixes, but Samuel and Garton (1985) illustrate a method for examining use patterns and determining core areas.

The MCP and MMA estimates are simple, flexible and easily calculated (White and Garrott 1990). Nevertheless, they are very sensitive to movement on the perimeter of the home range (Macdonald *et al.* 1979) and especially, as seen here, to irregularities in the

distribution of activity. These irregularities may result in the inclusion of many unused areas in the MCP, which may be corrected for by the MMA (Harvey and Barbour 1965; Macdonald *et al.* 1979). Previous research has also shown that the MCP estimate is dependent on sample size, when the sample size is small (Jennrich and Turner 1969; Macdonald *et al.* 1979; Schoener 1981; Anderson 1982; Bowen 1982; White and Garrott 1990). Implicit in the MCP and MMA methods is an assumption that the habitat and utilization distribution are uniform throughout the range (Schoener 1981; Bowen 1982; Samuel and Garton 1985). This assumption means that while the MCP and MMA may be appropriate for quick approximations of home range size (Anderson 1982), their validity for most animals must be questioned.

In almost all cases the JT ellipse included areas not included by other methods and excluded areas other methods included. To some extent this exclusion should be expected since the JT ellipse only gives the estimated area for 95 % of the activity. The assumption of the JT ellipse is that activity is distributed in a bivariate normal manner about the centre of the range (Jennrich and Turner 1969; Samuel and Garton 1985; White and Garrott 1990). For beavers, when their home range came close to meeting the assumptions (one area of concentrated use close to the centre of the home range) the JT ellipse generally gave the smallest home range estimate. Therefore when the assumptions are met, the ellipse can be useful. But, rarely is the bivariate normal model biologically justifiable (Ford and Krumme 1979; Macdonald *et al.* 1979; Anderson 1982; White and Garrott 1990) although it may fit in a homogeneous environment (Van Winkle 1975).

APPLICATION OF METHODS TO ESTIMATE HOME RANGE SIZE

In the examples given here, it can be seen that home range shape often reflects shape of the habitat. In boreal forest shield areas,

water availability for beavers is regulated by irregularities of the land. Hence, home ranges tend to be irregular in shape. In areas where habitat has a more uniform "grain", such as a series of oxbow lakes of similar shape and size, home ranges should be more regular in shape. However, even areas which look homogeneous to the human eye may not be homogeneous to beaver. For example, a group of trees which all appear the same are not necessarily identical to beavers, who will sample them before leaving some and harvesting others (Jenkins, 1978).

With beaver, one can see that the habitat is not homogeneous, because they use both land and water. In addition, their home ranges frequently include a variety of vegetation types which make the land heterogeneous. However, as noted above, even areas which appear homogeneous to us are not necessarily homogeneous in what they provide to beavers. Similarly Roze (1989) reports porcupines (*Erethizon dorsatum*) using only selected trees in a forest. Pruitt (pers. comm.) noted that multiple caribou (*Rangifer tarandus*) entering muskegs eat one willow and ignore every other willow in the bog (Pruitt, pers. comm.).

Ford and Krumme (1979) discussed the importance of the basic physical structure of the environment in which an animal lives in determining the parts to which the animal truly has access. One must be careful when one looks at the apparent environment within which any animal lives. Burt (1943) noted that rarely if ever is an animal's home range in any convenient geometric design and that many were probably amoeboid in outline. The only method which will result in amoeboid shaped home range maps is the grid method. It is interesting to note that while most authors working on home range estimation cite Burt's (1943) definition of home range, they fail to mention this caution about home range shape.

Geist (1971) noted that home range may be laid out contrary to convenience and logic. The ellipse and polygon methods are logical, but not necessarily realistic, and usually do not recognize the physical

characteristics of the land. Mohr and Stumpf (1966) asserted that practical and theoretical considerations require that the real shape of the home range be recognized. Metzgar (1973) declared it unwise to assume that a particular shape or activity distribution occurs in any population at any one time. These assumptions are built into many of the methods.

Most animals do not use their entire home range with equal intensity (Dixon and Chapman 1980). However, the MCP and MMA assume uniform habitat and uniform use of the habitat. In order to understand the biological significance of an animal's home range, one must include some knowledge of the intensity of use, by the animal, of various parts of the area (Hayne 1949) because only when home range size and shape are coupled with ecological and behavioural information do they become meaningful (Bowen 1982). Only the grid method truly allows recognition of different intensities of use without any assumptions about the distribution of activity around the centres of activity.

Non-statistical techniques (MCP, MMA, grid) frequently have a sample size bias, and statistical techniques (JT ellipse) frequently lack biological meaning (Hutton 1989). The more mathematically complicated models (JT ellipse) do not necessarily give greater biological insight (Macdonald *et al.* 1979). Van Winkle (1975) and Voigt and Tinline (1979) both warned that one must keep the objective in mind of using sound statistical techniques that can take us beyond estimating home range parameters and look at how the animal is affected by its physical and biological environment. Of all the methods discussed here, only the grid method really allows for delineation of different intensities of use.

CONCLUSIONS

White and Garrott (1990) argued for emphasizing the actual map of locations which cannot be distorted. If this is done first, the pattern of use can be identified and the appropriate method used. If the distribution of points is fairly evenly spread, with no apparent arms protruding, then the MMA and MCP may give reasonable estimates of home range size. If there is a concentration of observations towards the centre of the points, with less towards the edges and no protruding arms, the JT ellipse may be appropriate. If the distribution of points shows several areas of concentrated use and/or an irregular shape, the grid method may be the most appropriate method of estimating home range shape and size. The grid method also allows the analysis of space use patterns within the home range. While all the methods are potentially useful for some of the beavers in my study, only the grid method appears to give reasonable estimates in all the examples. Since comparison between results from one group using one method and results from another group using another method is not legitimate, I believe the grid method is the most suitable method for use in comparing home ranges that are not necessarily all uniform in structure.

LITERATURE CITED

Adams, L. and S.D. Davis. 1967. The internal anatomy of home range. Journal of Mammalogy 48:529-536.

Anderson, D.J. 1982. The home range: a new nonparametric estimation technique. Ecology 63:103-112.

Bowen, W.D. 1982. Home range and spatial organization of coyotes in Jasper National Park, Alberta. Journal of Wildlife Management 46:201-216.

Brown, J.L. and G.H. Orians. 1970. Spacing patterns in mobile animals. Annual Review of Ecology and Systematics 1:239-262.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346-352.

Craig, E.H. and Keller, B.L. 1986. Movements and home range of porcupines, *Erethizon dorsatum*, in Idaho shrub desert. Canadian Field-Naturalist 100:167-173.

Dixon, K.R. and J.A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040-1044.

Don, B.A.C. and K. Rennolls. 1983. A home range model incorporating biological attraction points. Journal of Animal Ecology 52:69-81.

Ford, R.G. and D.W. Krumme. 1979. The analysis of space use patterns. Journal of Theoretical Biology 76:125-155.

Galbraith, D.A., M.W. Chandler and R.J. Brooks. 1987. The fine structure of home ranges of male *Chelydra serpentina*: are snapping turtles territorial? Canadian Journal of Zoology 65:2623-2629.

Geist, V. 1971. Mountain Sheep: A Study in Behavior and Evolution. University of Chicago Press, Chicago.

Harvey, M.J. and R.W. Barbour. 1965. Home range of *Microtus ochrogaster* as determined by a modified minimum area method. Journal of Mammalogy 46:398-402.

Hayne, D.W. 1949. Calculation of size of home range. Journal of Mammalogy 30:1-18.

Hutton, J. 1989. Movements, home range, dispersal and the separation of size classes in Nile crocodiles. American Zoologist 29:1033-1049.

Jenkins, S.H. 1978. Food selection by beavers: sampling behavior. Breviora 447:1-8.

Jennrich, R.I. and F.B. Turner. 1969. Measurement of non-circular home range. Journal of Theoretical Biology 22:227-237.

Macdonald, D.W., F.G. Ball and N.G. Hough. 1979. The evaluation of home range size and configuration using radio tracking data. In C.J. Amlaner, Jr. and D.W. Macdonald (Eds.), A Handbook on Biotelemetry and Radio Tracking. Oxford, Pergamon Press, pp. 405-424.

Metzgar, L.H. 1973. Home range shape and activity in *Peromyscus leucopus*. Journal of Mammalogy 54:383-390.

Miller, D.R. 1964. Colored plastic ear markers for beavers. Journal of Wildlife Management 28:859-861.

Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223-249.

Mohr, C.O. and W.A. Stumpf. 1966. Comparison of methods for calculating areas of animal activity. Journal of Wildlife Management 30:293-304.

Pruitt, W.O., Jr.. Personal communication, 1993. Department of Zoology, University of Manitoba, Winnipeg, Manitoba, R3T 2N2.

Roze, U. 1989. The North American Porcupine. Washington D.C.: Smithsonian Institution Press.

Samuel, M.D. and E.O. Garton. 1985. Home range: a weighted normal estimate and tests of underlying assumptions. Journal of Wildlife Management 49:513-519.

Samuel, M.D., D.J. Pierce and E.O. Garton. 1985. Identifying areas of concentrated use within the home range. Journal of Animal Ecology 54:711-719.

SAS Institute Inc. 1988. SAS/STAT® User's Guide Release 6.03 Edition. Cary, N.C: SAS Institute.

Schoener, T.W. 1981. An empirically based estimate of home range. Theoretical Population Biology 20:281-325.

Swihart, R.K. and N.A. Slade. 1985a. Influence of sampling interval on estimates of home-range size. Journal of Wildlife Management 49:1019-1025.

Swihart, R.K. and N.A. Slade. 1985b. Testing for independence of observations in animal movements. Ecology 66:1176-1184.

Van Winkle, W. 1975. Comparison of several probabilistic home-range models. Journal of Wildlife Management 39:118-123.

Van Winkle, W., Jr., D.C. Martin and M.J. Sebetich. 1973. A home-range model for animals inhabiting an ecotone. Ecology 54:205-209.

Voigt, D.R. and R.R. Tinline. 1979. Strategies for analyzing radio tracking data. In C.J. Amlaner, Jr. and D.W. Macdonald (Eds.), A Handbook on Biotelemetry and Radio Tracking. Oxford, Pergamon Press, pp. 387-404.

Wheatley, M. 1989. Ecology of Beaver (*Castor canadensis*) in the Taiga of Southeastern Manitoba. M.Sc. Thesis, University of Manitoba, Winnipeg, Manitoba, 167 pp.

White, G.C. and R.A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data. San Diego: Academic Press.

Whitten, A.J. 1982. Home range use by Kloss gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. Animal Behaviour 30:182-198.

CHAPTER 3

HOME RANGE SIZES OF BEAVER IN SUMMER

ABSTRACT

I studied beavers (*Castor canadensis*) in the boreal forest of eastern Manitoba from 1986 to 1992. I captured and ear tagged 60 different beavers, and outfitted 42 of these animals with transmitters. I collected sufficient data to determine summer home range size for 34 beavers. All beavers except one had core areas. Beavers living in river habitat had the largest summer home ranges, those living in pond habitats had the smallest home ranges, and lake beavers were intermediate. Adult males usually had the largest home ranges, and adult females the smallest. Adult females usually had home ranges centred closer to the lodge, and adult males farther from the lodge, than other family members. Percent of area in the core and percent of activity in the core were similar for all habitats and sex and age classes (27 % and 74 % respectively).

INTRODUCTION

Analysis of size and patterns of use of home range gives us a better understanding of the relationship between an animal and its environment or habitat. By assessing home range size and use it is possible to infer the real requirements of a species and how these might vary in different habitats and for different sex and age classes. Much early work on beavers relied on examining evidence of beaver activity: lodges; dams; food piles; and cutting areas (Morgan 1868 in Morgan 1986; Warren 1927). Only with the advent of radio-telemetry has the study of the actual movements of this nocturnal mammal been possible.

Many authors have provided a variety of definitions of home range (Brown and Orians 1970; Burt 1943). There is a general acceptance of Burt's (1943) definition of home range as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young". Home range is different from territory which Burt (1943) defines as the "protected part of the home range". Brown and Orians (1970) list 3 conditions which must be met for an area to be considered a territory: 1) a fixed area; 2) a defended area; 3) exclusive use of area. In this paper I will consider home ranges only. The issue of territoriality will be dealt with separately in Chapter 6.

Animals use areas disproportionately within their home range (Samuel *et al.* 1985), and there may be regions of more concentrated use or core areas (Springer 1982). Core areas are "those areas used more frequently than any other areas and probably contain the home sites, refuges and most dependable food sources ... that is those portions of the animal's home range that exceed an equal use pattern" (Samuel *et al.* 1985).

Busher (1975) and Davis (1984) quantified daily movements of beaver but did not delineate actual home range sizes. Brady and Svendsen (1981), Bergerud and Miller (1977) and Green (1936) all

described beaver activities without quantifying movements or home range size. Only Gillespie (1975) provided details of beaver home range size. Hodgdon and Larson (1973) and Busher and Jenkins (1985) reported differences in behavioural patterns of different age class and sexes of beavers, while Davis (1984) assumed that there was no significant difference in movement or behaviour patterns between sex and age classes. No authors appear to have examined variations in home range size among beavers in different sex and age classes. Nor have any attempts been made to identify core areas of beavers.

The purpose of this paper is to examine use of home range by beavers in summer. This lasts from breakup of ice cover in early May to the beginning of fall activity (construction of food pile and/or lodge) in late August or early September. Kits are born in late May or early June. The summer months are spent raising the kits and/or feeding and growing.

The null hypotheses for my study are: H_o1 All areas of the home range are used equally, that is there are no core areas; H_o2 There is no correlation between size of core areas (if present), size of home range, proportion of area in the core and proportion of activity in the core; H_o3 There are no differences in these parameters for beavers living in different habitats; H_o4 There are no differences in these parameters for beavers of different sex and age classes; H_o5 There are no differences in the locations of activity of different family members.

METHODS

I live-trapped beavers using Hancock traps baited with a piece of trembling aspen (*Populus tremuloides*) 30 cm long and 2 to 5 cm in diameter and a scent bait consisting of ground up beaver castor, anise extract and glycerine (Aleksiuk, 1968). For each animal I took measurements of total length, tail length, hind foot length, length of ear from notch, neck circumference, and tail circumferences at the base and at the widest point. I also weighed each animal and determined its sex by palpating externally for the baculum.

To facilitate visual identification of individuals, I attached to both ears uniquely numbered metal ear tags (Monel, Number 3) to which I affixed uniquely coloured flags of reinforced vinyl as described by Miller (1964).

RADIOTELEMETRY

I installed radio-transmitter using 2 methods: intraperitoneal implantation (42 transmitters); and tail collars (3 transmitters) (Wheatley 1989). The implanted packages (Austec Electronics) consisted of a transmitter coupled with a C cell lithium battery, all encased in beeswax and then Elvax (Mini-mitter Co.) which is biologically inert. The entire package measured about 6 x 4 cm and weighed about 80 g. The tail collars (Wildlife Materials Inc.) measured 12.5 x 7.5 x 4.5 cm and weighed about 295 g including the webbing used for attachment to the base of the tail.

For tracking beavers I used an H-shaped antenna and 24 channel receiver (Wildlife Materials Inc.). For beavers residing on the river or lake, I generally tracked and observed from a 6.5 m freighter canoe. When observing at ponds, I chose a high ridge or similar good vantage point nearby from which to make observations. In general, I used the

telemetry to locate the beaver and then, as much as possible, continued with visual observations of activities and movements. After dark, my observations were based on using telemetry to locate animals, and sounds of chewing or tree felling or visual observation of water ripples to determine activity.

I recorded information about the location, time, type of activity, and any movement to another location during the period of observation. Observation periods varied in length from 5 minutes to 13 hours depending upon weather conditions and the number of animals being observed in one night. Most observations were made between 1800 and 2400 h. I recorded data directly in a field book or on cassette audio tape for later transcription into the field book. I later transferred the data onto forms for each beaver.

I drew maps of appropriate size and scale to encompass the home range of each beaver or group of beavers. I then made a grid overlay on an acetate sheet, equivalent to a 50 m by 50 m grid (0.25 ha) on the ground. I transferred each beaver's data onto the appropriate grid. For this I considered 1 minute as 1 observation. A beaver can swim approximately 50 m in one minute. While this does not allow for true independence of observations (Swihart and Slade 1985a; 1985b), the beavers move throughout their home ranges too much to be able to reflect accurately home range use by 1 observation per night. I separated seasons by identifying apparent shifts in patterns of use, such as new areas of use or previously used areas that were no longer frequented.

I tallied the number of observations in each grid cell and the total number of observations for each beaver for each season. I also recorded the total number of grid cells used. To determine the core area of each individual's home range, I calculated the proportion of observations in each grid cell (number of observations in cell/total number of observations) and compared these proportions to those expected in each grid cell if the beaver's use of the cells was uniform (1/number

of grid cells). I compared the ordered observed cumulative distribution function with the hypothesized uniform cumulative distribution function for each beaver using the Kolmogorov-Smirnov one tailed goodness of fit procedure in which N equals the number of grid squares (Samuel *et al.* 1985). If this test showed that a core area was present, I classed all cells with a greater proportion of observations than uniform as core areas (Samuel *et al.* 1985). I then transferred to the map the outline of the home range and core areas within the home range.

TERMS AND DEFINITIONS

I calculated the home range size in hectares by dividing the total number of grid cells used by 4. In all following discussions, I refer to this as the Total Size. I determined the size of the core area (Core Size) by totalling the number of grid cells identified as constituting the core area and dividing these by 4 in the same manner as for Total Size. I calculated the percent of the Total Size that was included in the Core Size for each beaver by dividing the Core Size by total size and multiplying by 100. This I refer to as the Core Percent. To calculate the percent of activity which occurred within the core area (Core Activity), I divided the total number of observations in cells identified as comprising the core area by the total number of observations of each beaver and multiplied by 100.

To separate different age classes, I used the classification system of Buckley and Libby (1955). "Kits" were any beavers less than 12 months of age. "Yearlings" refers to all beaver in their second year of life and "two-year-olds" to those in their third year of life. The term "adult" refers to any beaver older than 36 months of age. I classified beavers as pond, lake or river beavers based on the location of their primary residence (the lodge or bank burrow used most).

ANALYSIS

I analyzed the data for all beavers by habitat type and by sex and age class within family groups. I calculated the means for Total Size, Core Size, Core Percent and Core Activity. Results are given as mean ± 2 standard errors. I employed Spearman Rank Correlation (r_s) to determine correlations between different variables (pairwise correlations between Total Size, Core Size, Core Percent and Core Activity) for all beavers and broken down by habitat. I used the Mann-Whitney U-test for analysis of habitat differences in the variables. For determining differences in the variables between family members within families I used the Wilcoxon Matched Pairs Test.

I used SAS (SAS Institute Inc. 1988) to calculate a weighted centroid of all the observations on each beaver and the associated variance. Hayne (1949) uses the term "centre of activity" to refer to the geometric centre of all the locations of an animal, while Dixon and Chapman (1980) use the term "centre of activity" to mean an area in which there is a large amount of activity. For this reason I have chosen an alternate term, the "centroid" to denote the geometric centre of all the points. For beavers residing in family groups, I then tested for similarity between the calculated centroids using F and t tests with weighted degrees of freedom.

RESULTS

I captured and ear tagged 60 different beavers, and outfitted 42 of these animals with transmitters. Some animals had more than 1 transmitter during the course of this study. I had sufficient data to determine summer home range size for 34 beavers.

Total Size ranged from 2.25 to 42.75 ha ($\bar{X}$=10.34±2.75 ha, N=34) (Figure 1). All beavers had core areas (Kolmogorov one-sided test, $p<0.05$ to $p<0.005$) except one adult female (TB1508, lake habitat, $p>0.05$, N=11)(Appendices 2 and 3). Core Size varied from 0.75 to 14.25 ha ($\bar{X}$=2.864±0.9070 ha, N=33)(Figure 1). The core area accounted for 16.36 to 37.5 % of the total home range ($\bar{X}$=27.27±1.9 %, N=33)(Figure 2), and included 60.9 to 84.4 % of the activity ($\bar{X}$=74.05±2.5 %, N=33) (Figure 2) (See also Appendix 1).

Core Size and Total Size were highly correlated (Spearman Rank Correlation, r_s=0.9340, $p<0.0005$, N=33). There was no significant correlation between Total Size and Core Activity (r_s=0.0391, $p>0.25$, N=33) or Core Percent (r_s=-0.2463, $p>0.05$, N=33). Neither was the Core Size correlated with Core Percent (r_s=0.0528, $p>0.25$, N=33) or Core Activity (r_s=0.1897, $p>0.1$, N=33). Core Activity and Core Percent also were not significantly correlated (r_s=0.2445, $p>0.05$, N=33).

Beaver home ranges tended to follow shorelines and never included large expanses of open water (Appendix 1). I only found beavers in open water areas (on lakes) when they were crossing from one point of land to another, and then they appeared to select areas that furnished the narrowest expanse of water. Even pond beavers did not often use the central part of their ponds. Main lodges were usually at one side or end of a home range, and rarely towards the centre. Core areas always included both land and water and were never exclusively one or the other. While beavers did not use their entire home range every night, I found that during overnight observations, beavers did use most of their

Figure 1. Summer home range area size (open symbols) and core area size (closed symbols) (hectares) for all beavers combined and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range.

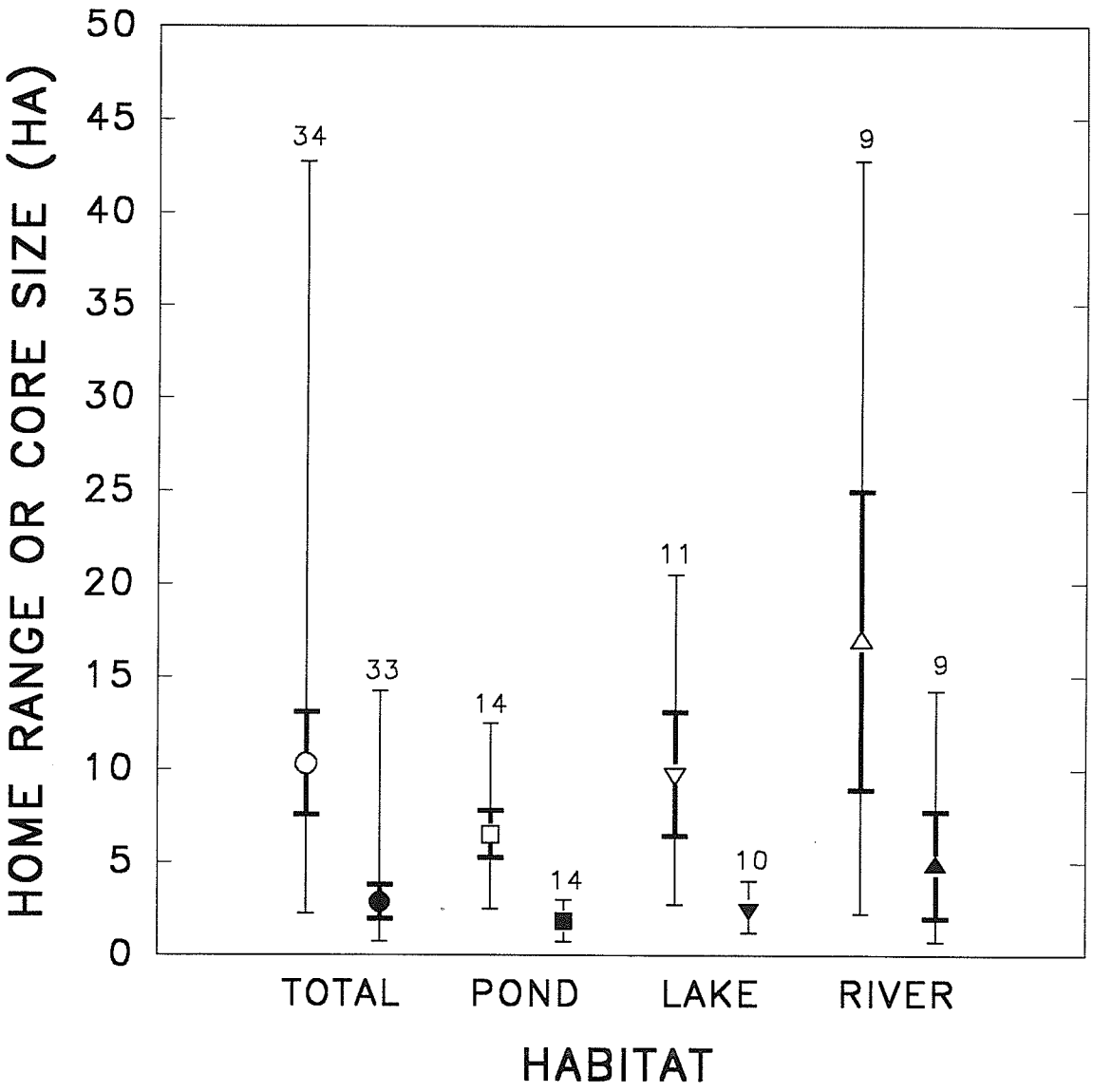
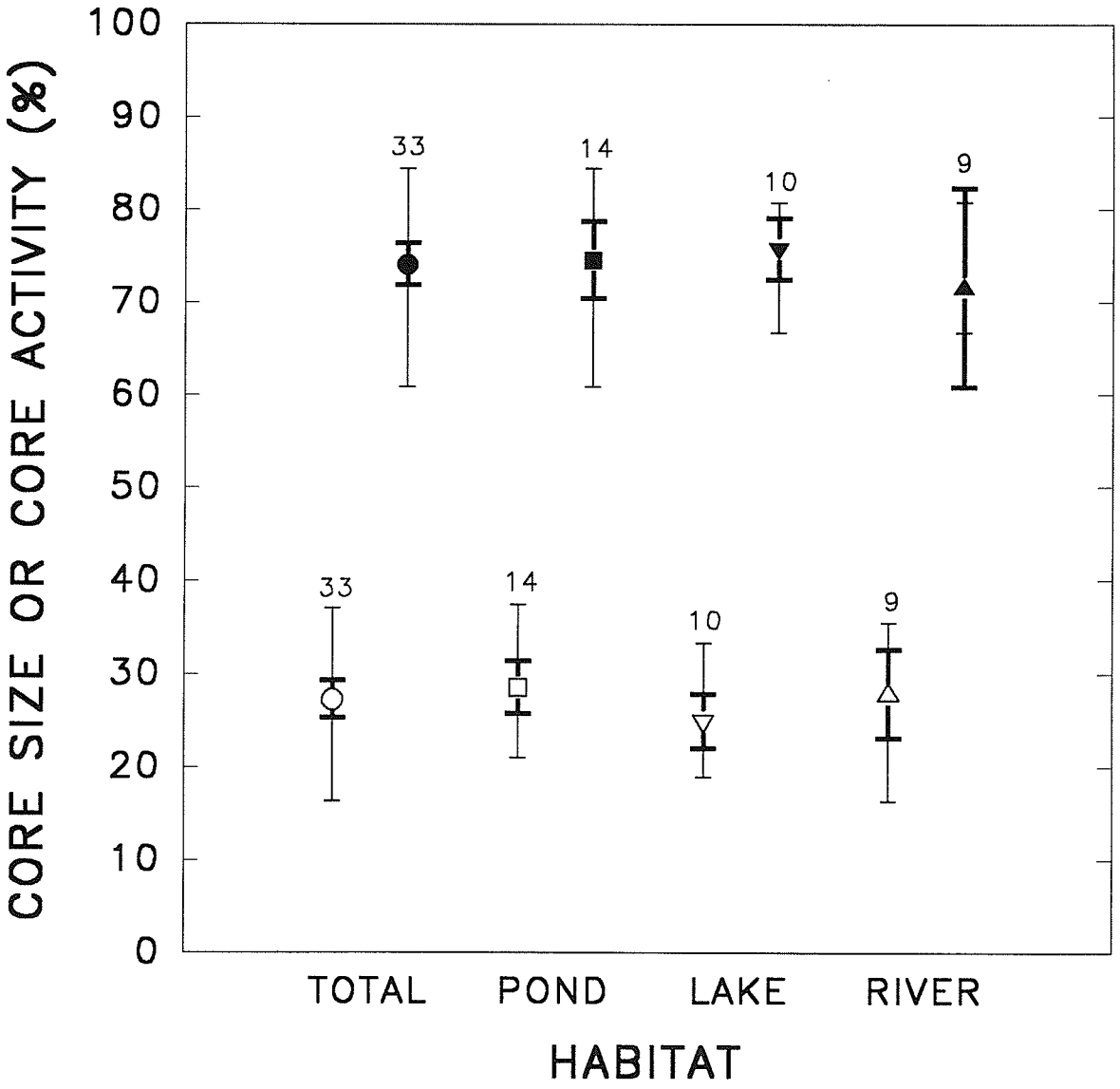

HOME RANGE OR CORE SIZE (HA)
50
45
40
35
30
25
20
15
10
5
0
34
33
14
14
11
10
9
9
TOTAL
POND
LAKE
RIVER
HABITAT

Figure 2. Summer core size as percent of total home range size (open symbols) and percent of all activity in core area (closed symbols) for all beavers combined and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range.


CORE SIZE OR CORE ACTIVITY (%)
100
90
80
70
60
50
40
30
20
10
0
33
14
10
9
33
14
10
9
TOTAL
POND
LAKE
RIVER
HABITAT

home range every night. (See Appendix 1) During the night, beavers residing in family groups made frequent trips to the lodge from their feeding areas, often taking vegetation into the lodge at that time. Beavers not resident in family groups usually spent most of the night out of the lodge with no visits to the lodge.

HABITAT

Total Size was larger for river beavers than pond beavers (Mann-Whitney U-test, U=17, $p<0.005$, n=14,9)(Figure 1). There was no significant difference in Total Size between beavers inhabiting ponds and lakes (U=53.5, $p>0.1$, N=14,11)(Figure 1) or lakes and rivers (U=31, $p>0.05$, N=11,9)(Figure 1). Likewise Core Size was larger in rivers than ponds (U=23.5, p,0.01, N=14,9)(Figure 1), but there was no difference in Core Size between pond and lake (U=45, $p>0.05$, N=14,10) or river and lake (U=28, $p>0.05$, N=9,10). The Core Percent was not significantly different between pond and lake (U=44, $p>0.05$, N=14,10), pond and river (U=62, $p>0.01$, N=14,9) or river and lake (U=32, $p>0.1$, N=9,10)(Figure 2). Neither was there any difference in the Core Activity between pond and lake (U=64, $p>0.1$, N=14,10), pond and river (U=62, $p>0.1$, N=14,9) or river and lake (U=32, $p>0.1$, N=9,10)(Figure 2).

Pond

For pond beavers the Core Size and Total Size were highly positively correlated ($r_s=0.9188$, $p<0.0005$, N=14). The Total Size was also significantly positively correlated with Core Activity ($r_s=0.4796$, $p<0.05$, N=14) but was not positively correlated with Core Percent ($r_s=0.0858$, $p>0.25$, N=14). The Core Size was positively correlated with both Core Percent ($r_s=0.4094$, $p<0.05$, N=14) and Core Activity ($r_s=0.7342$,

$p<0.0025$, N=14). Core Percent and Core Activity were highly correlated ($r_s=0.7143$, $p<0.005$, N=14).

Lake

Total Size was highly positively correlated with Core Size ($r_s=0.9326$, $p<0.0005$, N=10) and negatively correlated with Core Percent ($r_s=-0.6485$, $p<0.025$, N=10). Total Size was not positively correlated with Core Activity ($r_s=0.1043$, $p>0.25$, N=10). Core Size was not significantly positively correlated with Core Percent ($r_s=-0.4049$, $p>0.1$, N=10) or Core Activity ($r_s=0.1043$, $p>0.25$, N=10). Neither were Core Percent and Core Activity positively correlated ($r_s=-0.0667$, $p>0.25$, N=10).

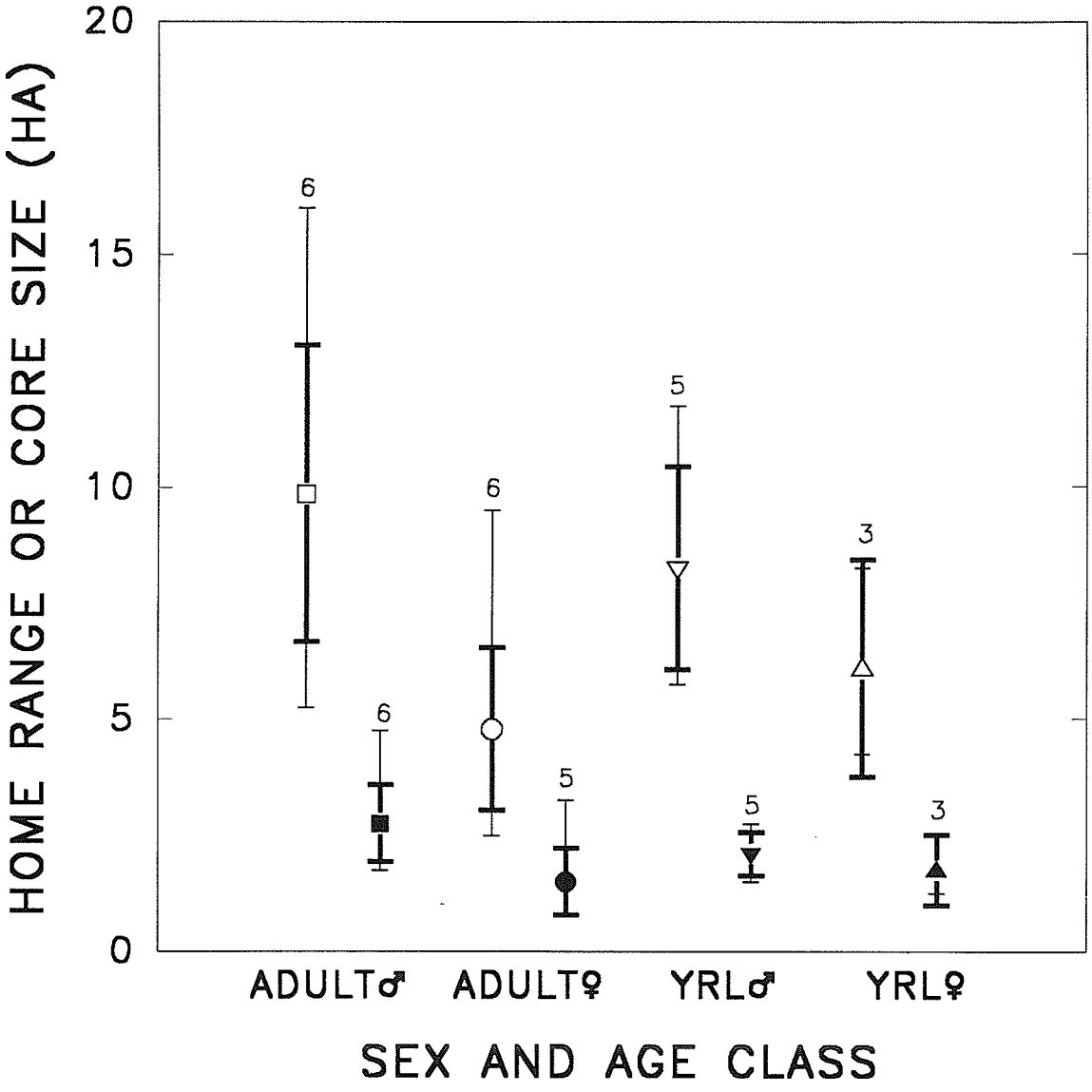
River

Total Size was highly positively correlated with Core Size ($r_s=0.9289$, $p<0.0005$, N=9) but not with Core Percent ($r_s=0.1172$, $p>0.25$, N=9) or Core Activity ($r_s=0$, $p>0.25$, N=9). Core Size was not positively correlated with Core Percent ($r_s=0.3697$, $p>0.1$, N=9) or Core Activity ($r_s=0.1088$, $p>0.25$, N=9). Neither was there a significant positive correlation between Core Activity and Core Percent ($r_s=-0.0418$, $p>0.25$, N=9).

FAMILY

Within known family groups, Total Size of adult males was significantly larger than that of adult females (Wilcoxon Signed Rank Test, T=0, p=0.0078, N=6)(Figure 3). Total Size of yearling males was also larger than that of adult females (T=0, p=0.0132, N=5), but adult

Figure 3. Summer home range area size (open symbols) and core area size (closed symbols) (hectares) for beavers living in family groups, by sex and age class. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range.


20
15
10
5
0
HOME RANGE OR CORE SIZE (HA)
6
6
6
5
5
5
3
3
ADULT♂
ADULT♀
YRL♂
YRL♀
SEX AND AGE CLASS

males were no different from yearling males (T=3.5, p=0.1562, N=5). There were insufficient yearling females (N=3) for comparison to any of the other groups, but the yearling females' home ranges tended to be intermediate in size between sizes of the adult female and yearling male (Figure 3).

The adult males' Core Sizes were larger than the adult females' (T=0, p=0.0156, N=5)(Figure 3). Yearling males' Core Sizes tended to be next largest after the adult males', but were not significantly different from the adult males' (T=3, p=0.3125, N=5). These were followed in size by the yearling females and adult females, but numbers in each group are too few for statistical comparison.

The Core Percent was very similar for all family members (Figure 4). There was no significant difference between adult males and adult females (T=7, p=0.2812, N=6) or between adult males and yearling males (T=3, p=0.1562, N=5). There were insufficient numbers to compare other groups.

There was no difference in Core Activity between adult males and females (T=10, p=0.5, N=6), but the yearling males had greater Core Activity than the adult males (T=0, p=0.0312, N=5) (Figure 4). Numbers within other groups were insufficient for statistical comparisons.

Centroids

The centroids of activity were different for each family member within each family group (t-test, $p<0.025$ to $p<0.0005$)(Figures 5,6,7,8 and 9). A significant difference in either the X or Y direction results in a difference in the centroids. Within each family, the adult female's activity centroid was closer to the lodge than that of any other member of the family. The adult male's centroid was farther from the lodge than all other family members for Implant Pond, Twin Bays and Gatlan Pond (1991)(Figures 5,6 and 9). In the JRB Bay and Gatlan Pond

Figure 4. Summer core size as percent of total home range size (open symbols) and percent of all activity in core area (closed symbols) for beavers living in family groups, by sex and age class. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range.

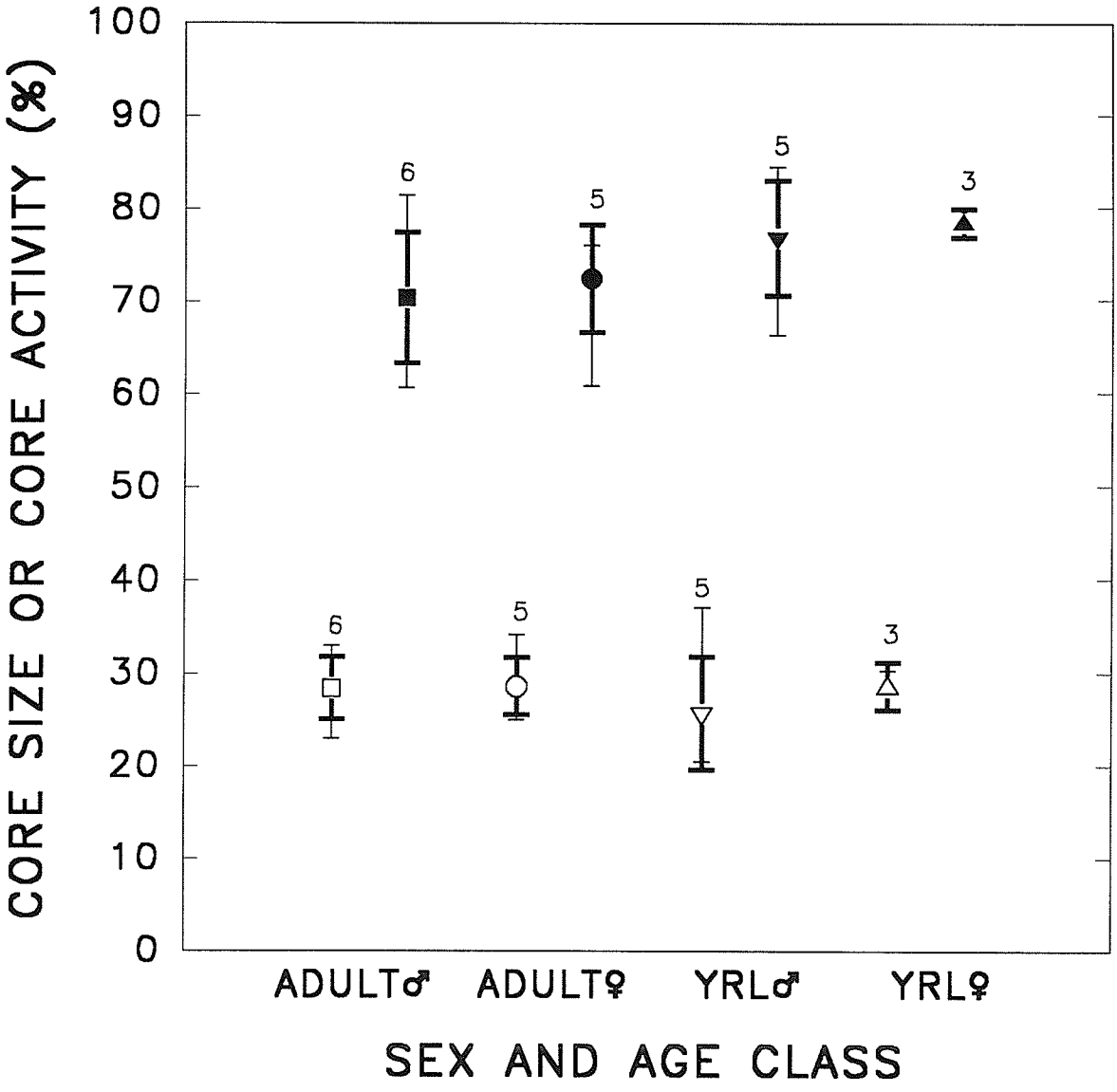

CORE SIZE OR CORE ACTIVITY (%)
100
90
80
70
60
50
40
30
20
10
0
6
5
5
3
6
5
5
3
ADULT♂
ADULT♀
YRL♂
YRL♀
SEX AND AGE CLASS

Figure 5. Centroids of activity for Implant Pond Family, Summer, 1989. Centroids are shown ± 2 standard errors in both the X and Y directions. Adult Male = IP491, Adult Female = IP414, Yearling Male = IP433, Juvenile Female = IP403.

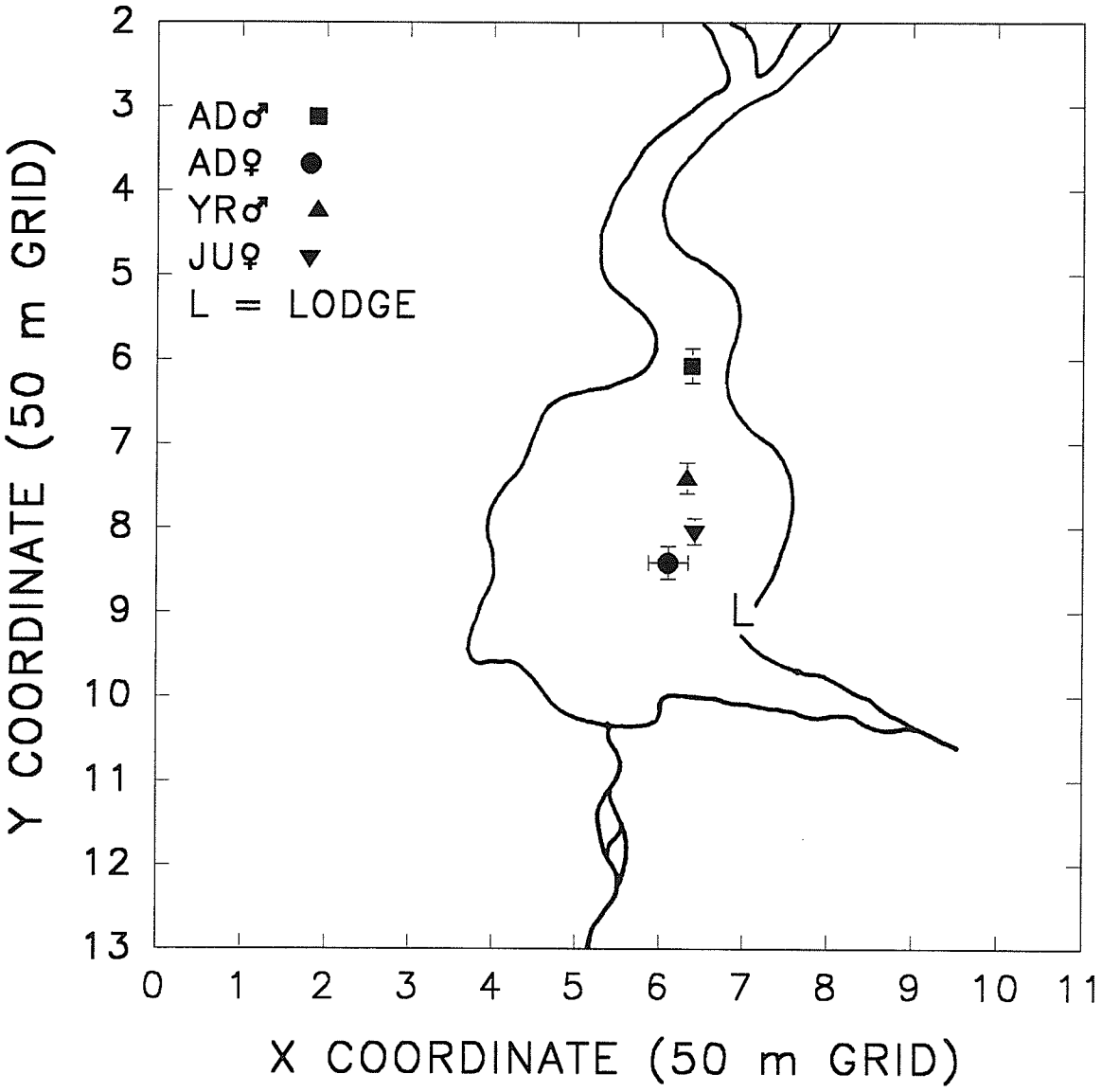

AD♂
AD♀
YR♂
JU♀
L = LODGE
L
Y COORDINATE (50 m GRID)
X COORDINATE (50 m GRID)
2
3
4
5
6
7
8
9
10
11
12
13
0
1
2
3
4
5
6
7
8
9
10
11

Figure 6. Centroids of activity for Twin Bays Family, Summer, 1991. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = TB1510, Adult Female = TB1508, Yearling Male = TB1528, Yearling Female = TB1502.

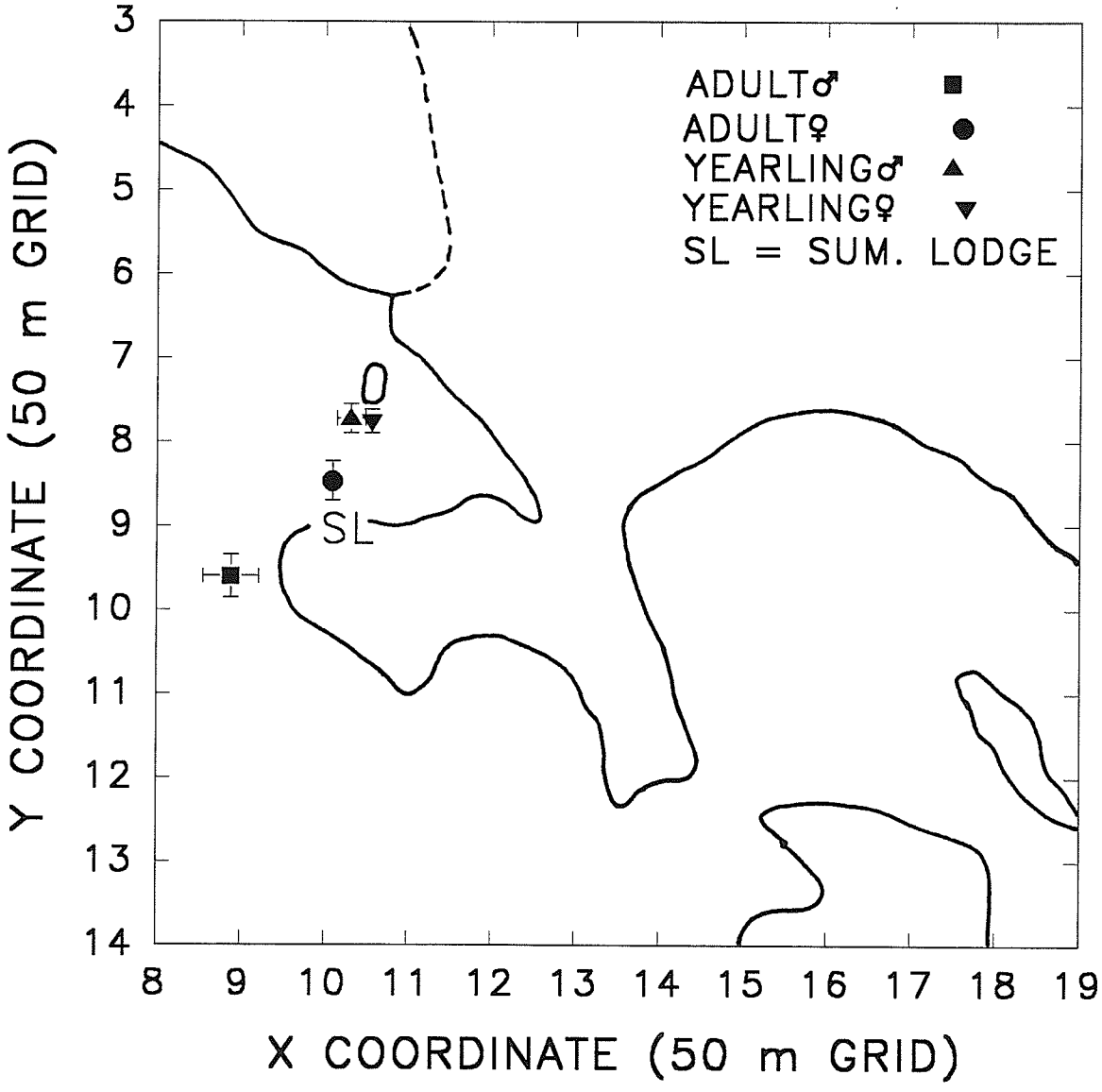

ADULT♂
ADULT♀
YEARLING♂
YEARLING♀
SL = SUM. LODGE
SL
Y COORDINATE (50 m GRID)
X COORDINATE (50 m GRID)
3
4
5
6
7
8
9
10
11
12
13
14
8
9
10
11
12
13
14
15
16
17
18
19

Figure 7. Centroids of activity for JRB Bay Family, Summer, 1990. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = JRB1617, Adult Female = JRB1629, Yearling Male (Triangle Down) = JRB1641, Yearling Male (Triangle Up) = JRB1649.

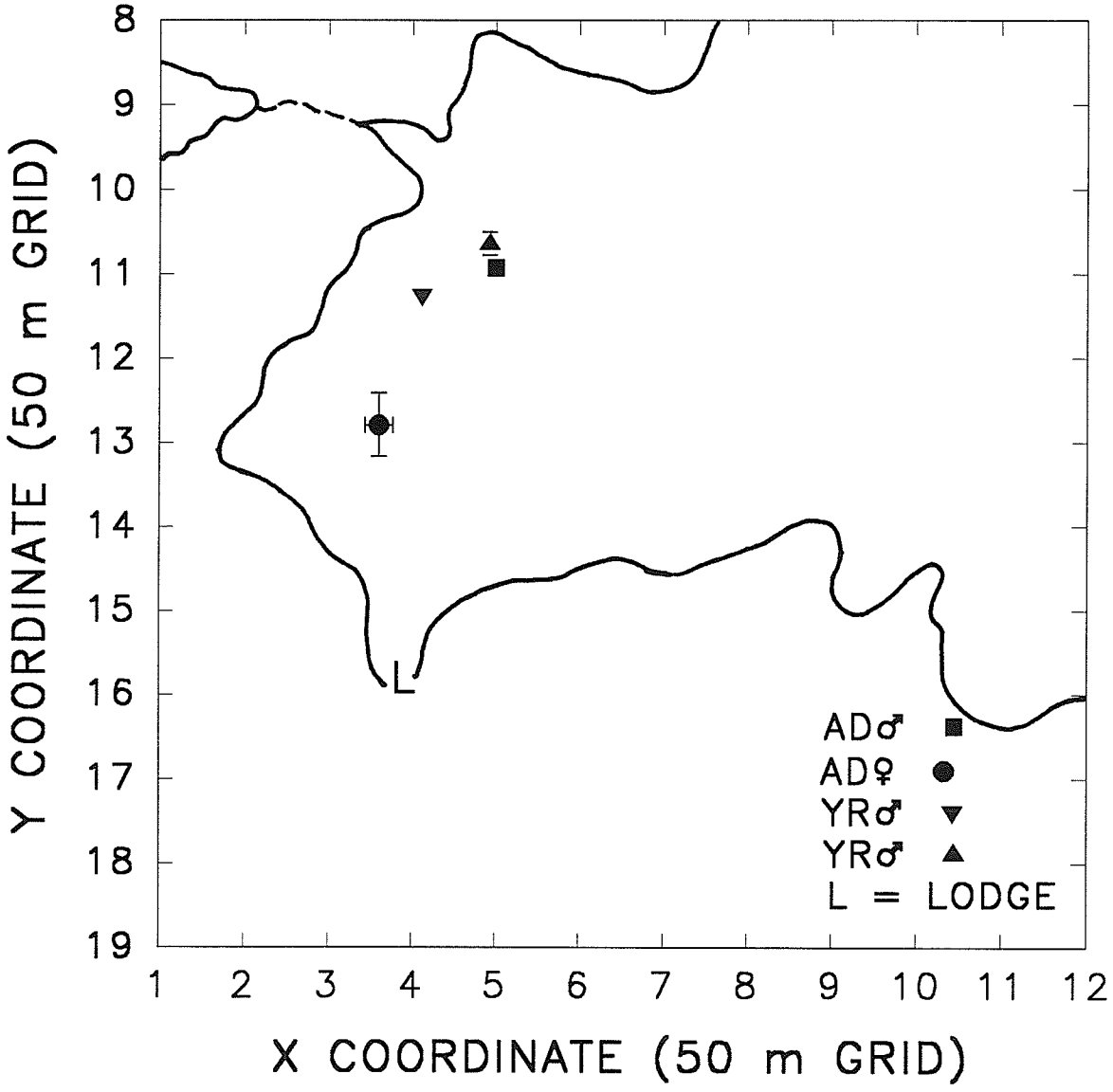

Y COORDINATE (50 m GRID)
8
9
10
11
12
13
14
15
16
17
18
19
1
2
3
4
5
6
7
8
9
10
11
12
X COORDINATE (50 m GRID)
L
AD♂
AD♀
YR♂
YR♂
L = LODGE

Figure 8. Centroids of activity for Gatlan Ponds Family, Summer, 1990. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = GP1611, Adult Female GP1676, Yearling Male = GP1684, Yearling Female = GP1623.

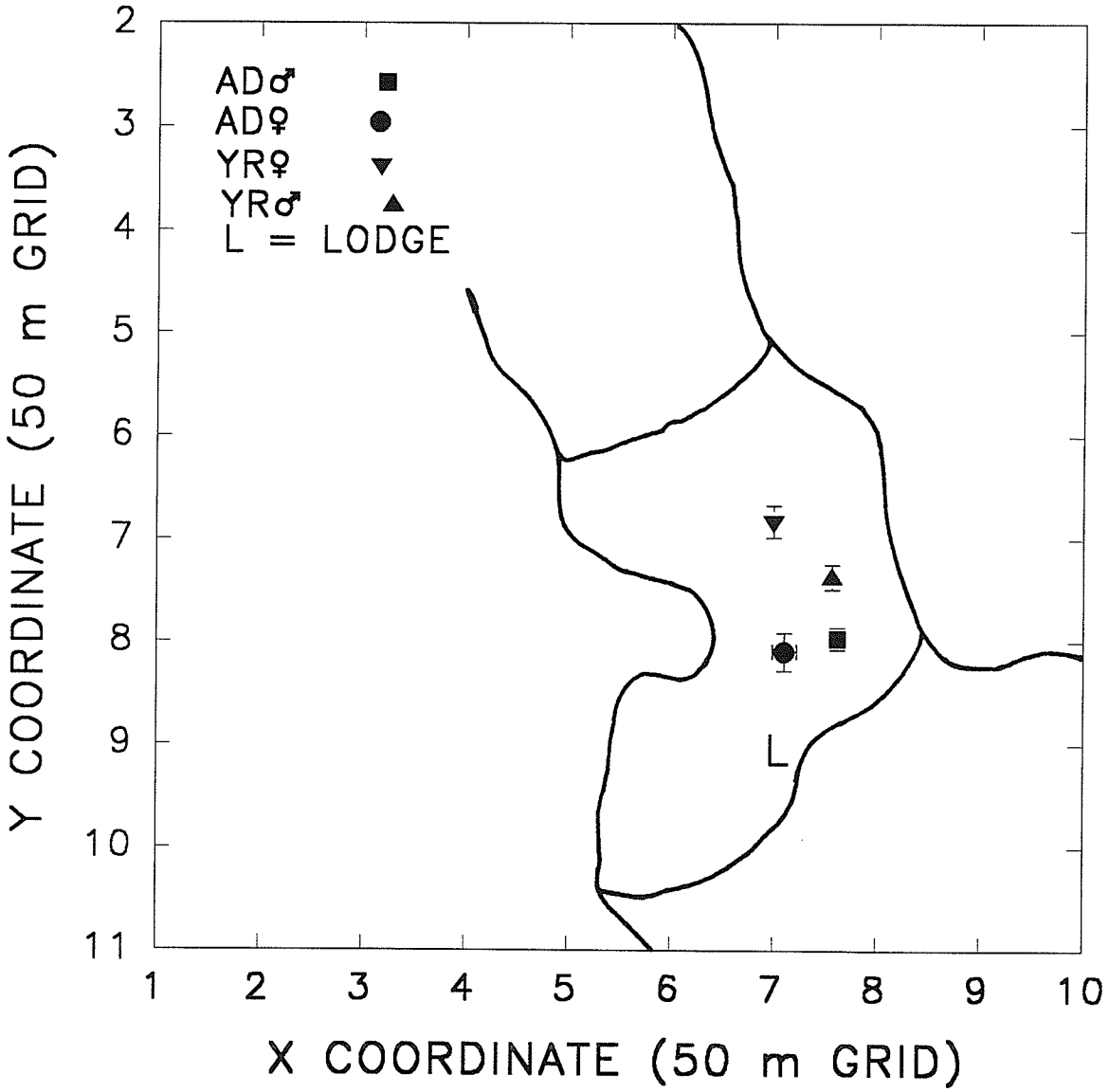
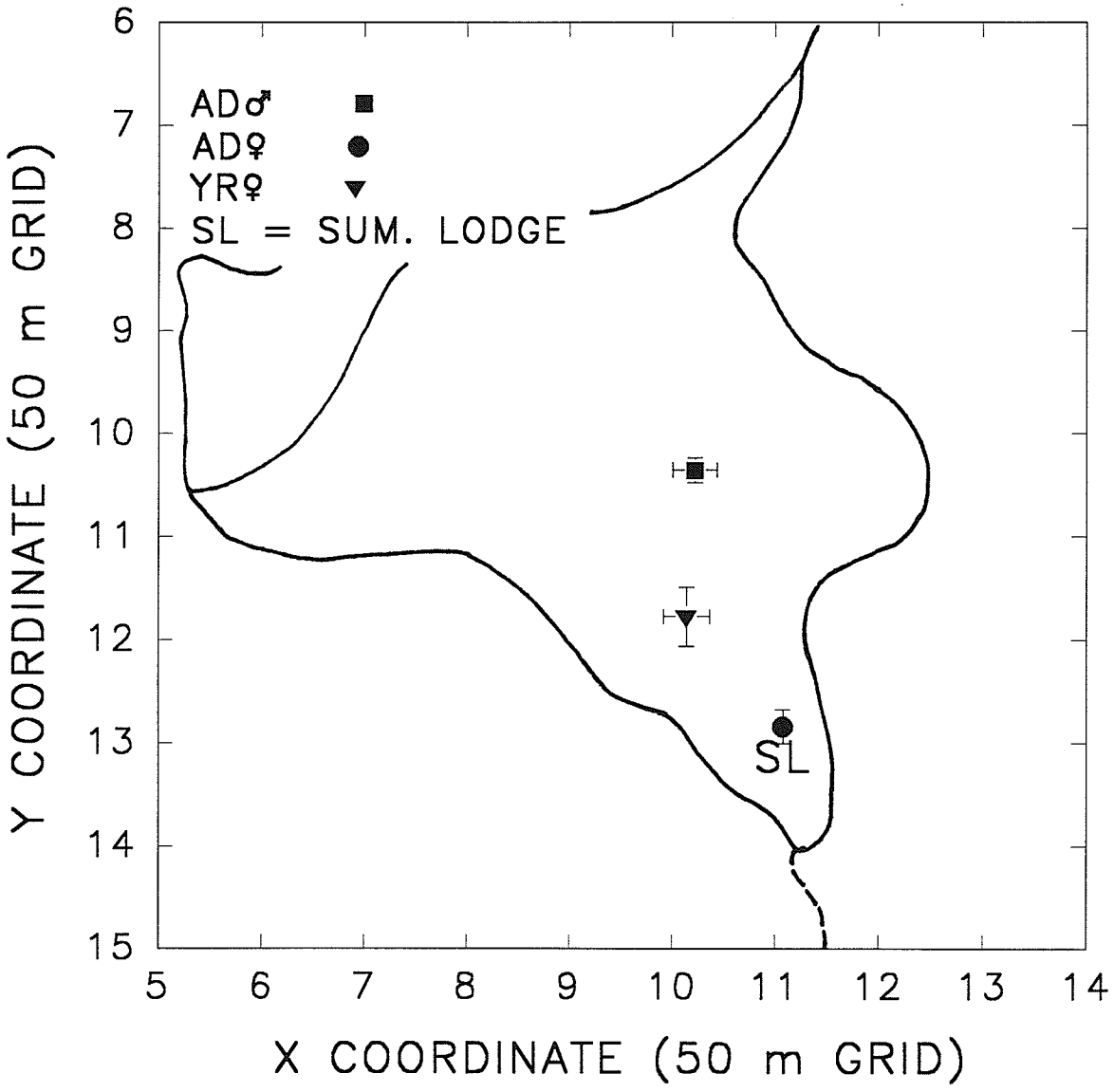

AD♂
AD♀
YR♀
YR♂
L = LODGE
L
Y COORDINATE (50 m GRID)
X COORDINATE (50 m GRID)
2
3
4
5
6
7
8
9
10
11
1
2
3
4
5
6
7
8
9
10

Figure 9. Centroids of activity for Gatlan Ponds Family, Summer, 1991. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = GP1611, Adult Female = GP1676, Yearling Female = GP1526.


AD♂
AD♀
YR♀
SL = SUM. LODGE
SL
Y COORDINATE (50 m GRID)
X COORDINATE (50 m GRID)
6
7
8
9
10
11
12
13
14
15
5
6
7
8
9
10
11
12
13
14

(1990) families, the adult male's centroid was closer to the lodge than one or both yearlings (Figures 7 and 8). The adult male tended to have a home range that extended farther from the lodge than those of other members of the family while the adult female's home range usually was closer to the lodge than those of other family members (See Appendix 1).

DISCUSSION

HOME RANGE SIZE AND SHAPE

I found beaver home ranges to average 10.34 ha in size. Beavers use most of their home range each day. This is unlike many other animals for which home ranges have been determined. Georgii (1980) found that red deer (*Cervus elaphus*) used only a small part of their home range each day. Hutton (1989) found similar results with Nile crocodiles (*Crocodilus niloticus*) as did Galbraith *et al.* (1987) with snapping turtles (*Chelydra serpentina*). Both crocodiles and turtles are similar to beavers in being semi-aquatic, however they differ in being ectotherms not endotherms. Gillespie (1975) found beaver summer home ranges from 1.76 to 22.0 ha in southern Ontario. No other authors have quantified home range size, but Busher (1975) found home range lengths of 200 to 800 m in California, and Davis (1984) found distances between extreme points of daily movement to be 84 to 1863 m in South Carolina. The values given by these authors are similar, although somewhat smaller than, my home range values.

Beaver home ranges are not uniform in shape. They do not conform to any regular shape such as the ellipse described by Jennrich and Turner (1969) the circular home ranges of Van Winkle (1975) nor the multiple circles around centres of activity of Dixon and Chapman (1980) or Don and Rennolls (1983) (Chapter 2). Rather, the home ranges follow the convoluted shorelines of lakes, the meandering routes of rivers, or the natural, irregular outlines of ponds. Shorelines are the primary source of beaver food, either as leaves and bark of terrestrial trees or the aquatic plants growing in shallow water near the shore.

When moving between feeding sites or lodges, beavers tend to stick close to shore except to cross to an island. Tevis (1950) also reported frequent movement by beavers along shorelines. The eyesight of beavers

is poor compared to their senses of smell and hearing. By travelling near shore they may be better able to track their location by smell. The Nile crocodiles and snapping turtles cited earlier also show movement patterns in which they stay close to the water's edge and avoid deep water except to cross (Hutton 1989; Galbraith *et al.* 1987). The beavers often followed very similar routes each day. While this might be expected on the river, it seems unusual on the lake or ponds. While nothing is visible to the human eye, it is as if the beaver is following a set of pathways between feeding and rest spots, similar to those reported for Kloss Gibbons (Whitten 1982).

CORE AREAS

All beavers except one adult female had core areas. These averaged 2.864 ha in size and accounted for 27.27 % of the home range and 74 % of the activity. Core areas usually included the lodge, but were not usually at the geographic or geometric centre of the home range. Springer (1982) reported 82.9 % of activity in 6.9 % of the home range for coyotes (*Canis latrans*), and Samuel *et al.* (1985) recorded 76 % of activity in 34 % of the home range for black bears (*Ursus americanus*). As with beavers, both coyotes and black bears had multiple core areas. For beavers, the core areas are primarily associated with feeding or food gathering sites and lodge(s) and bank burrows. Most of the remaining home range serves as travel routes between core areas or may be the result of exploration or scouting of new sites by beavers. Beavers with more extensive regions of non-core home range were generally non-family subadults or adult males and occasionally yearlings in family groups.

Core Size varied with habitat and sex and age class. However, Core Percent and Core Activity showed no such variation except that yearling males showed slightly greater degree of activity in the core

than adult males. Despite this, the means are still similar. It would seem that regardless of habitat or sex or age, beavers use about one-quarter of their home range as core area, and about 3/4 of their activity occurs in this core area. While this might be a mathematical artefact, I believe this unlikely due to the range of values for core size and core percent (Figure 2). This would seem to indicate that beavers have some basic patterns of use of the area in which they live. Regardless of habitat or sex or age, about 3/4 of their home range is not used intensively. The lack of core area in the one adult female probably resulted from her fairly constant movement to and from the lodge.

HABITAT

Home range size and Core Size were both largest for river beavers and smallest for pond beavers with lake beavers intermediate between the two. The pond has an area that is more definitively delineated than the river or lake. However, the pond beavers did not always remain within the boundaries of their own pond. Tevis (1950) found beavers were restricted to their own pond. This may be dependent on the density of beavers in the area. There were no other beavers living in the immediate vicinity of the pond beavers I studied.

A pond, with the dam which creates it, requires a greater energy input than lake or river habitats. I hypothesize that in order for the beavers to put the extra effort into building and/or maintaining a pond, there must be a certain quality to the habitat. If the pond has a greater abundance of food, then they will not require a larger home range to supply sufficient food. Similarly if food is more concentrated, core areas will be smaller. Ponds also tend to be shallow with little water flow which encourages growth of aquatic plants which are sometimes eaten by beaver (Jenkins 1979)(Chapter 7).

The large home ranges of river beavers may be an artefact of the grid method due to the relative widths of the grid and the river. However, food supply may also be the cause of larger river home ranges. The river is primarily bordered by bogs, with occasional ridge areas. Most of the bogs contain species not usually selected by beavers (*Larix laricina*, *Picea mariana*)(See Chapter 7). Ridges are the most frequent sites for growth of more favoured beaver food such as Trembling Aspen (*Populus tremuloides*). The Gatlan Ponds are surrounded by very little bog, and Implant Pond had ridges or drier land only a short distance back from shore. The lake also has more ridge areas along the shore than the river. Ponds and lakes therefore had a greater number of potential areas of suitable beaver food than rivers and beavers may have had correspondingly smaller home ranges. Beavers living on the river, especially near the mouth, often had home ranges that included lake habitat possibly for food. Most of the river beavers in this study were lone subadult beavers. They may therefore have been travelling farther in order to search for suitable areas for permanent residence or for a mate.

FAMILY

Within family groups, the adult male had the largest home range and the adult female the smallest. The centroids showed that the adult male tended to be farther from the lodge, and the adult female closer to the lodge. There have been many different findings about the behaviour and roles of different family members. Adult males have been found to have much summer movement (Tevis 1950), and greater variation in rest sites than adult females (Busher 1991). From time to time, I saw all members of the beaver families taking food into the lodge, apparently for the kits. While all family members are capable of taking this food in, the kits are also nursing at this time and the adult female is the

only one capable of nursing the kits. Hence, the adult female may be required to remain closer to the lodge in order to meet the needs of the kits.

Previous studies have described many different roles for the adult male while kits are present. The adult male may stay away from the lodge while the kits are around (Seton 1909; Bradt 1938), or not associate much with the adult female (Busher 1975), or the adult male may help with care of the young (Brady and Svendsen 1981; Busher and Jenkins 1985). As I found for members of family groups, Tevis (1950) found that beavers were independent of each other during the night and visited the lodge throughout the night.

CONCLUSIONS

H_o1 was disproved. Beavers do not use all areas of their summer home range equally, core areas are almost always present. These core areas usually include the lodge and major feeding areas. Beavers tend to travel close to shore and only venture into open water in order to cross to another shore. H_o2 was also disproved. Home range size was positively correlated with core area size for all beavers combined and within each habitat. H_o3 was disproved. River beavers had larger home ranges, probably as a result of fewer areas of food availability. Pond beavers had smaller home ranges, possibly due to a higher quality of habitat in areas where ponds are constructed. All beavers had similar percentages of home range and activity in their core areas indicating that there is a basic pattern of use of the home range common to all beavers regardless of habitat. H_o4 was disproved. Adult males usually have a larger home range and core area than other family members and adult females tend to have a smaller home range and core area than other family members. H_o5 was also disproved. Adult males are generally active farther from the lodge than other family members, while adult females are generally active closer to the lodge.

LITERATURE CITED

Aleksiuk, M. 1968. Scent-mound communication, territoriality, and population regulation in beaver (*Castor canadensis* Kuhl). Journal of Mammalogy 49:759-762.

Bergerud, A.T. and D.R. Miller. 1977. Population dynamics of Newfoundland beaver. Canadian Journal of Zoology 55:1480-1492.

Bradt, G.W. 1938. A study of beaver colonies in Michigan. Journal of Mammalogy 19:139-162.

Brady, C.A. and G.E. Svendsen. 1981. Social behaviour in a family of beaver, *Castor canadensis*. Biology of Behaviour 6:99-114.

Brown, J.L. and G.H. Orians. 1970. Spacing patterns in mobile animals. Annual Review of Ecology and Systematics 1:239-262.

Buckley, J.L. and W.L. Libby. 1955. Growth rates and age determination in Alaskan beaver. Transactions of the twentieth North American Wildlife Conference, Washington. pp.495-507.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346-352.

Busher, P.E. 1975. Movements and activities of beavers, *Castor canadensis*, on Sagehen Creek, California. M.A. Thesis, San Francisco State University, California, 86 pp.

Busher, P.E. 1991. Resting association patterns of adult beavers. American Society of Mammalogists 71st Annual Meeting, Abstract.

Busher, P.E. and S.H. Jenkins. 1985. Behavioral patterns of a beaver family in California. Biology of Behaviour 10:41-54.

Davis, J.R. 1984. Movement and Behavior Patterns of Beaver in the Piedmont of South Carolina. M.Sc. Thesis, Clemson University, Clemson, South Carolina, 83pp.

Dixon, K.R. and J.A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040-1044.

Don, B.A.C. and K. Rennolls. 1983. A home range model incorporating biological attraction points. Journal of Animal Ecology 52:69-81.

Galbraith, D.A., M.W. Chandler and R.J. Brooks. 1987. The fine structure of home ranges of male *Chelydra serpentina*: are snapping turtles territorial? Canadian Journal of Zoology 65:2623-2629.

Georgii, B. 1980. Home range patterns of female red deer (*Cervus elaphus* L.) in the Alps. Oecologia 47:278-285.

Gillespie, P.S. 1975. Summer Activities, Home Range and Habitat Use of Beaver. M.Sc. Thesis, University of Toronto, Toronto, Ontario, 149 pp.

Green, H.U. 1936. The beaver of the Riding Mountain, Manitoba: An ecological study and commentary. Canadian Field-Naturalist 50:1-8, 21-23, 36-50, 61-67, 85-92.

Hayne, D.W. 1949. Calculation of size of home range. Journal of Mammalogy 30:1-18.

Hodgdon, H.E. and J.S. Larson. 1973. Some sexual differences in behaviour within a colony of marked beavers (*Castor canadensis*). Animal Behaviour 21:147-152.

Hutton, J. 1989. Movements, home range, dispersal and the separation of size classes in Nile crocodiles. American Zoologist 29:1033-1049.

Jenkins, S.H. 1979. Seasonal and year-to-year differences in food selection by beavers. Oecologia 44:112-116.

Jennrich, R.I. and F.B. Turner. 1969. Measurement of non-circular home range. Journal of Theoretical Biology 22:227-237.

Miller, D.R. 1964. Colored plastic ear markers for beavers. Journal of Wildlife Management 28:859-861.

Morgan, L.H. 1986. The American Beaver: A Classic of Natural History and Ecology. Dover Publications Inc., New York.

Samuel, M.D., D.J. Pierce and E.O. Garton. 1985. Identifying areas of concentrated use within the home range. Journal of Animal Ecology 54:711-719.

SAS Institute Inc. 1988. SAS/STAT® User's Guide Release 6.03 Edition. Cary, N.C: SAS Institute.

Seton, E.T. 1909. Life Histories of Northern Animals. Charles Scribner's Sons, New York.

Springer, J.T. 1982. Movement patterns of coyotes in south central Washington. Journal of Wildlife Management 46:191-200.

Swihart, R.K. and N.A. Slade. 1985a. Influence of sampling interval on estimates of home-range size. Journal of Wildlife Management 49:1019-1025.

Swihart, R.K. and N.A. Slade. 1985b. Testing for independence of observations in animal movements. Ecology 66:1176-1184.

Tevis, L., Jr. 1950. Summer behavior of a family of beavers in New York State. Journal of Mammalogy 31:40-65.

Van Winkle, W. 1975. Comparison of several probabilistic home-range models. Journal of Wildlife Management 39:118-123.

Warren, E.R. 1927. The Beaver Its Works and Its Ways. American Society of Mammalogists Monographs 2, Baltimore, The Williams and Wilkins Company.

Wheatley, M. 1989. Ecology of Beaver (*Castor canadensis*) in the Taiga of Southeastern Manitoba. M.Sc. Thesis, University of Manitoba, Winnipeg, Manitoba, 167 pp.

Whitten, A.J. 1982. Home range use by Kloss gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. Animal Behaviour 30:182-198.

CHAPTER 4

HOME RANGE SIZES OF BEAVER IN FALL

ABSTRACT

I studied beavers (*Castor canadensis*) in the boreal forest of eastern Manitoba from 1986 to 1992. I captured and ear tagged 60 different beavers, and outfitted 42 of these animals with transmitters. I collected sufficient data to determine fall home range size for 27 beavers. Fall home ranges averaged 3.07 ha in size, and core areas were present in 21 of 27 beavers. Home range size, Core area size and percent of total home range area in the core were positively correlated. Home ranges were larger for river beavers than pond or lake beavers, but lake beavers had more activity in their core area than pond or river beavers. Adult females tended to have smaller home ranges than other family members.

INTRODUCTION

In the taiga and other areas where ice-cover in winter restricts access to food, fall is the time of year when beavers construct food piles and build or repair lodges and dams. Winter survival may depend on fall activities. Despite the importance of this season to beavers, few authors have investigated activities of beavers at this time of year. Jenkins (1979) reports seasonal differences in food preference and seasonal variation in site selection (Jenkins 1981) by beavers. Busher and Jenkins (1985) included fall data in their examination of behavioural patterns of a beaver family. Davis (1984) includes data on seasonal variation in beaver movements, but his study area was not subject to ice-cover, so fall activities did not have to include food cache construction. Gillespie (1977) is the only author to have examined home range size, but she does not differentiate between the seasons in her study.

Burt (1943) defined home range as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young". Core areas are "those areas used more frequently than any other areas and probably contain the home sites, refuges and most dependable food sources ... that is, those portions of the animal's home range that exceed an equal use pattern" (Samuel *et al.* 1985).

The purpose of this study was to examine patterns of use of home range by beavers in fall. The hypotheses I tested are: H_o1) All areas of the home range are used equally, that is, there are no core areas; H_o2) There are no correlations between Total Size of home range, Core Size, Core Percent and Core Activity; H_o3) There are no differences in these parameters between different habitats (pond, lake and river); H_o4) There are no difference in these parameters for different sex and age classes; H_o5) There are no differences in centres of activity for different family members.

METHODS

I live-trapped beavers using Hancock traps baited with a piece of trembling aspen (*Populus tremuloides*) 30 cm long and 2 to 5 cm in diameter and a scent bait consisting of ground up beaver castor, anise extract and glycerine (Aleksiuk, 1968). For each animal I took measurements of total length, tail length, hind foot length, length of ear from notch, neck circumference, and tail circumference at the base and at the widest point. I also weighed each animal and determined its sex by palpating externally for the baculum.

To facilitate visual identification of individuals, I attached to both ears uniquely numbered metal ear tags (Monel, Number 3) to which I affixed uniquely coloured flags of reinforced vinyl as described by Miller (1964).

RADIOTELEMETRY

I installed radio-transmitters using 2 methods: intraperitoneal implantation (42 transmitters); and tail collars (3 transmitters) (Wheatley 1989). The implanted packages (Austec Electronics) consisted of a transmitter coupled with a C cell lithium battery, all encased in beeswax and then Elvax (Mini-mitter Co.) which is biologically inert. The entire package measured about 6 x 4 cm and weighed about 80 g. The tail collars (Wildlife Materials Inc.) measured 12.5 x 7.5 x 4.5 cm and weighed about 295 g including the webbing used for attachment to the base of the tail.

For tracking beavers I used an H-shaped antenna and 24 channel receiver (Wildlife Materials Inc.). For beavers residing on the river or lake, I generally tracked and observed from a 6.5 m freighter canoe. When observing at ponds, I chose a high ridge or similar good vantage point nearby from which to make observations. In general, I used the

telemetry to locate the beaver and then, as much as possible, continued with visual observations of activities and movements. After dark, my observations were based on using telemetry to locate animals, and sounds of chewing or tree felling or visual observation of water ripples to determine activity.

I recorded information about the location, time, type of activity, and any movement to another location during the period of observation. Observation periods varied in length from 5 minutes to 13 hours depending upon weather conditions and the number of animals being observed in one night. Most observations were made between 1800 and 2400 h. I recorded data directly in a field book or on cassette audio tape for later transcription into the field book. I later transferred the data onto forms for each beaver.

I drew maps of appropriate size and scale to encompass the home range of each beaver or group of beavers. I made up a grid overlay on an acetate sheet, equivalent to a 50 m by 50 m grid (0.25 ha) on the ground. I transferred each beaver's data onto the appropriate grid. For this I considered 1 minute as 1 observation. A beaver can swim approximately 50 m in one minute. While this does not allow for true independence of observations (Swihart and Slade 1985a; 1985b), the beavers move throughout their home range too much to be able to reflect accurately home range use by 1 observation per night. I separated seasons by identifying apparent shifts in patterns of use, such as new areas of use or previously used areas that were no longer frequented.

I tallied the number of observations in each grid cell and the total number of observations for each beaver for each season. I also recorded the total number of grid cells used. To determine the core area of each individual's home range, I calculated the proportion of observations in each grid cell (number of observations in cell/total number of observations) and compared these proportions to those expected in each grid cell if the beaver's use of the cells was uniform (1/number

of grid cells). I compared the ordered observed cumulative distribution function with the hypothesized uniform cumulative distribution function for each beaver using the Kolmogorov-Smirnov one tailed goodness of fit procedure in which N equals the number of grid squares (Samuel *et al.* 1985). If this test showed that a core area was present, I classed all cells with a greater proportion of observations than uniform as core areas (Samuel *et al.* 1985). I then transferred to the map the outline of the home range and core areas within the home range.

TERMS AND DEFINITIONS

I calculated the home range size in hectares by dividing the total number of grid cells used by 4. In all following discussions I refer to this as the Total Size. I determined the size of the core area (Core Size) by totalling the number of grid cells identified as constituting the core area and dividing these by 4 in the same manner as for Total Size. I calculated the percent of the Total Size that was included in the Core Size for each beaver by dividing the Core Size by Total Size and multiplying by 100. This I refer to as the Core Percent. To calculate the percent of activity which occurred within the core area (Core Activity), I divided the total number of observations in cells identified as comprising the core area by the total number of observations of each beaver and multiplied by 100.

To separate different age classes, I used the classification system of Buckley and Libby (1955). "Kits" were any beavers less than 12 months of age. "Yearlings" refers to all beavers in their second year of life and "two-year-olds" to those in their third year of life. The term "adult" refers to any beaver older than 36 months of age. I classified beavers as pond, lake or river beavers based on the location of their primary residence (lodge or bank burrow).

ANALYSIS

I analysed the data for all beavers by habitat type and by sex and age class within family groups. I calculated the means for Total Size, Core Size, Core Percent and Core Activity. Results are given as mean ± 2 standard errors. I employed Spearman Rank Correlation (r_s) to determine correlations between different variables (pairwise correlations between Total Size, Core Size, Core Percent and Core Activity) for all beavers and broken down by habitat. I used the Mann-Whitney U-test for analysis of habitat differences in the variables. For determining differences in the variables between family members within families I used the Wilcoxon Matched Pairs Test.

I used SAS (SAS Institute Inc. 1988) to calculate a weighted centroid of all the observations on each beaver and the associated variance. Hayne (1949) uses the term "centre of activity" to refer to the geometric centre of all the locations of an animal, while Dixon and Chapman (1980) use the term "centre of activity" to mean an area in which there is a large amount of activity. For this reason I have chosen an alternate term, the "centroid" to denote the geometric centre of all the points. For beavers residing in family groups, I then tested for similarity between the calculated centroids using F and t tests with weighted degrees of freedom.

RESULTS

I captured and ear tagged 60 different beavers, and outfitted 42 of these animals with transmitters. Some animals had more than 1 transmitter during the course of this study. I had sufficient data to determine fall home range size for 27 beavers.

Fall Total Size ranged from 1.0 to 8.0 ha ($\bar{X}$=3.074±0.7126 ha, N=27)(Figure 1). Twenty-one of the 27 beavers had core areas (Kolmogorov-Smirnov One-sided test, $p<0.05$ to $p<0.005$) (Appendix 2 and 3). Three adult females (JRB1629, IP414, TB1508), one adult male (GP1611 (1991)) and two yearling females (BR1603, GP1526) did not have core areas ($p>0.1$, N=4 to N=17). Core Size was 0.25 to 2.75 ha ($\bar{X}$=1.012±0.3246, N=21)(Figure 1). The core area accounted for 16.66 to 47.06 % of the total area ($\bar{X}$=27.3±4.104 %, N=21)(Figure 2) and 63.4 to 89.4 % of the activity ($\bar{X}$=75.51±2.996 %, N=21)(Figure 2)(See also Appendix 1 and 2).

Core Size and Total Size were highly positively correlated (Spearman Rank Correlation, r_s=0.8892, $p<0.0005$, N=21). Total Size was also significantly positively correlated with Core Percent (r_s=0.4985, $p<0.025$, N=21). Core Percent was significantly positively correlated with Core Size (r_s=0.8093, $p<0.0005$, N=21). There was a slightly negative, though non-significant correlation between Core Activity and Total Size (r_s=-0.2833, $p>0.1$, N=21). There was no significant correlation between Core Activity and Core Percent (r_s=0.0998, $p>0.25$, N=21) or Core Activity and Core Size (r_s=0.1052, $p>0.25$, N=21).

Home ranges were usually located close to shorelines and followed shorelines. Core areas occasionally included areas of open water, but these were usually associated with food piles. Main lodges were usually to one side or one end of the home range, and rarely towards the centre. Beavers used almost all of their home range each night.

Figure 1. Fall home range area size (open symbols) and core area size (closed symbols) (hectares) for all beavers combined and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range.

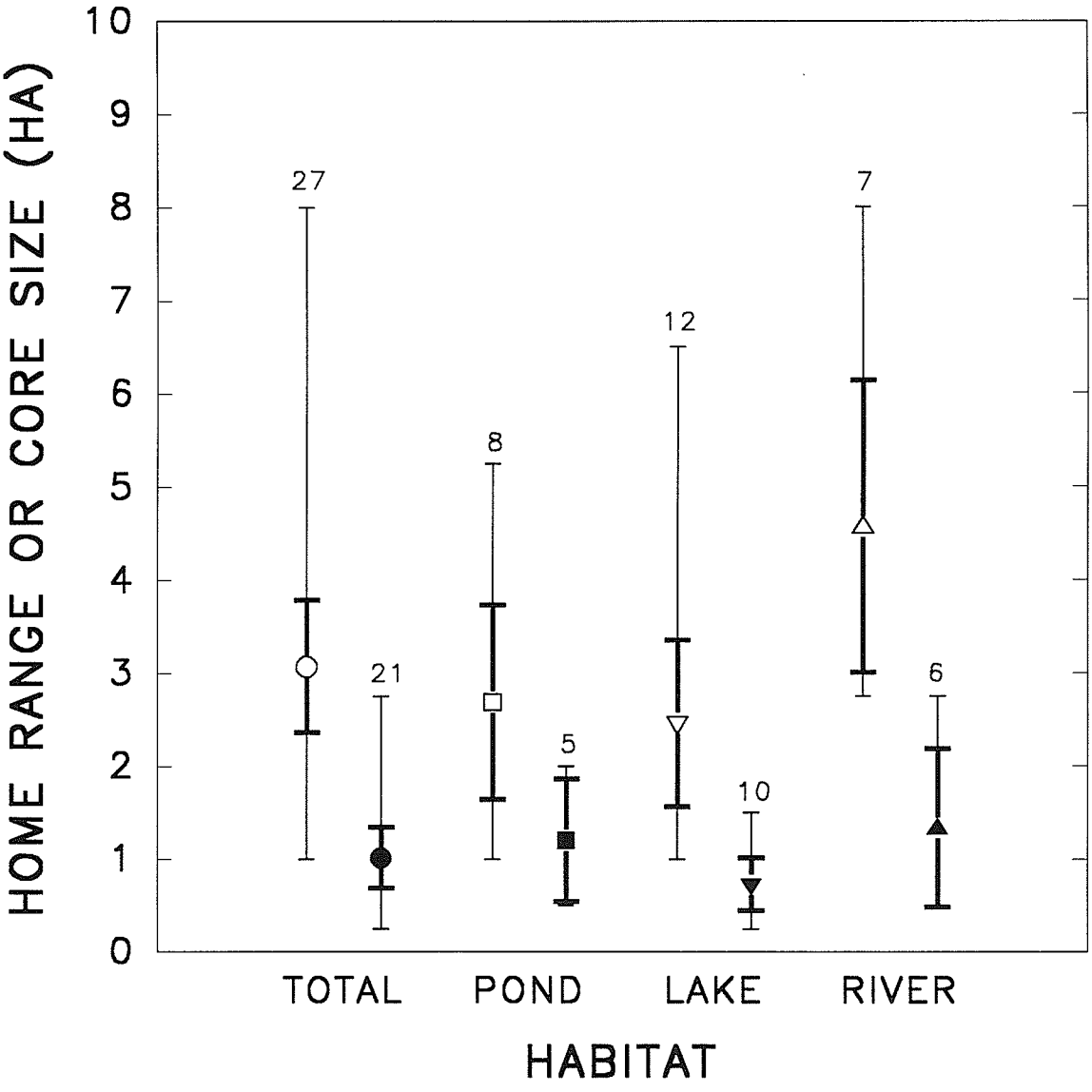
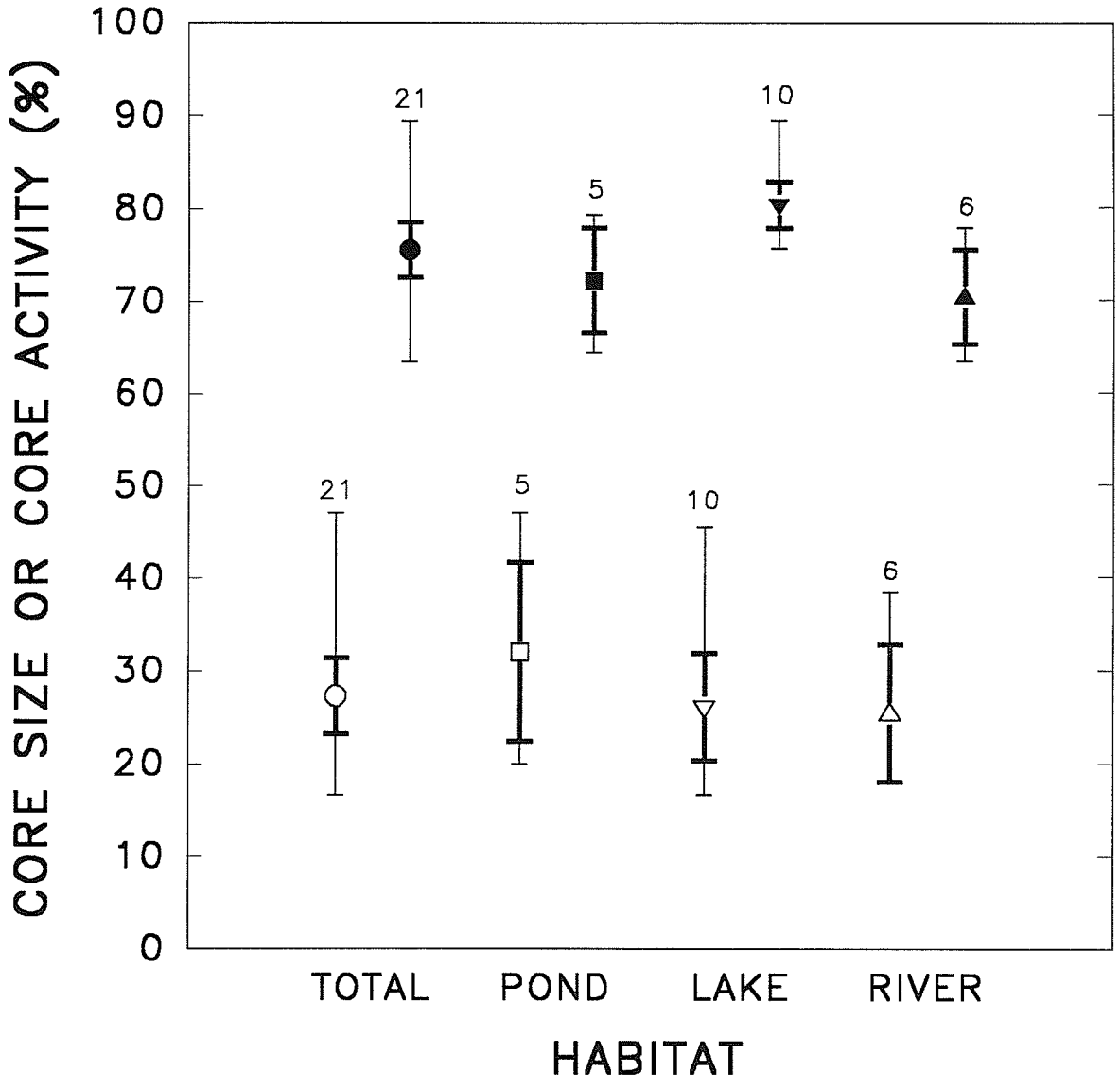

HOME RANGE OR CORE SIZE (HA)
10
9
8
7
6
5
4
3
2
1
0
27
21
8
5
12
10
7
6
TOTAL
POND
LAKE
RIVER
HABITAT

Figure 2. Fall core size as percent of total home range size (open symbols) and percent of all activity in core area (closed symbols) for all beavers combined and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range.


CORE SIZE OR CORE ACTIVITY (%)
100
90
80
70
60
50
40
30
20
10
0
21
5
10
6
21
5
10
6
TOTAL
POND
LAKE
RIVER
HABITAT

HABITAT

Total Size of river beavers was greater than those for both pond beavers (Mann-Whitney U Test, $U=11.5$, $p<0.05$, $N=7,8$) and lake beavers ($U=14.5$, $p<0.01$, $N=7,12$). There was no difference in Total Size between pond and lake beavers ($U=45$, $p>0.1$, $N=8,12$). There was no difference in Core Size between pond and river ($U=14.5$, $p>0.1$, $N=5,6$), pond and lake ($U=15$, $p>.1$, $N=5,10$) or river and lake ($U=19.5$, $p>0.1$, $N=6,10$). Core Activity was greater for lake beavers than river beavers ($U=4.0$, $p<0.001$, $N=10,6$) and pond beavers ($U=5.5$, $p<0.01$, $N=5,10$). There was no difference between pond and river beavers ($U=12.0$, $p>0.1$, $N=5,6$). There was no difference in the Core Percent between pond and river ($U=8.5$, $p>0.1$, $N=5,6$), pond and lake ($U=16.0$, $p>0.1$, $N=5,10$) or river and lake ($U=29.5$, $p>0.1$, $N=6,10$).

Pond

For pond beavers, the Core Size was not significantly positively correlated with Total Size ($r_s=0.8922$, $p>0.05$, $N=5$) but was significantly positively correlated with Core Percent ($r_s=0.9487$, $p<0.05$, $N=5$). There was no significant positive correlation between Core Percent and Core Activity ($r_s=0.7000$, $p>0.1$, $N=5$) or between Core Activity and Core Size ($r_s=0.7370$, $p>0.1$, $N=5$). Neither was Core Activity positively correlated with Total Size ($r_s=0.5643$, $p>0.1$, $N=5$) or Core Percent positively correlated with Total Size ($r_s=0.7182$, $p>0.1$, $N=5$).

Lake

Core Size was highly positively correlated with Total Size ($r_s=0.8809$, $p<0.001$, $N=10$) and with Core Percent ($r_s=0.6502$, $p<0.01$,

N=10) but showed almost no correlation with Core Activity (r_s=-0.0062, p>0.25, N=10). Core Activity was not significantly positively correlated with Core Percent (r_s=0.3161, p>0.1, N=10) or with Total Size (r_s=-0.3877, p>0.1, N=10). Core Percent was not significantly positively correlated with Total Size (r_s=0.3087, p>0.1, N=10).

River

Total Size and Core Size were highly positively correlated (r_s=1.0, p<0.005, N=6), as were Core Size and Core Percent (r_s=0.9355, p<0.025, N=6) and Total Size and Core Percent (r_s=0.9355, p<0.025, N=6). There was no significant positive correlation between Core Activity and Core Percent (r_s=0.0304, p>0.25, N=6), between Core Activity and Core Size (r_s=0.1518, p>0.25, N=6) or between Total Size and Core Activity (r_s=0.1518, p>0.25, N=6).

FAMILY

Within family groups, statistical comparison of matched pairs was not possible due to insufficient numbers of pairs for the Wilcoxon Matched Pairs Test. However, the trend was for adult males and yearling males to have larger Total Sizes than adult and yearling females (Figure 3). Core Size was very similar for all members of family groups which had core areas (Figure 3). Likewise, Core Activity and Core Percent were very similar for all members of families which had core areas (Figure 4).

Figure 3. Fall home range area size (open symbols) and core area size (closed symbols) (hectares) for beavers living in family groups, by sex and age class. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range.

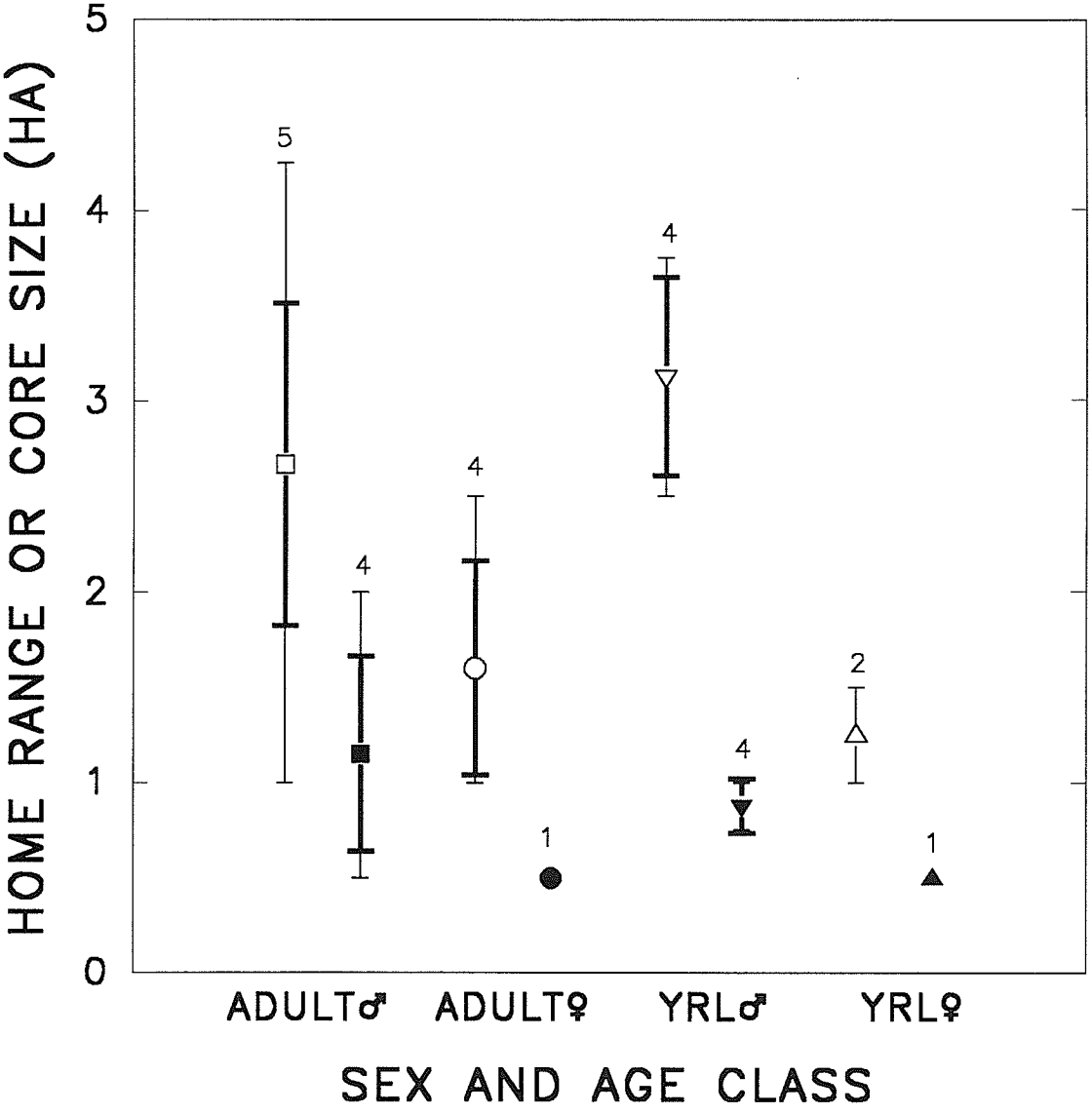
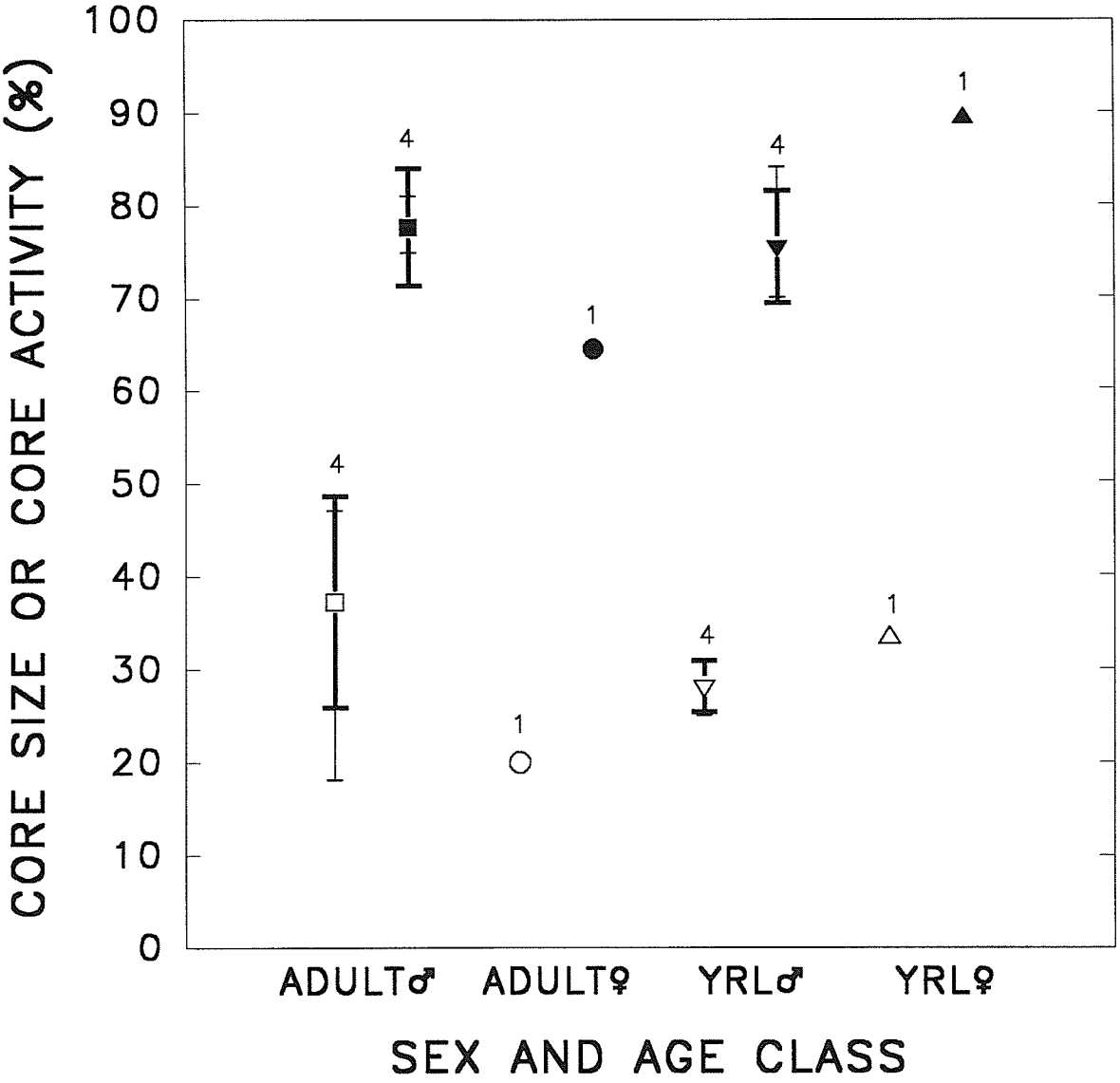

HOME RANGE OR CORE SIZE (HA)
0
1
2
3
4
5
5
4
4
1
4
4
2
1
ADULT♂
ADULT♀
YRL♂
YRL♀
SEX AND AGE CLASS

Figure 4. Fall core size as percent of total home range size (open symbols) and percent of all activity in core area (closed symbols) for beavers living in family groups, by sex and age class. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range.


CORE SIZE OR CORE ACTIVITY (%)
100
90
80
70
60
50
40
30
20
10
0
4
1
4
1
4
1
4
1
ADULT♂
ADULT♀
YRL♂
YRL♀
SEX AND AGE CLASS

Centroids

Within most known family groups, the activity centroids were different for each member of the family (t-test, $p<0.01$ to $p<0.0005$ (Figures 5, 6, 7, 8 and 9)(See also Appendix 1). However in the Twin Bays Family, all three kits had very similar centroids ($p>0.05$ to $p>0.25$), and the centroids of the adult male and yearling female were not significantly different ($t(X)=0.4037$, $p>0.25$, $N=334$, $t(Y)=0.3043$, $p>0.25$, $N=285$), although the variances were different ($F(X)=1.553$, $p<0.001$, $N=315,142$, $F(Y)=1.106$, $p<0.001$, $N=315, 142$)(Figure 6). In the JRB Bay Family, the adult male and one of the yearling males had centroids that were not significantly different ($t(X)=0.226$, $p>0.25$ $N=459$, $t(Y)=0.1114$, $p>0.45$, $N=437$), but again the variances were different ($F(X)=1.262$, $p<0.001$, $N=200,307$, $F(Y)=1.0799$, $p<0.001$, $N=200,307$)(Figure 7). In these last two cases, therefore, although the location of the centroid may be similar, the distribution of the home range about the centroid is different. The centroid of the adult female was located closer to the lodge than any other family member in the Implant Pond, JRB Bay and Gatlan Pond (1990) families (Figures 5, 7 and 8).

Figure 5. Centroids of activity for Implant Pond Family, Fall, 1989. Centroids are shown ± 2 standard errors in both the X and Y directions. Adult Male = IP491, Adult Female = IP414, Yearling Male = IP433, Juvenile Female = IP403.

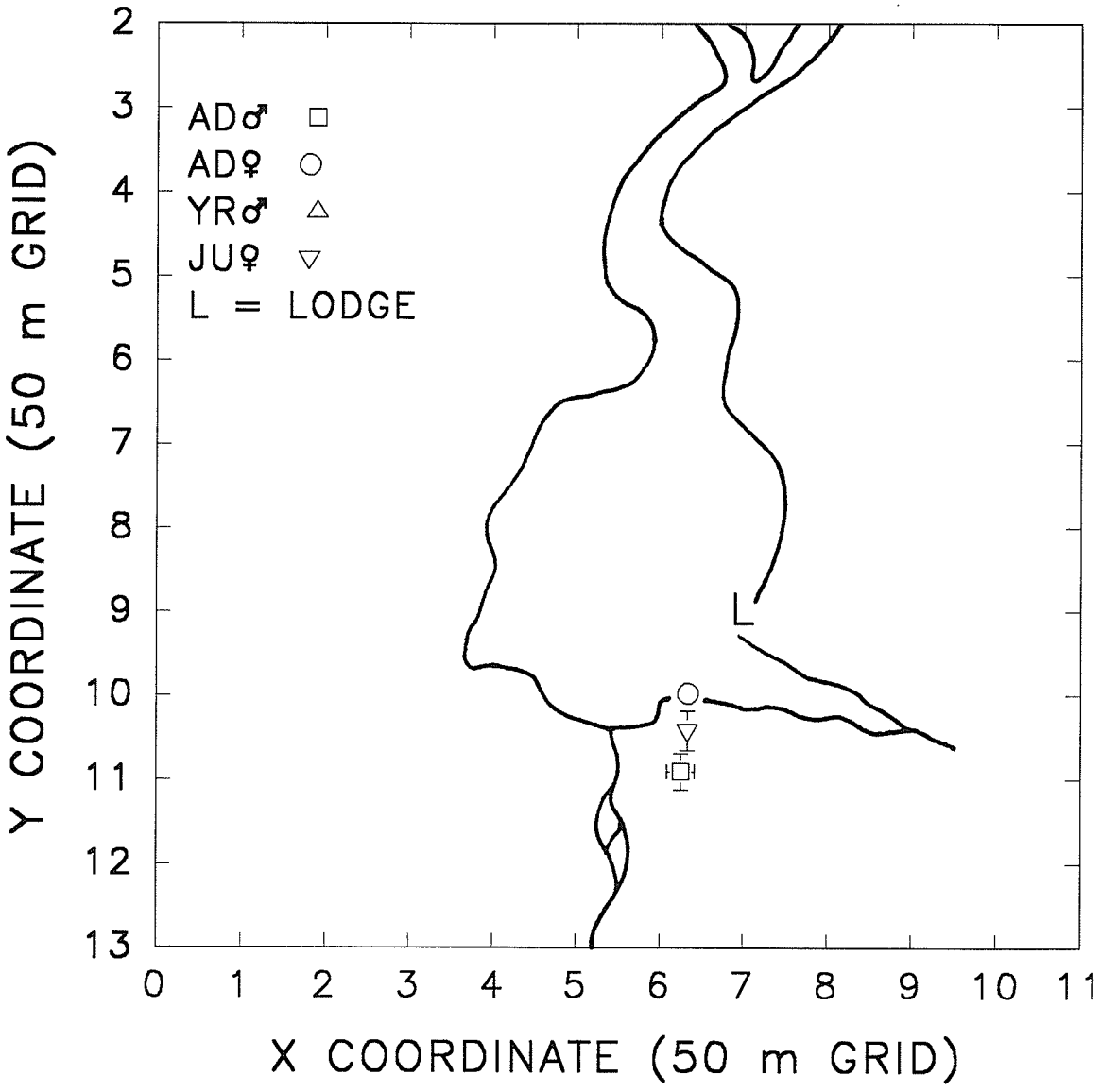

AD♂
AD♀
YR♂
JU♀
L = LODGE
Y COORDINATE (50 m GRID)
X COORDINATE (50 m GRID)
2
3
4
5
6
7
8
9
10
11
12
13
0
1
2
3
4
5
6
7
8
9
10
11

Figure 6. Centroids of activity for Twin Bays Family, Fall, 1991. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = TB1510, Adult Female = TB1508, Yearling Male = TB1528, Yearling Female = TB1502, Kits = TB1518, TB1520, TB1522.

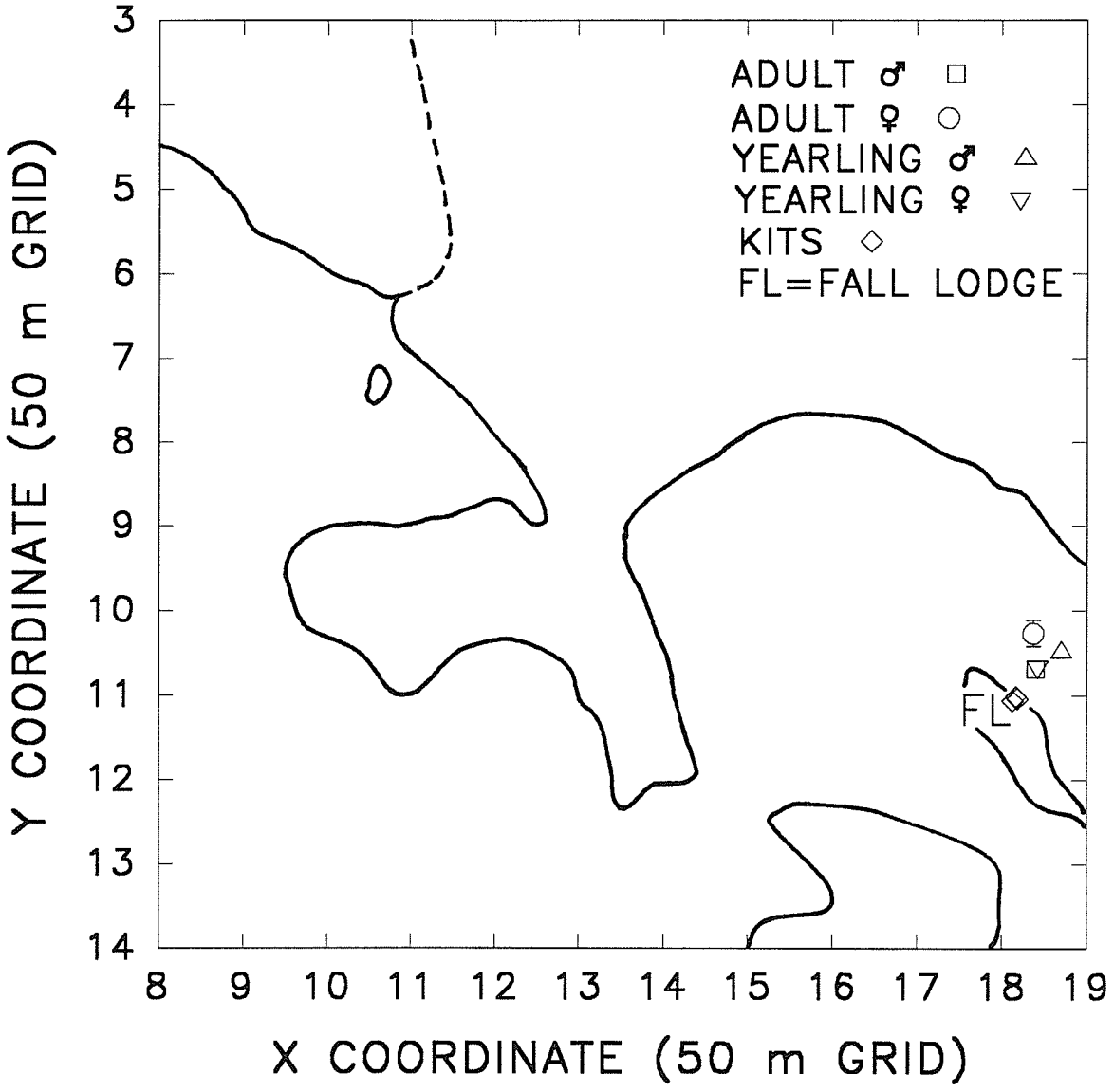

ADULT ♂
ADULT ♀
YEARLING ♂
YEARLING ♀
KITS
FL=FALL LODGE
FL
Y COORDINATE (50 m GRID)
X COORDINATE (50 m GRID)
3
4
5
6
7
8
9
10
11
12
13
14
8
9
10
11
12
13
14
15
16
17
18
19

Figure 7. Centroids of activity for JRB Bay Family, Fall, 1990. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = JRB1617, Adult Female = JRB1629, Yearling Male (Triangle Down) = JRB1641, Yearling Male (Triangle Up) = JRB1649.

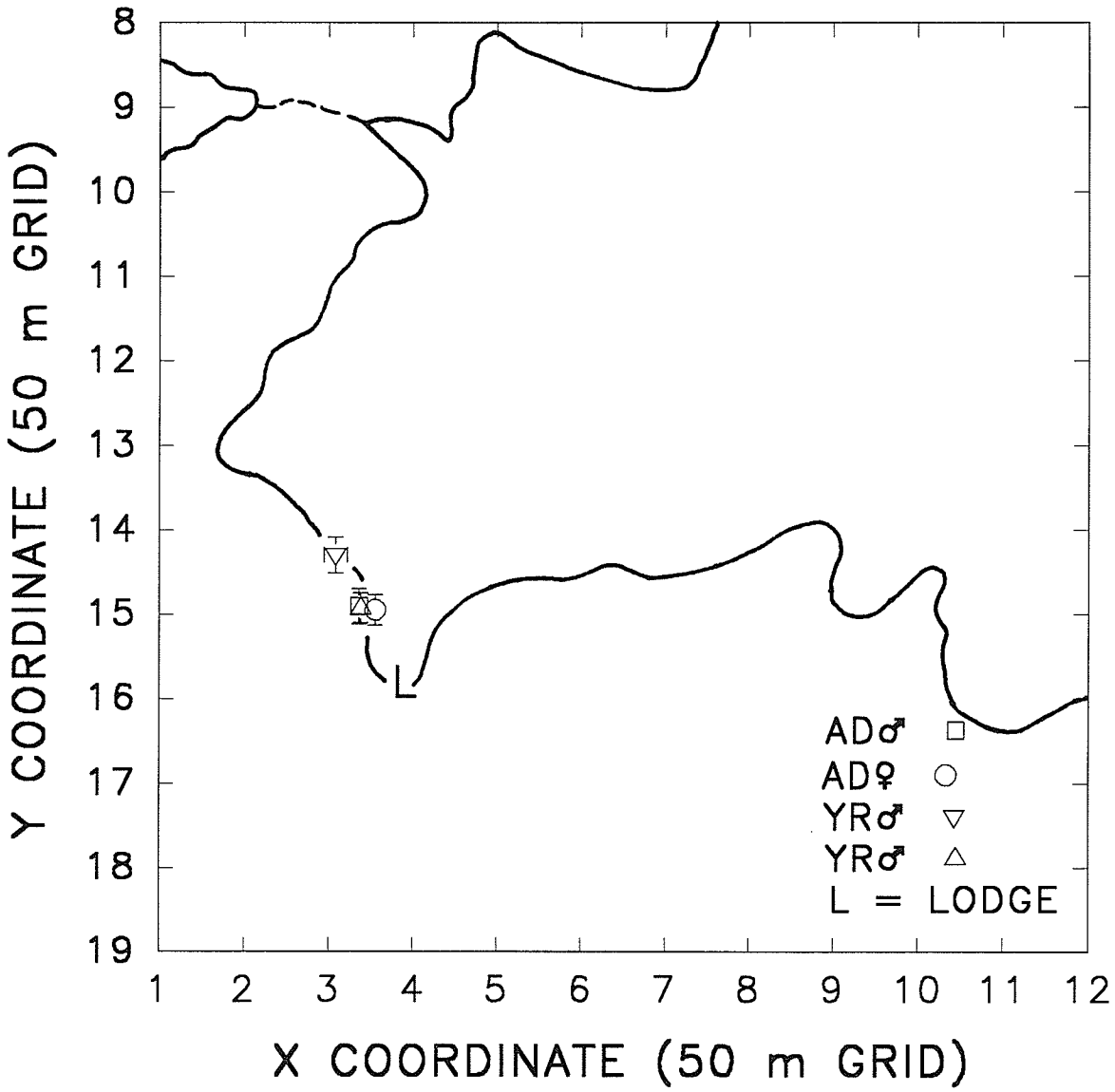

Y COORDINATE (50 m GRID)
8
9
10
11
12
13
14
15
16
17
18
19
1
2
3
4
5
6
7
8
9
10
11
12
X COORDINATE (50 m GRID)
L
AD♂
AD♀
YR♂
YR♂
L = LODGE

Figure 8. Centroids of activity for Gatlan Ponds Family, Fall, 1990. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = GP1611, Adult Female GP1676, Yearling Male = GP1684.

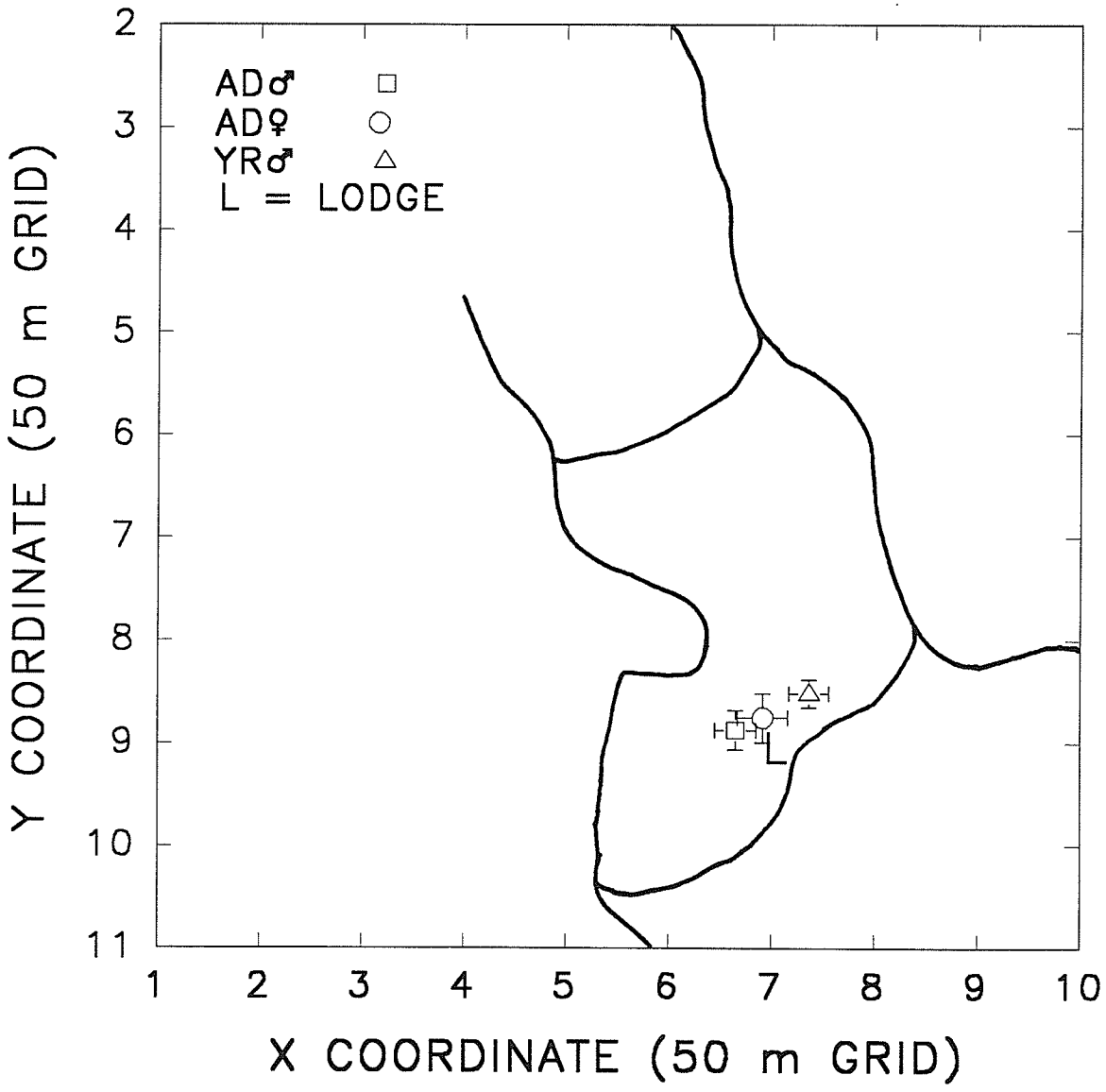
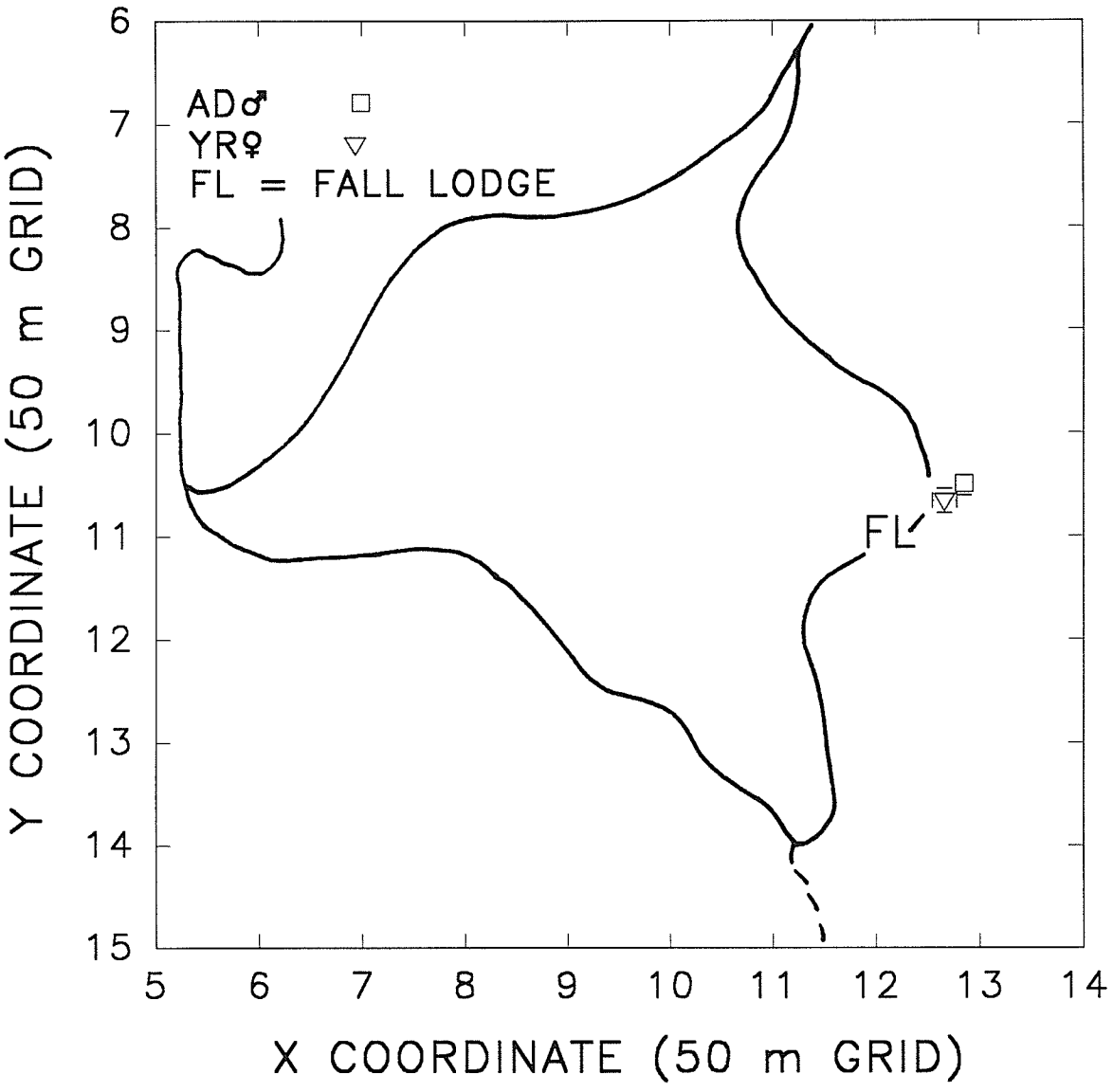

AD♂ □
AD♀ ○
YR♂ △
L = LODGE
Y COORDINATE (50 m GRID)
X COORDINATE (50 m GRID)
2
3
4
5
6
7
8
9
10
11
1
2
3
4
5
6
7
8
9
10

Figure 9. Centroids of activity for Gatlan Ponds Family, Fall, 1991. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = GP1611, Yearling Female = GP1526.


AD♂ □
YR♀ ▽
FL = FALL LODGE
FL
Y COORDINATE (50 m GRID)
X COORDINATE (50 m GRID)
6
7
8
9
10
11
12
13
14
15
5
6
7
8
9
10
11
12
13
14

DISCUSSION

HOME RANGE SIZE AND USE

In areas with long-term ice cover, fall is the time of year when beavers construct food piles and build or repair lodges and dams in preparation for winter. Most of this activity requires working in the vicinity of the lodge. I found that fall home ranges of beaver averaged 3.074 ha in size and were usually concentrated close to the lodge and to shores. Little research has been done on fall home ranges of beavers. Davis (1984), working in South Carolina, reported total daily movement to be greatest in October (fall) and distance between extreme points to be greatest in September (fall) for his lake colony. The stream colony showed maximum values of both these measurements in March (spring) (Davis 1984). The large amount of movement in fall may be related to food supply. If these beavers ate many pond lily roots in the lodge vicinity in the summer, more travel would be required in fall to find other sources of food. McIlroy (1973) reported comparable results for Wombats (*Vombatus ursinus*) in southeastern Australia, finding that they tended to use a larger home range in fall and winter due to a need to search farther for food. In addition, during fall the activity period for beavers is longer due to the longer night (Davis 1984). This allows more time for travel to greater distances from the lodge. These data of Davis' at first appear contradictory to what I describe in the present study. However, the South Carolina beavers had open water year round. Therefore, it was not necessary for them to spend the fall period gathering food and constructing a food pile as is required in areas with long term ice cover. In my study area, ice-cover lasted for up to 6 months, necessitating the expenditure of considerable energy on food cache construction in the fall.

Core areas were present for most beavers. Those beavers without core areas either had very small home ranges (JRB1629, TB1508, GP1611(1991) and GP1526) or had a larger home range which included frequent movement back and forth for provisioning the food cache (BR1603, IP414). Three of these six beavers were adult females, and two were yearling females. The three kits I studied with radiotelemetry stayed close to the lodge in the fall. It is also possible that while constant care of the kits was not necessary in fall, the females stayed closer to the lodge, or made more frequent trips to the lodge in order to supervise the kits.

River home ranges were larger than pond or lake home ranges. Core Activity was greater in lake beavers than pond or river beavers. River habitat in the study area was bordered by numerous bogs containing black spruce (*Picea mariana*), Jack pine (*Pinus banksiana*), alder (*Alnus crispa*) and tamarack (*Larix laricina*), with a few ridges containing Jack pine and trembling aspen (*Populus tremuloides*). Lakes and ponds tend to have more numerous ridges and fewer bogs along their shores. Trembling aspen is a favoured food of beavers (Jenkins and Busher 1979). There is a greater abundance of trembling aspen along lake and pond shores than along river banks. River beavers must therefore travel farther in search of food than either pond or lake beavers. Lake core areas were smaller than pond or river core areas, although not significantly, and Core Activity was greater in lake habitats. The difference from river habitats is explainable by the larger Core Size as discussed above. The ponds in the study area are old and established. The lake lodges are much newer. Suitable food is likely still available in closer proximity to lake lodges than to pond lodges.

Although the numbers were too small for a statistical comparison within family groups, the trend was for adult females to have the smallest home ranges. All beavers' centroids were quite close to the lodge, but the adult female was usually closest. As explained above,

the females may have been closer to the lodge because of providing care for the kits. Busher and Jenkins (1985) found that all family members except the kits had similar behaviour patterns in the fall, and that much more time was spent outside the rest site in fall (>80% of active time) than in summer. Gillespie (1977) did not separate out fall (September and October) data from summer data, so comparison with her results for fall, from southern Ontario, is not possible.

CONCLUSIONS

H_o1 was disproved. Beavers do not use their home range equally during the fall. Core areas were present for most beavers. H_o2 was disproved. Total Size of home range, Core Size and Core Percent were all positively correlated for all beavers combined. H_o3 was disproved. River home ranges were larger than pond or lake home ranges and lake beavers had more activity in their core areas than pond or river beavers. These differences are probably related to differences in food availability in the different habitats. H_o4 and H_o5 were not proved or disproved. Adult females tended to have smaller home ranges than adult males or yearling males and these home ranges were centred closer to the lodges, possibly in order to provide maternal care for the kits, gut other parameters were similar for all animals.

LITERATURE CITED

Aleksiuk, M. 1968. Scent-mound communication, territoriality, and population regulation in beaver (*Castor canadensis* Kuhl). Journal of Mammalogy 49:759-762.

Buckley, J.L. and W.L. Libby. 1955. Growth rates and age determination in Alaskan beaver. Transactions of the twentieth North American Wildlife Conference, Washington. pp.495-507.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346-352.

Busher, P.E. and S.H. Jenkins. 1985. Behavioral patterns of a beaver family in California. Biology of Behaviour 10:41-54.

Davis, J.R. 1984. Movement and Behavior Patterns of Beaver in the Piedmont of South Carolina. M.Sc. Thesis, Clemson University, Clemson, South Carolina, 83pp.

Dixon, K.R. and J.A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040-1044.

Gillespie, P.S. 1977. Summer Activities, Home Range and Habitat Use of Beaver. M.Sc. Thesis, University of Toronto, Toronto, Ontario, 149 pp.

Hayne, D.W. 1949. Calculation of size of home range. Journal of Mammalogy 30:1-18.

Jenkins, S.H. 1979. Seasonal and year-to-year differences in food selection by beavers. Oecologia 44:112-116.

Jenkins, S.H. 1981. Problems, progress, and prospects in studies of food selection by beavers. Proceedings of the Worldwide Furbearer Conference 1:559-579.

Jenkins, S.H. and P.E. Busher. 1979. *Castor canadensis*. Mammalian Species 120:1-8.

McIlroy, J.C. 1973. Aspects of the ecology of the common wombat, *Vombatus ursinus* (Shaw 1800). Ph.D. Thesis, Australian National University.

Miller, D.R. 1964. Colored plastic ear markers for beavers. Journal of Wildlife Management 28:859-861.

Samuel, M.D., D.J. Pierce and E.O. Garton. 1985. Identifying areas of concentrated use within the home range. Journal of Animal Ecology 54:711-719.

SAS Institute Inc. 1988. SAS/STAT® User's Guide Release 6.03 Edition. Cary, N.C: SAS Institute.

Swihart, R.K. and N.A. Slade. 1985a. Influence of sampling interval on estimates of home-range size. Journal of Wildlife Management 49:1019-1025.

Swihart, R.K. and N.A. Slade. 1985b. Testing for independence of observations in animal movements. Ecology 66:1176-1184.

Wheatley, M. 1989. Ecology of Beaver (*Castor canadensis*) in the Taiga of Southeastern Manitoba. M.Sc. Thesis, University of Manitoba, Winnipeg, Manitoba, 167 pp.

CHAPTER 5

SEASONAL VARIATION IN HOME RANGE SIZES OF BEAVER

ABSTRACT

I studied beavers (*Castor canadensis*) in the boreal forest of eastern Manitoba from 1986 to 1992. I captured and ear tagged 60 different beavers, and outfitted 42 of these animals with transmitters. I collected sufficient data to determine summer home range size for 34 beavers and fall home range size for 27 beavers. Home ranges and core areas were larger in summer than fall and were centred closer to the lodge in fall than summer. Winter home ranges were restricted to the vicinity of the lodge. Summer home range size was positively correlated with fall home range size, and summer and fall core sizes were also positively correlated.

INTRODUCTION

Burt (1943) defined home range as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young". Animals use areas disproportionately within their home range (Samuel *et al.* 1985) and within the home range, there may be regions of more concentrated use or core areas (Springer 1982). Core areas are "those areas used more frequently than any other areas and probably contain the home sites, refuges and most dependable food sources ... that is those portions of the animal's home range that exceed an equal use pattern" (Samuel *et al.* 1985).

Activities and behaviour of beavers vary seasonally (Green 1936; Aleksiuk and Cowan 1969; Potvin and Bovet 1975; Jenkins 1981; Lancia 1979; Lancia *et al.* 1982; Davis 1984; Busher and Jenkins 1985; Buech *et al.* 1989; Busher 1991). This seasonal variation is most noticeable in regions with distinct climatic variation among seasons, and especially in regions where beaver must cope with extended periods of ice cover. Beaver kits are born in late May or early June and for beaver families much of the summer is devoted to raising these young. Summer is also the primary time of year for growth and fat deposition. Fall is a busy and important season, when beavers build food caches and repair or construct lodges and dams. Winter is spent almost entirely in the lodge and under the ice, feeding on the stored food. Growth is rare in winter, except in kits, and weight loss is more the rule. Beavers generally leave their parents' lodge at 2 years of age, but occasionally leave at their first birthday or stay beyond their second birthday. Despite this acknowledged seasonal variation in activities, few attempts have been made to quantify home range size and how it varies seasonally.

Considering this seasonal variation in activities, I endeavoured to compare patterns of home range use by beavers in different seasons. The hypotheses I tested are: H_o1) There are no differences in home

range size, core area size, core percent or core activity in different seasons (summer and fall) for all beavers as a whole; H_o2) There are no differences in these parameters for beavers in different habitats; H_o3) There are no correlations between seasons for any of the above parameters; H_o4) There are no differences in the location of centroids of activity for different seasons for individual beavers.

METHODS

I live-trapped beavers using Hancock traps baited with a piece of trembling aspen (*Populus tremuloides*) 30 cm long and 2 to 5 cm in diameter and a scent bait consisting of ground up beaver castor, anise extract and glycerine (Aleksiuk, 1968). For each animal I took measurements of total length, tail length, hind foot length, length of ear from notch, neck circumference, and tail circumferences at the base and at the widest point. I also weighed each animal and determined its sex by palpating externally for the baculum.

To facilitate visual identification of individuals, I attached uniquely numbered and coloured ear tags (Monel, Number 3) to both ears. I made the coloured tags from reinforced vinyl as described by Miller (1964).

RADIOTELEMETRY

I installed radio-transmitters using 2 methods: intraperitoneal implantation (42 transmitters); and tail collars (3 transmitters) (Wheatley, 1989). The implanted packages (Austec Electronics) consisted of a transmitter coupled with a C cell lithium battery, all encased in beeswax and then Elvax (Mini-mitter Co.) which is biologically inert. The entire package measured about 6 x 4 cm and weighed about 80 g. The tail collars (Wildlife Materials Inc.) measured 12.5 x 7.5 x 4.5 cm and weighed about 295 g including the webbing used for attachment to the base of the tail.

For tracking beavers I used an H-shaped antenna and 24 channel receiver (Wildlife Materials Inc.). For beavers residing on the river or lake, I generally tracked and observed from a 6.5 m freighter canoe. When observing at ponds, I chose a high ridge or similar good vantage point nearby from which to make observations. In general, I used the

telemetry to locate the beaver and then, as much as possible, continued with visual observations of activities and movements. After dark, my observations were based on using telemetry to locate animals, and sounds of chewing or tree felling or visual observation of water ripples to determine activity.

I recorded information about the location, time, type of activity, and any movement to another location during the period of observation. Observation periods varied in length from 5 minutes to 13 hours depending upon weather conditions and the number of beavers observed in one night. In open water seasons, most observations were made between 1800 and 2400 h. I recorded data directly in a field book or on cassette audio tape for later transcription into the field book. I later transferred the data onto forms for each beaver.

I drew maps of appropriate size and scale to encompass the home range of each beaver or group of beavers. I then made a grid overlay on an acetate sheet, equivalent to a 50 m by 50 m grid (0.25 ha) on the ground. I transferred each beaver's data onto the appropriate grid. For this I considered 1 minute as 1 observation. A beaver can swim approximately 50 m in one minute. While this does not allow for true independence of observations (Swihart and Slade 1985a; 1985b), the beavers move throughout their home range too much to be able to reflect accurately home range use by 1 observation per night. I separated seasons by identifying apparent shifts in patterns of use, such as new areas of use or previously used areas that were no longer frequented.

I tallied the number of observations in each grid cell and the total number of observations for each beaver for each season. I also recorded the total number of grid cells used. To determine the core area of each individual's home range, I calculated the proportion of observations in each grid cell (number of observations in cell/total number of observations) and compared these proportions to those expected in each grid cell if the beaver's use of the cells was uniform (1/number

of grid cells). I compared the ordered observed cumulative distribution function with the hypothesized uniform cumulative distribution function for each beaver using the Kolmogorov-Smirnov one tailed goodness of fit procedure in which N equals the number of grid squares (Samuel *et al.* 1985). If this test showed that a core area was present, I classed all cells with a greater proportion of observations than uniform as core areas (Samuel *et al.* 1985). I then transferred to the map the outline of the home range and core areas within the home range. I did this for each season identified for each beaver.

TERMS AND DEFINITIONS

I calculated the home range size in hectares by dividing the total number of grid cells used by 4. From here on in I refer to this as the Total Size. I determined the size of the core area (Core Size) by totalling the number of grid cells identified as constituting the core area and dividing these by 4 in the same manner as for Total Size. I calculated the percent of the Total Size that was included in the Core Size for each beaver by dividing the Core Size by Total Size and multiplying by 100. This I refer to as the Core Percent. To calculate the percent of activity which occurred within the core area (Core Activity), I divided the total number of observations in cells identified as comprising the core area by the total number of observations of each beaver and multiplied by 100.

To separate different age class, I used the classification system of Buckley and Libby (1955). "Kits" were any beavers less than 12 months of age. "Yearlings" refers to all beavers in their second year of life and "two-year-olds" to those in their third year of life. The term "adult" refers to any beaver older than 36 months of age. I classified beavers as pond, lake or river beavers based on the location of their primary residence (lodge or bank burrow).

ANALYSIS

I analyzed the data for all beavers by habitat type and by sex and age class within family groups. I calculated the means for Total Size, Core Size, Core Percent and Core Activity. I employed Wilcoxon Matched Pairs Test or Mann-Whitney U-test to determine differences in the variable values between summer and fall, and Spearman Rank Correlation to determine correlations between the same variables for summer and fall for all beavers and for beavers by habitat. There were insufficient numbers of beavers with home ranges in other seasons for statistical comparison.

I used SAS (SAS Institute Inc. 1988) to calculate a weighted centroid of all the observations on each beaver and the associated variance. Hayne (1949) uses the term "centre of activity" to refer the geometric centre of all the locations of an animal, while Dixon and Chapman (1980) use the term "centre of activity" to mean an area in which there is a large amount of activity. For this reason I have chosen an alternate term, the "centroid" to denote the geometric centre of all the points. For beavers residing in family groups, I then tested for similarity between the summer and fall calculated centroids using F and t tests with weighted degrees of freedom.

RESULTS

All beavers had different summer and fall home ranges based on differences in location, size, shape and intensity of use the home ranges. Most fall home ranges consisted of a smaller part of the summer home range, but some included some new home range and a new lodge (JRB Bay Family and BR1848(1987)) or new home range while using the same lodge as the summer (Implant Pond Family, Gatlan Pond Family (1990)).

Winter home ranges were limited to the immediate lodge area or one grid square (0.25 ha, N=21). This is smaller than any other seasonal home range I recorded. Winter excursions from the lodge were limited to the time necessary to gather food from the food pile except in years when water levels had dropped after freeze-up.

While most beavers moved directly from winter to summer to fall to winter home ranges, some beavers had other seasonal home ranges - spring, late spring and late summer (Appendix 1). Late summer home ranges were usually associated with building a new lodge and usually included both summer and fall home range. Spring and late spring home ranges only occurred in one 2-year old female. There were not sufficient beavers with each of these other seasonal home ranges for statistical comparison.

Total summer home range sizes were larger than fall home range sizes (Wilcoxon Matched Pairs Test, $T=-1$, $p<0.0001$, $N=23$)(Figure 1), but the two were highly correlated (Spearman Rank Correlation, $r_s=0.6259$, $p<0.001$, $N=23$). Summer Core Sizes were also larger than fall Core Sizes ($T=-4.5$, $p<0.0001$, $N=17$)(Figure 2) and also highly correlated ($r_s=0.5068$, $p<0.005$, $N=17$). Core Percent did not differ between summer and fall ($T=72$, $p=0.6697$, $N=17$)(Figure 3) and was not significantly correlated ($r_s=-0.0484$, $p>0.25$, $N=17$). Core Activity also did not differ between summer and fall ($T=72$, $p=0.3981$, $N=17$)(Figure 4) and was

Figure 1. Home range size (hectares) for summer (closed symbols) and fall (open symbols) for all beavers combined, and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range.

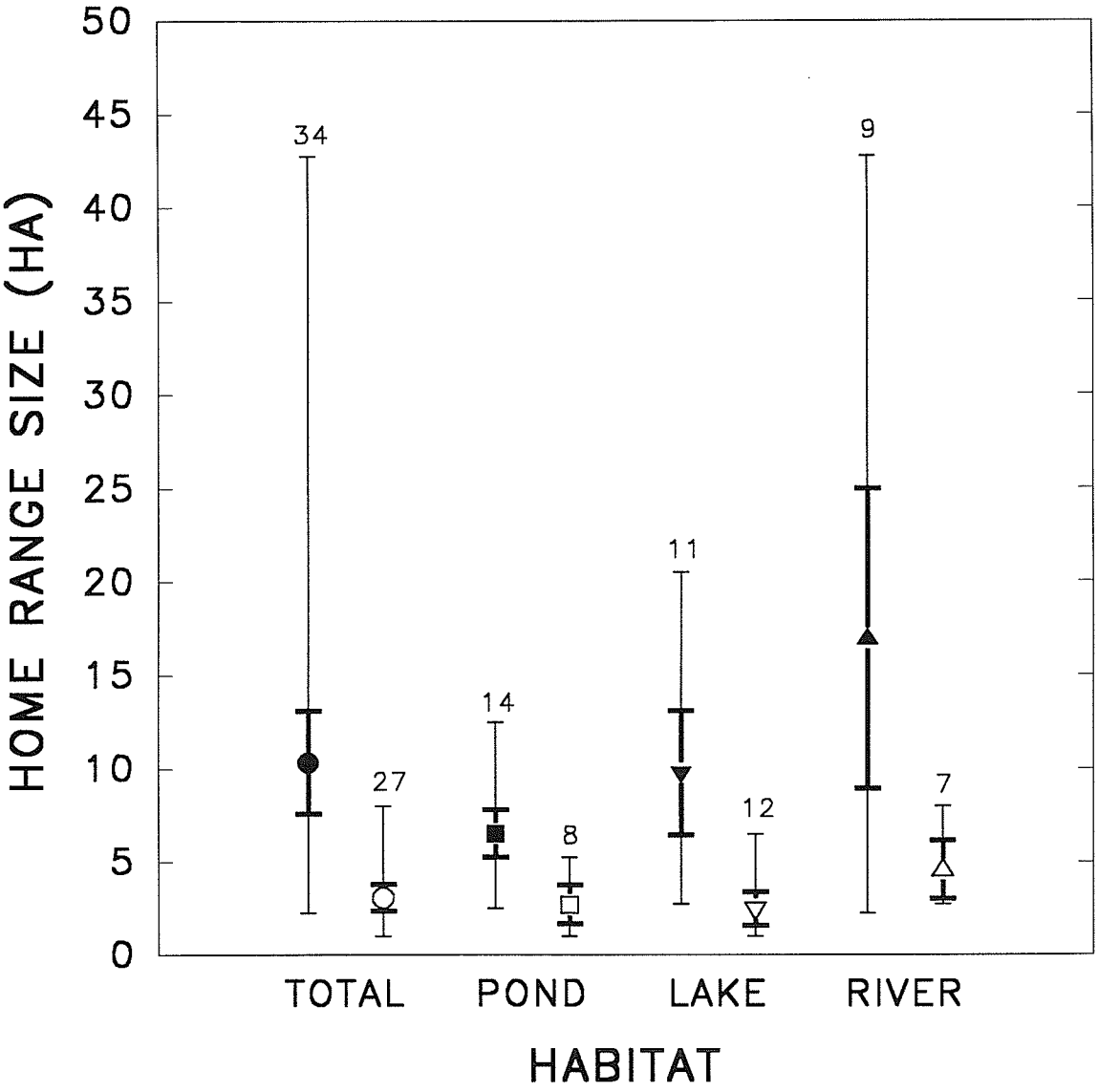

50
45
40
35
30
25
20
15
10
5
0
HOME RANGE SIZE (HA)
34
27
14
8
11
12
9
7
TOTAL
POND
LAKE
RIVER
HABITAT

Figure 2. Core area size (hectares) for summer (closed symbols) and fall (open symbols) for all beavers combined, and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range.

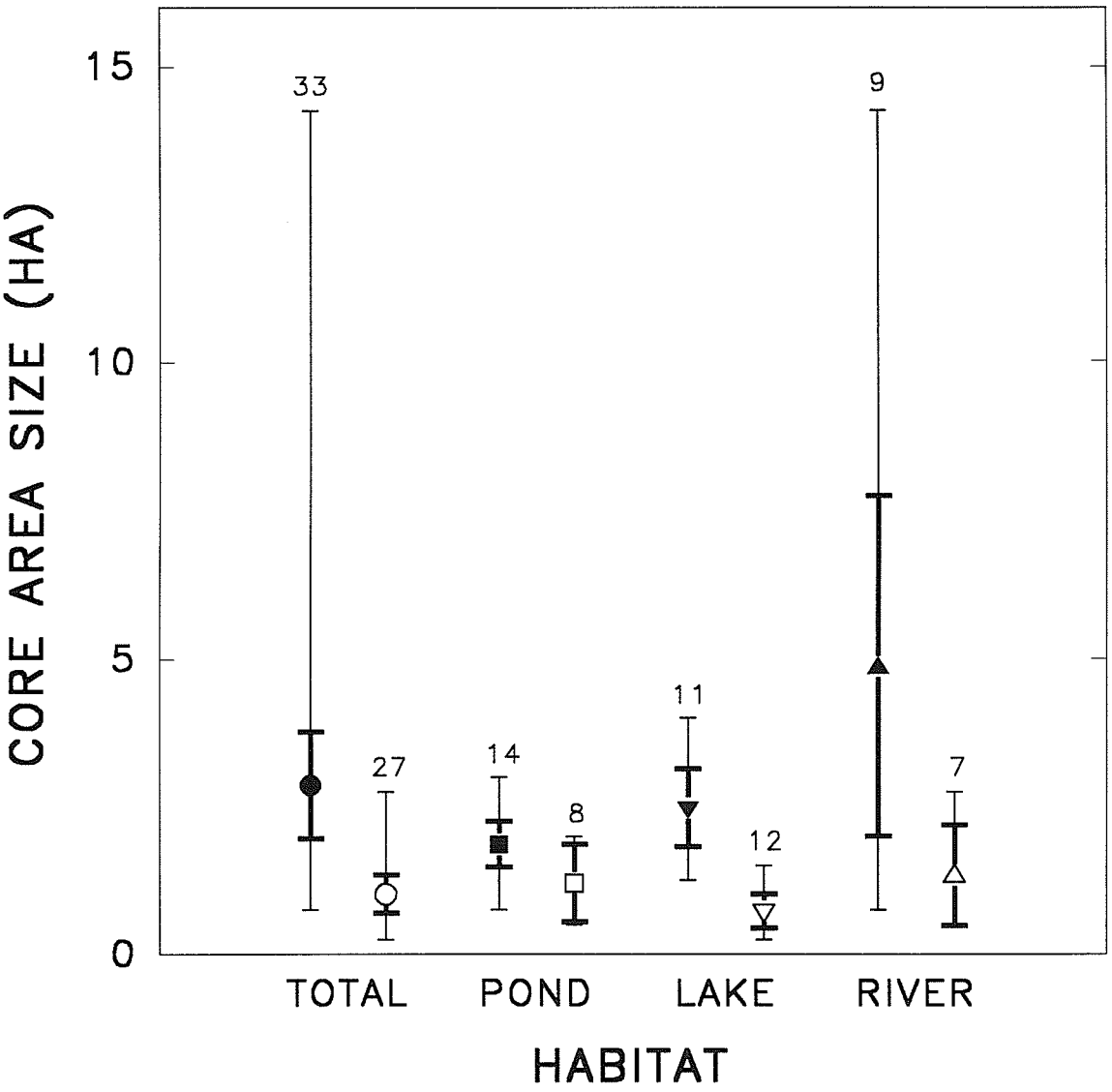

15
10
5
0
CORE AREA SIZE (HA)
33
27
14
8
11
12
9
7
TOTAL
POND
LAKE
RIVER
HABITAT

Figure 3. Core area size as percent of total home range size for summer (closed symbols) and fall (open symbols) for all beavers combined, and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range.

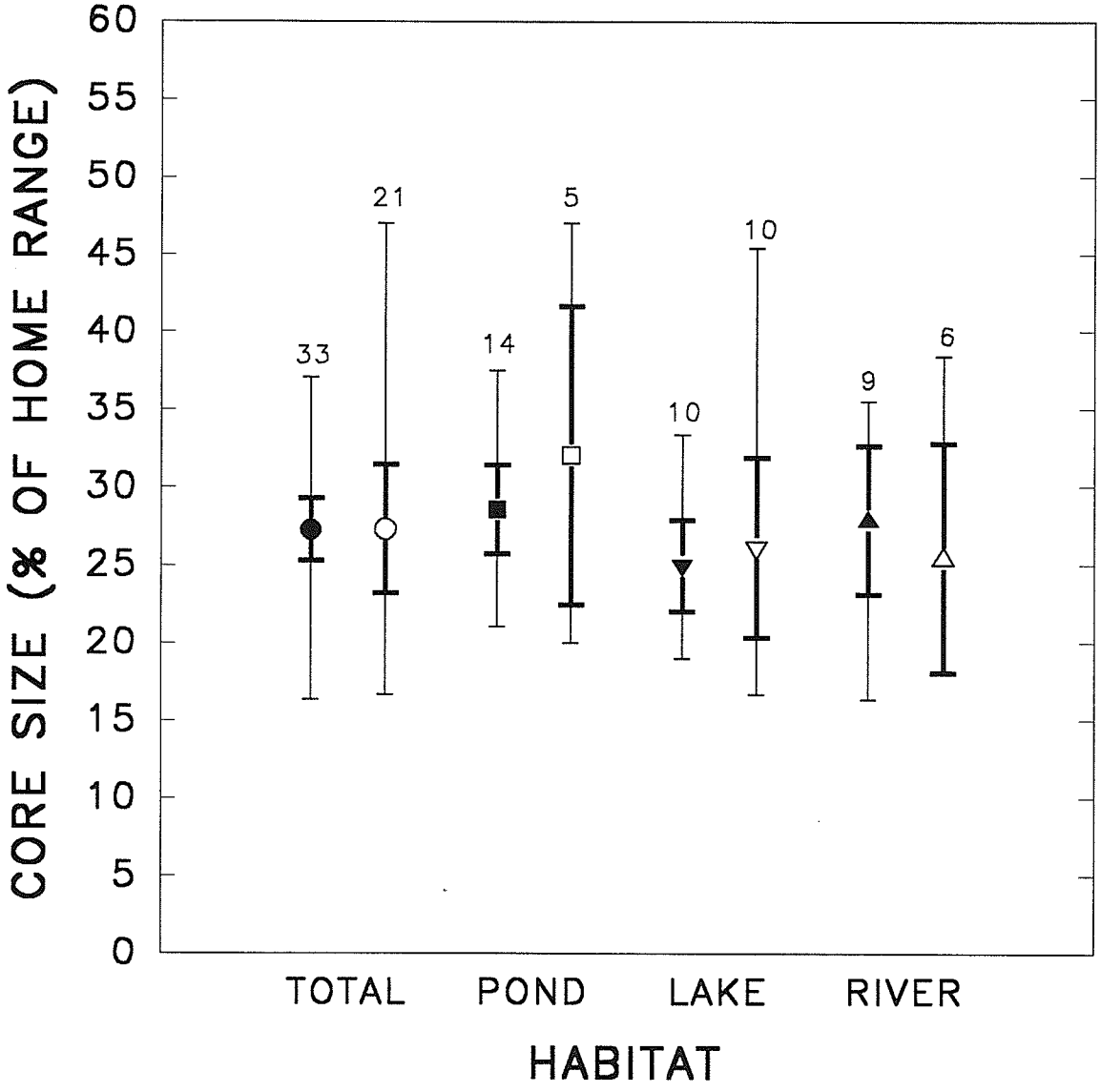
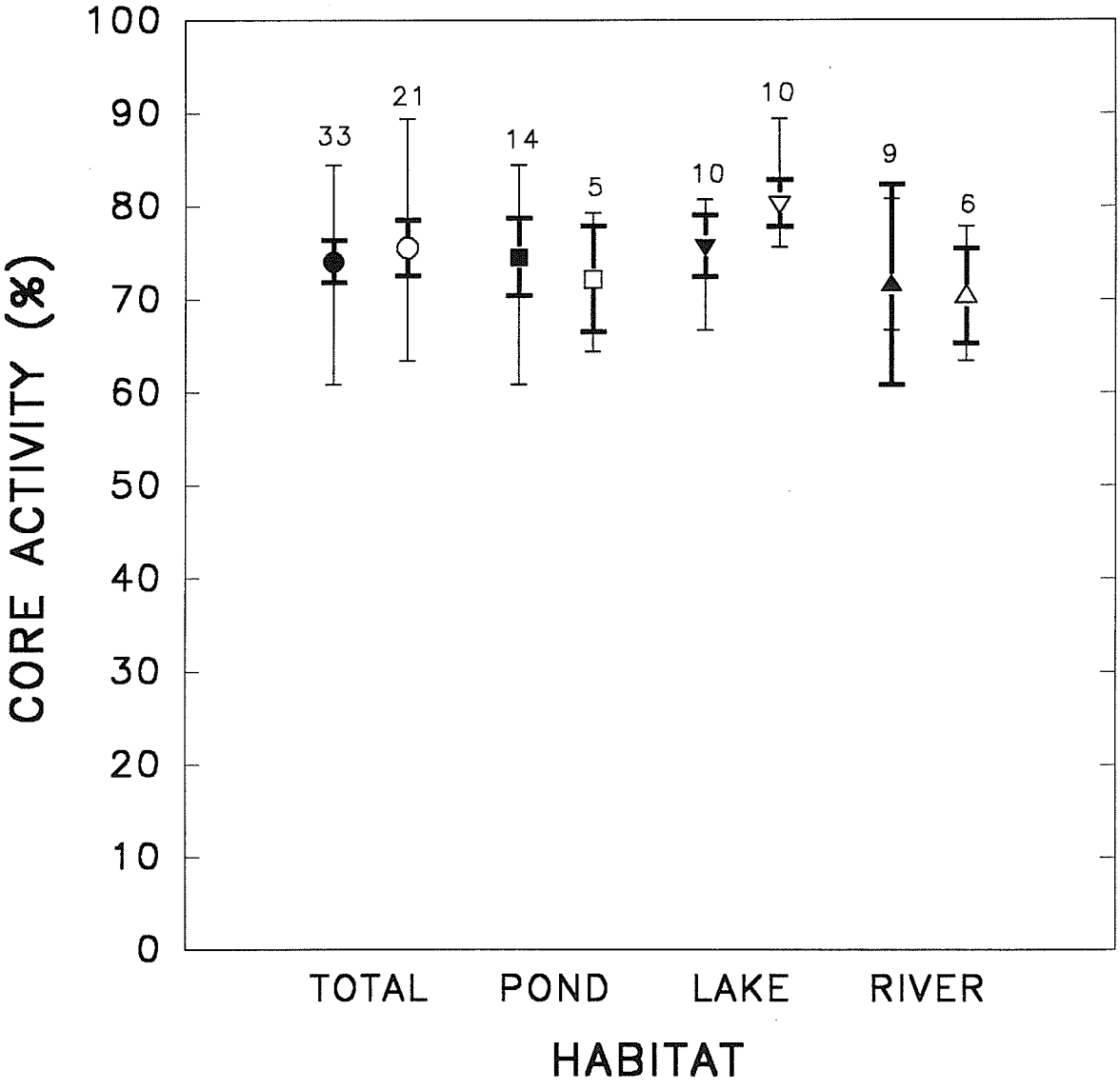

CORE SIZE (% OF HOME RANGE)
60
55
50
45
40
35
30
25
20
15
10
5
0
33
21
14
5
10
10
9
6
TOTAL
POND
LAKE
RIVER
HABITAT

Figure 4. Activity in the core area as percent of all activity for summer (closed symbols) and fall (open symbols) for all beavers combined, and by habitat. Symbols indicate means, wide bars show ± 2 standard errors, narrow lines show range.


100
90
80
70
60
50
40
30
20
10
0
CORE ACTIVITY (%)
33
21
14
5
10
10
9
6
TOTAL
POND
LAKE
RIVER
HABITAT

not significantly correlated (r_s=0.1435, p>0.25, N=17).(See also Appendix 1).

HABITAT

Pond

Beavers living in pond areas also had significantly larger home ranges in summer than in fall (Mann-Whitney U Test, U=8.5, p<0.001, N=14,8)(Figure 1). However, summer and fall Total Size were not correlated (r_s=-0.2271, p>0.25, N=8). Core Sizes were similar in summer and fall (U=19, p>0.05, N=14,5)(Figure 2), and were not significantly correlated (r_s=0.2163, p>0.25, N=5). Core Percent did not differ significantly between summer and fall (U=29.5, P>0.1, N=14,5)(Figure 3) and summer and fall Core Percent were not correlated (r_s=-0.6000, p>0.1, N=5). Summer Core Activity did not differ from fall Core Activity (U=28.5, p>0.1, N=14,5)(Figure 3) and the two were not correlated (r_s=0.1000, p>0.25, N=5).

Lake

Total summer home range size of lake beavers was significantly larger than fall home range size (U=8.0, p<0.001, N=11,12)(Figure 1) and the two were significantly correlated (r_s=0.8954, p<0.01, N=9). Core Size was also significantly larger in summer than in fall (U=3.5, p<0.001, N=10,10)(Figure2) and summer and fall Core Size were significantly correlated (r_s=0.8808, p<0.025, N=7). Core Percent did not differ between summer and fall (U=49.5, p>0.1, N=10,10)(Figure 3) and the two were not correlated (r_s=0.0714, p>0.25, N=7). Core Activity was greater in fall than in summer (U=24.5, p<0.05, N=10,10)(Figure 4) and the two were not correlated (r_s=0.25, p>0.25, N=7).

River

Total home range size of river beavers was significantly larger in summer than in fall ($U=7.0$, $p<0.005$, $N=9,7$)(Figure 1) and the two were not significantly correlated ($r_s=0.759$, $p>0.05$, $N=6$). Core Size was also larger in summer than in fall ($U=7.0$, $p<0.01$, $N=9,6$)(Figure 2) and the two were not correlated ($r_s=0.7826$, $p>0.1$, $N=5$). Core Percent did not differ between the two seasons ($U=26$, $p>0.1$, $N=9,6$)(Figure 3) and was not correlated between the two seasons ($r_s=0.8030$, $p>0.1$, $N=5$). Core Activity also did not differ between seasons ($U=20.5$, $p>0.1$, $N=9,6$)(Figure 4) but was negatively correlated between seasons ($r_s=-0.9000$, $p<0.05$, $N=5$).

CENTROIDS

Centroids for each beaver for each season were all significantly different from other seasonal centroids for the same beaver (t-test, $p<0.005$)(Figures 5,6,7,8 and 9 and see Appendix 4). Home ranges in the fall were centred closer to the lodge than in the summer. In fall, centroids for family members were more similar to each other than in summer (Figures 5,6,7,8 and 9).

Figure 5. Centroids of activity for Implant Pond Family, Summer and Fall, 1989. Centroids are shown ± 2 standard errors in both the X and Y directions. Adult Male = IP491, Adult Female = IP414, Yearling Male = IP433, Juvenile Female = IP403.

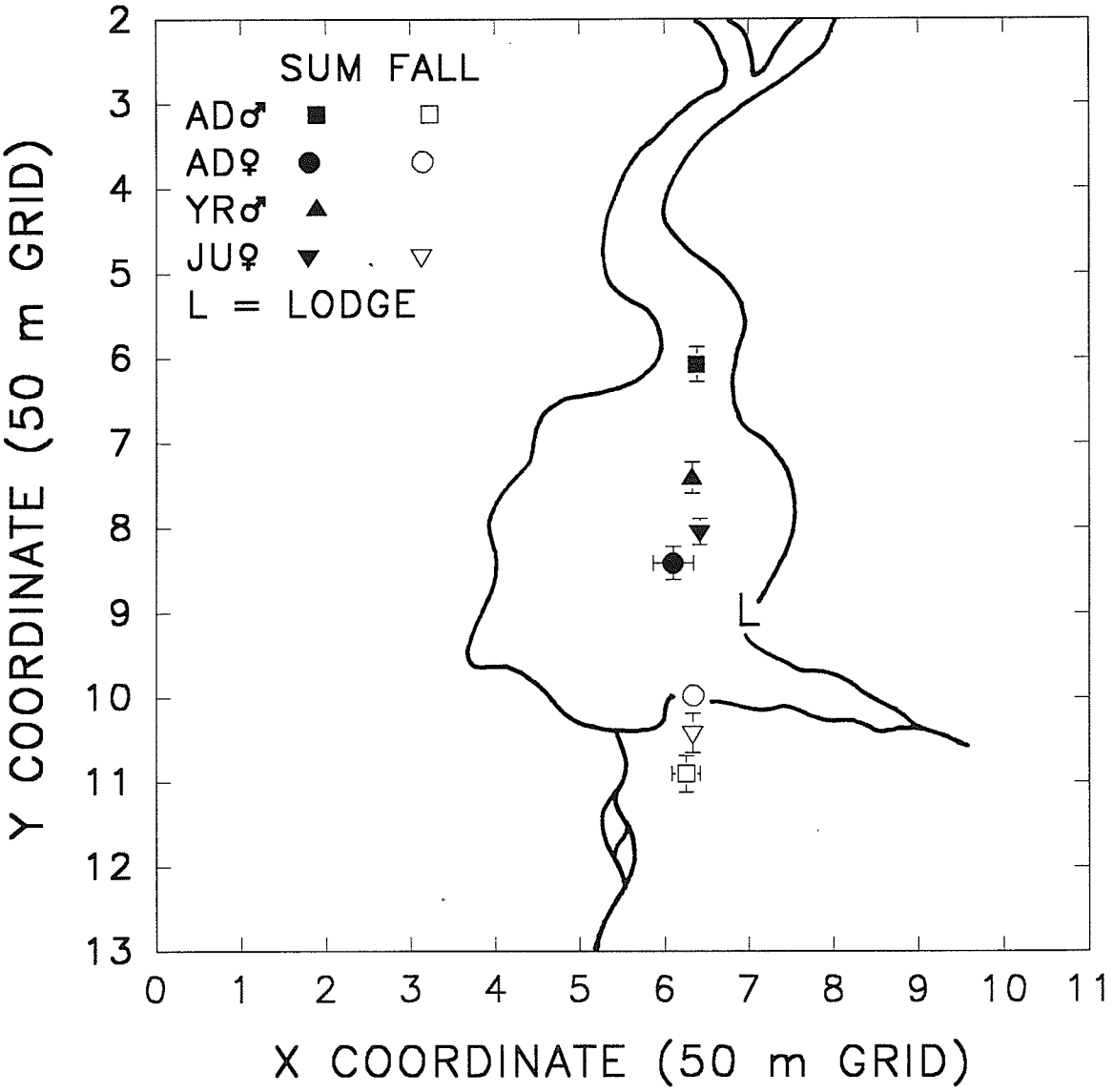

SUM FALL
AD♂
AD♀
YR♂
JU♀
L = LODGE
L
Y COORDINATE (50 m GRID)
X COORDINATE (50 m GRID)
2
3
4
5
6
7
8
9
10
11
12
13
0
1
2
3
4
5
6
7
8
9
10
11

Figure 6. Centroids of activity for Twin Bays Family, Summer, Late Summer and Fall, 1991. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = TB1510, Adult Female = 1508, Yearling Male = TB1528, Yearling Female = TB 1502, Kits = TB1518, TB1520, TB1522.

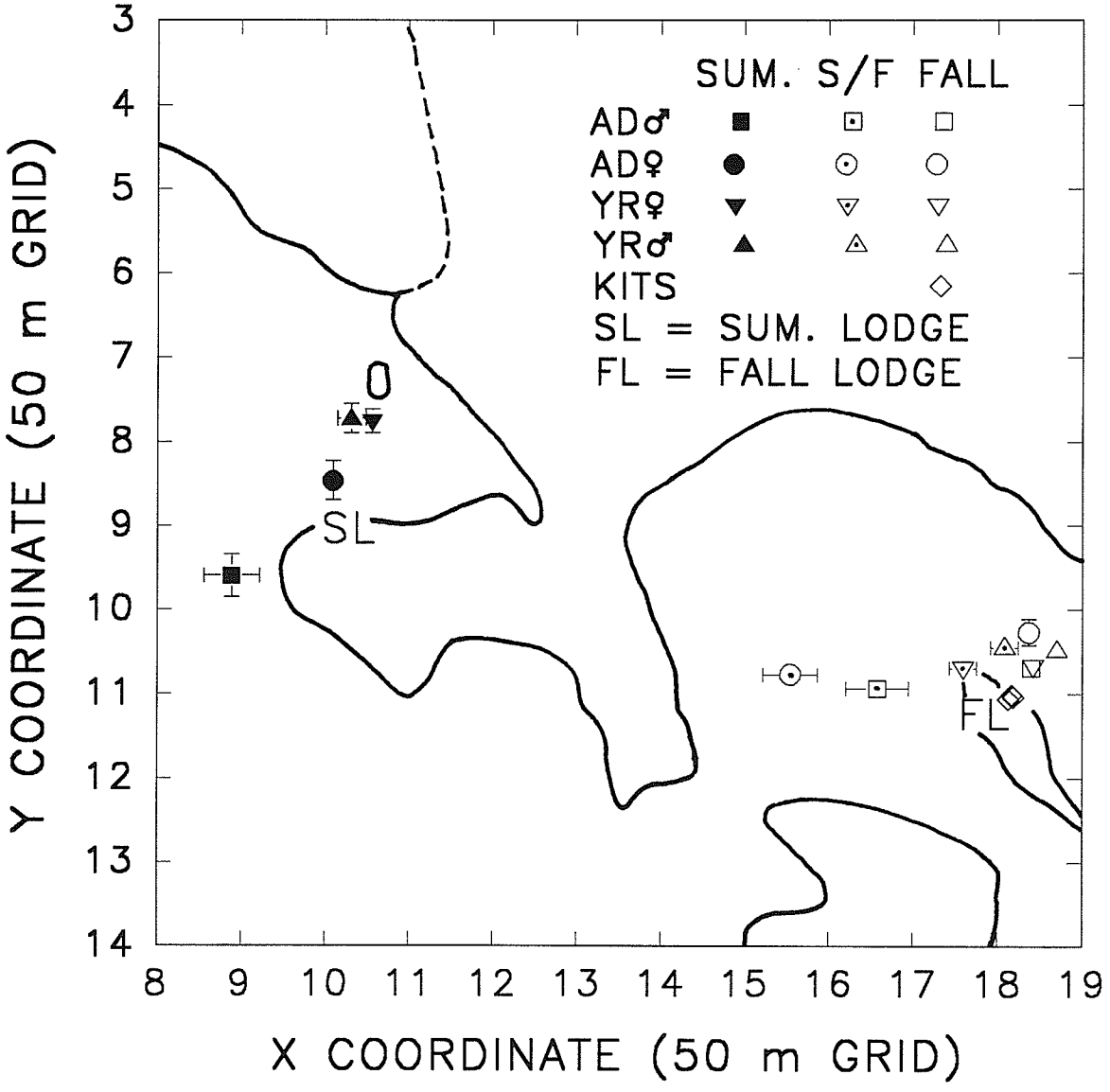

SUM. S/F FALL
AD♂
AD♀
YR♀
YR♂
KITS
SL = SUM. LODGE
FL = FALL LODGE
SL
FL
Y COORDINATE (50 m GRID)
X COORDINATE (50 m GRID)
3
4
5
6
7
8
9
10
11
12
13
14
8
9
10
11
12
13
14
15
16
17
18
19

Figure 7. Centroids of activity for JRB Bay Family, Summer and Fall, 1990. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = JRB1617, Adult Female = JRB1629, Yearling Male (Triangle Down) = JRB1641, Yearling Male (Triangle Up) = JRB1649.

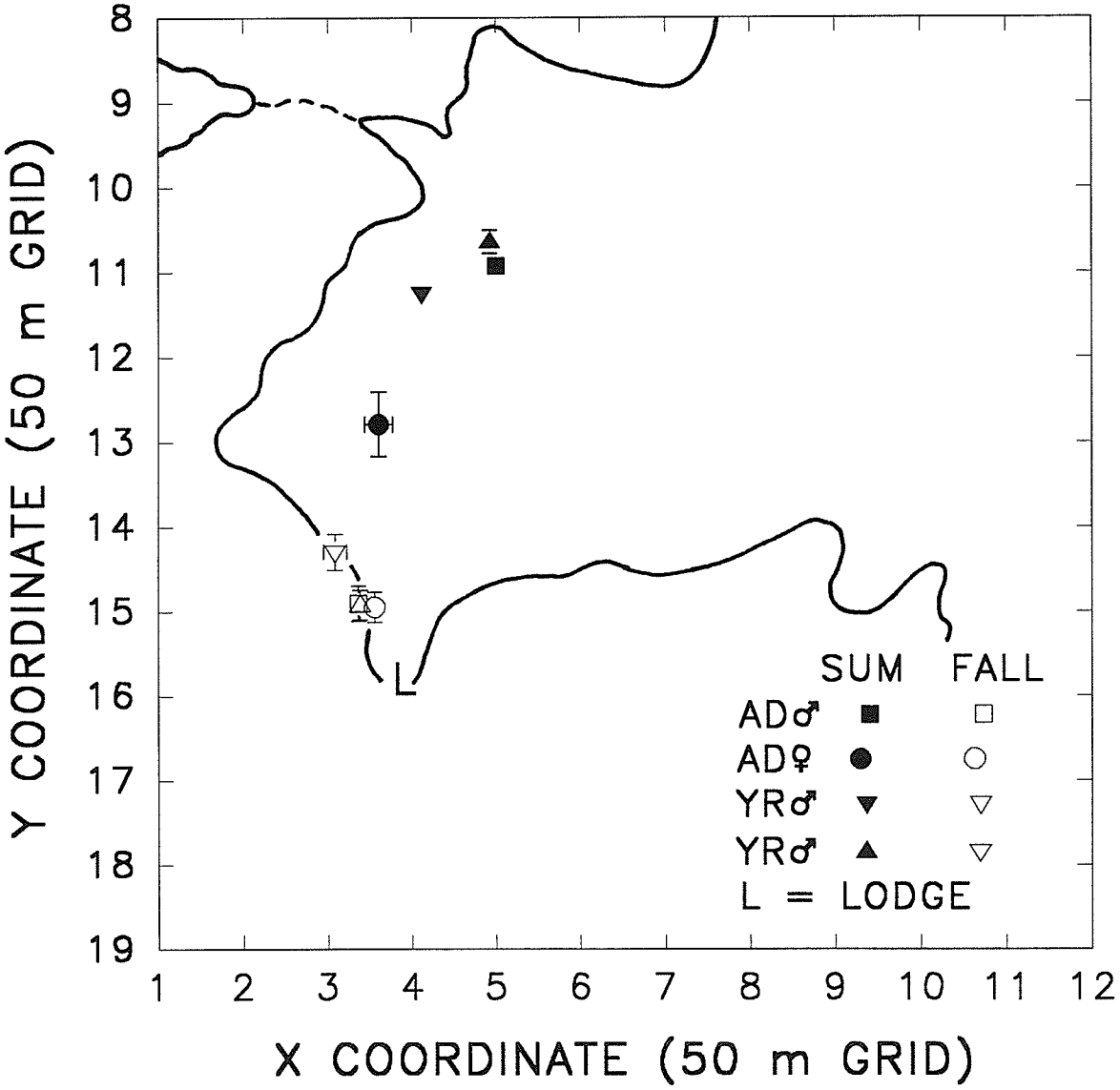

Y COORDINATE (50 m GRID)
8
9
10
11
12
13
14
15
16
17
18
19
1
2
3
4
5
6
7
8
9
10
11
12
X COORDINATE (50 m GRID)
L
SUM
FALL
AD♂
AD♀
YR♂
YR♂
L = LODGE

Figure 8. Centroids of activity for Gatlan Ponds Family, Summer and Fall, 1990. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = GP1611, Adult Female GP1676, Yearling Male = GP1684, Yearling Female = GP1623.

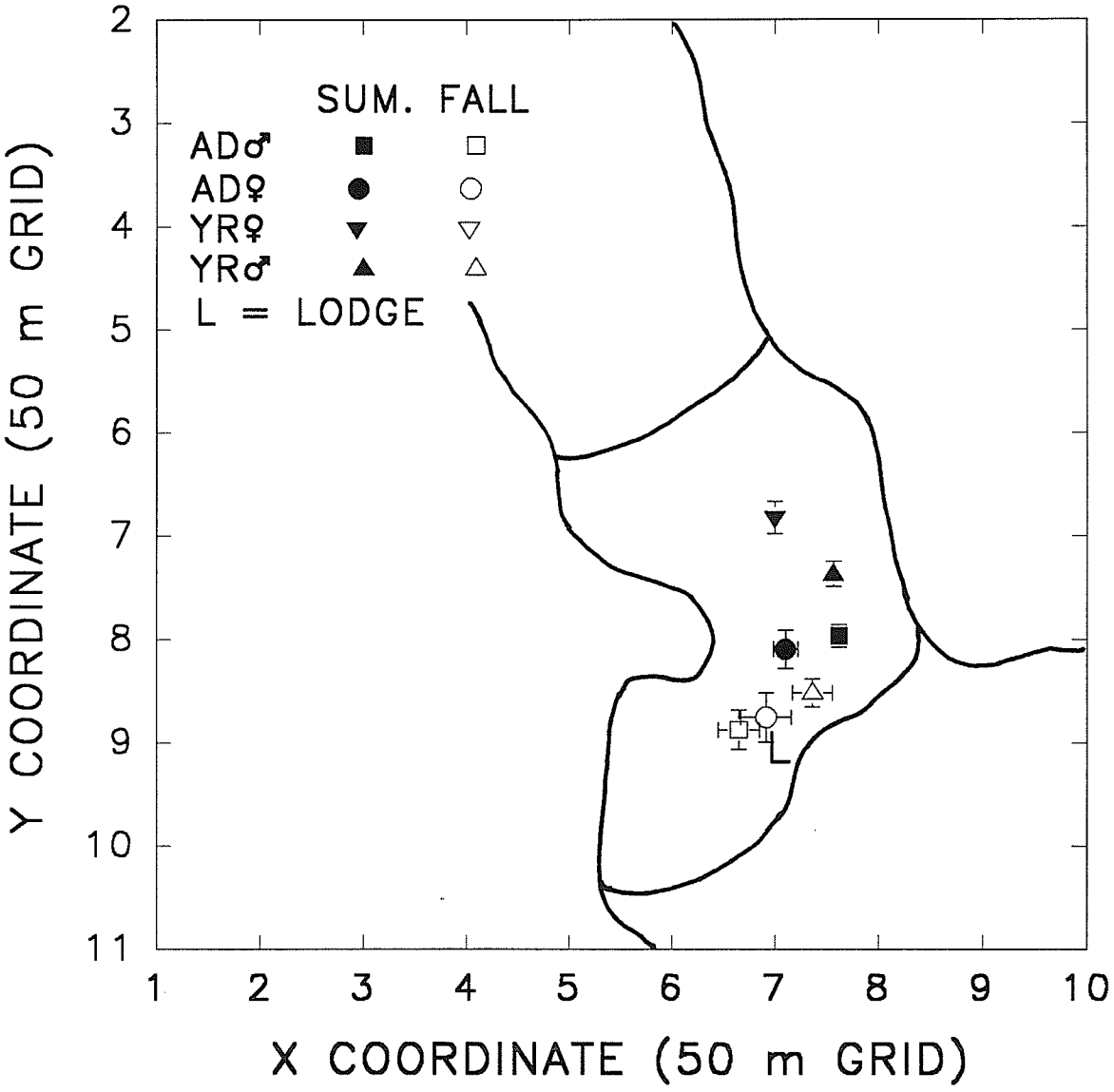
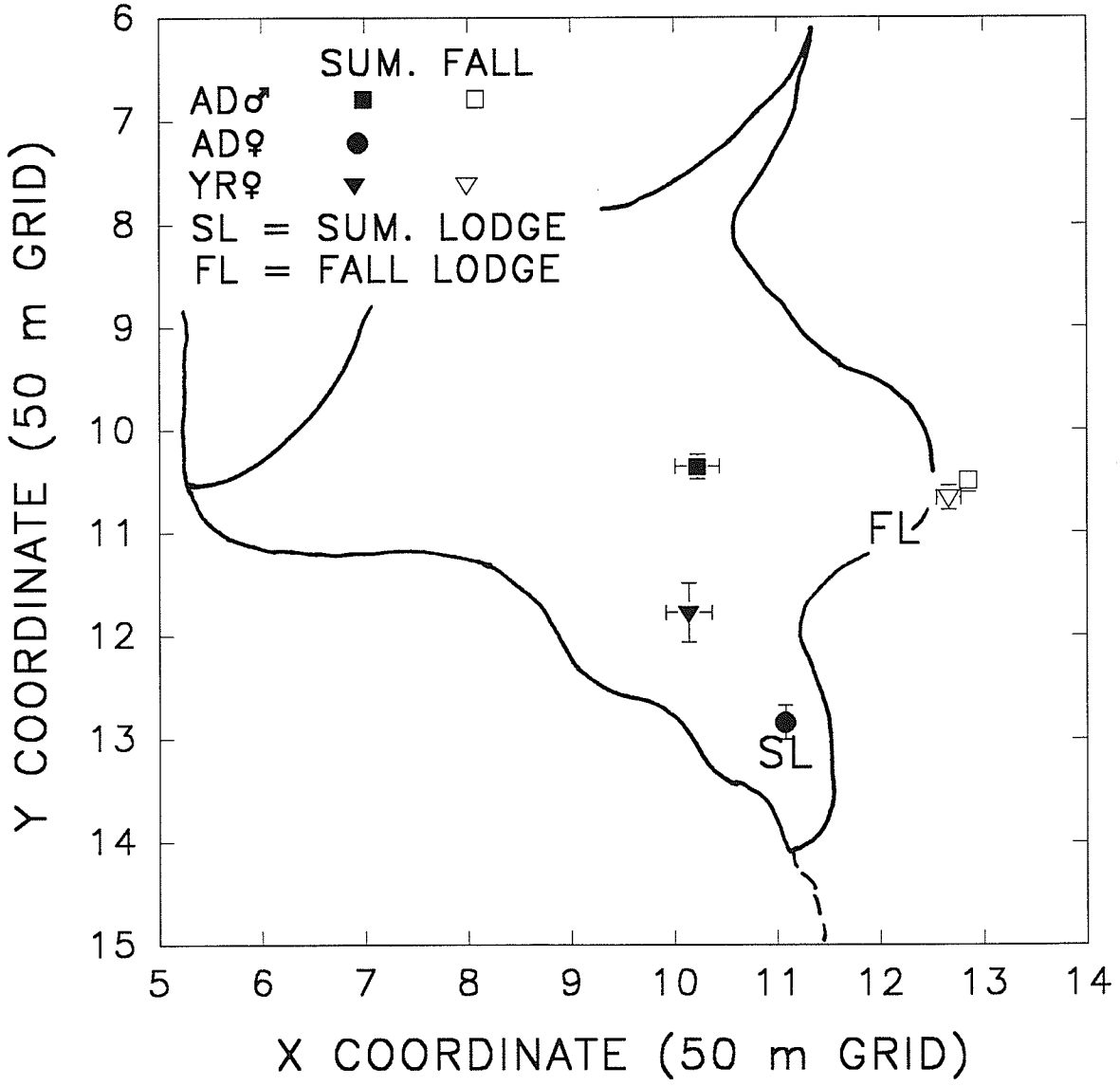

SUM. FALL
AD♂
AD♀
YR♀
YR♂
L = LODGE
Y COORDINATE (50 m GRID)
X COORDINATE (50 m GRID)
2
3
4
5
6
7
8
9
10
11
1
2
3
4
5
6
7
8
9
10

Figure 9. Centroids of activity for Gatlan Ponds Family, Summer and Fall, 1991. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = GP1611, Adult Female = GP1676, Yearling Female = GP1526.


SUM. FALL
AD♂
AD♀
YR♀
SL = SUM. LODGE
FL = FALL LODGE
FL
SL
Y COORDINATE (50 m GRID)
X COORDINATE (50 m GRID)
6
7
8
9
10
11
12
13
14
15
5
6
7
8
9
10
11
12
13
14

DISCUSSION

HOME RANGE SIZE AND USE

Seasonal variation in home range size has been described for many animals including mountain sheep (*Ovis* spp.) (Geist 1971), coyotes (*Canis latrans*) (Springer 1982) and porcupines (*Erethizon dorsatum*) (Craig and Keller 1986). My data show that beaver home ranges also vary seasonally in size, being largest in summer, smallest in winter and intermediate in fall. In contrast, Davis (1984) found that beavers showed greater movement in fall (lake colony) or winter (stream colony) than in spring and summer in South Carolina. In South Carolina, however, winter ice cover was not present, and nights are longer in winter allowing beavers more time to search farther afield for food. Beavers also do not have to build food caches in the fall or rely on these caches in winter. In my study area the beavers must build the food cache in fall and rely on this cache for up to 6 months of ice cover. Busher and Jenkins (1985) found that much more time was spent outside the rest site (lodge) in fall than in summer. Care of kits which requires activity around the lodge is not as crucial in fall as in summer. But, time away from the rest site does not necessarily imply a larger home range.

Jenkins (1981) reported a seasonal change in feeding site, possibly as a result of a seasonal preference for different species of trees, or because of seasonal variation in site accessibility. I discuss seasonal changes in food choice in Chapter 7. The changes in home range use, including size, which I describe coincided with changes in location of food cutting sites. In summer, beavers cut trees at much greater distance from the lodge than necessary to find food, and consumed the leaves and/or bark near the cutting site. In fall, beavers harvested trees much closer to the lodge and transported most of them to

the vicinity of the lodge for inclusion in the food pile. Home ranges may be larger than necessary in summer which could to reduce energy expenditure in the fall.

Semyonoff (1953) and Lancia (1979; 1982) have reported more winter movement than I found in beavers. However, Semyonoff's beavers used sushinetz (air spaces) under the ice and Lancia's beavers were active fairly frequently above the ice. Smith and Peterson (1991) found behaviour similar to Semyonoff when water levels under the ice dropped. They speculated that there was a thermal advantage to staying in the air spaces under the ice. I found similar results, with beavers remaining outside the lodge for extended periods of time in winter if the water level under the ice dropped during the winter. However, the shape of the shorelines or the location of the lodges on islands prevented the beavers from making extensive trips away from the lodge under the ice.

Core Areas

Core Sizes were larger in summer than fall for all beavers combined and for lake and river beavers. Core Sizes were similar in summer and fall for pond beavers. Two of the pond families used new area in the fall, and in the other pond family, none of the animals had a core area in the fall resulting in small numbers (N=5) for analysis. Springer (1982) showed that Core Size varied by season in *Canis latrans*. Davis (1984) found that maxima and minima in total daily movement and distance between extreme points were different for beavers living in river and lake habitats. In Davis's (1984) study, with year-round open water, maximum lake colony movement occurred in fall and minimum in spring, whereas for the stream colony, maximum movement occurred in winter and minimum in summer.

Core Percent and Core Activity were similar in both summer and fall. As demonstrated in Chapter 3, Core Percent and Core Activity were

also similar within all habitats and within sex and age classes. Beavers therefore seem to have some inherent pattern of use of their home range such that about 75 % of their activity takes place in about 25 % of their home range. This may be related to food availability in the area, to habitat types or to other factors which we cannot detect.

CORRELATIONS

Summer and fall home range size were positively correlated for all beavers combined and for lake beavers, but not for river or pond beavers. Similarly, summer and fall Core Sizes were positively correlated for lake, but not for river or pond. Numbers were small for correlations in pond and river habitats. Fall home ranges usually included a smaller part of the summer home range, but in some cases included new area not included in the summer range (Implant Pond, Gatlan Ponds 1990, Twin Bays). The presence of new home range in some pond beavers may have resulted in the lack of correlation. Different home ranges in late summer from summer or fall coincided with building a new lodge for the Twin Bays Family.

CENTROIDS

Fall centroids of family members were closer together and closer to the lodge than in summer. Winter centroids, though not calculated, would have been at the lodge with very low variance. The smaller fall home range that results in activity centres in the vicinity of the lodge for all family members results in this closer association between family members in fall. Similarly Busher (1991) noted the presence of seasonal differences in association and rest sites among members of beaver families. Pairs (adult male and adult female) were together more in winter and spring than in summer.

CONCLUSIONS

H_o1 was disproved. Home range sizes and Core Sizes were larger in summer than fall. However, Core Activity and Core Percent were not significantly different in summer and fall. H_o2 was disproved. Within each habitat, home range size was larger in summer than in fall. Within pond habitats, Core Size did not differ between summer and fall, while in river and lake habitats Core Size was larger in summer than in fall. Core Activity was greater in fall than summer for lake dwellers, but did not differ between summer and fall for pond or river beavers. However, there was no difference in Core Percent between summer and fall in any habitat. H_o3 was disproved. Home range size and Core Size were both significantly positively correlated between summer and fall, however, Core Percent and Core Activity were not. H_o4 was disproved. Centroids of activity were located much closer to the lodge in fall than summer.

LITERATURE CITED

Aleksiuk, M. 1968. Scent-mound communication, territoriality, and population regulation in beaver (*Castor canadensis* Kuhl). Journal of Mammalogy 49:759-762.

Aleksiuk, M. and I.McT. Cowan. 1969. Aspects of seasonal energy expenditure in the beaver (*Castor canadensis* Kuhl) at the northern limit of its distribution. Canadian Journal of Zoology 47:471-481.

Buckley, J.L. and W.L. Libby. 1955. Growth rates and age determination in Alaskan beaver. Transactions of the twentieth North American Wildlife Conference, Washington. pp.495-507.

Buech, R.R., D.J. Rugg and N.L. Miller. 1989. Temperature in beaver lodges and bank dens in a near-boreal environment. Canadian Journal of Zoology 67:1061-1066.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346-352.

Busher, P.E. 1991. Resting association patterns of adult beavers. American Society of Mammalogists 71st Annual Meeting, Abstract.

Busher, P.E. and S.H. Jenkins. 1985. Behavioral patterns of a beaver family in California. Biology of Behaviour 10:41-54.

Craig, E.H. and Keller, B.L. 1986. Movements and home range of porcupines, *Erethizon dorsatum*, in Idaho shrub desert. Canadian Field-Naturalist 100:167-173.

Davis, J.R. 1984. Movement and Behavior Patterns of Beaver in the Piedmont of South Carolina. M.Sc. Thesis, Clemson University, Clemson, South Carolina, 83pp.

Dixon, K.R. and J.A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040-1044.

Geist, V. 1971. Mountain Sheep: A Study in Behavior and Evolution. University of Chicago Press, Chicago.

Green, H.U. 1936. The beaver of the Riding Mountain, Manitoba: An ecological study and commentary. Canadian Field-Naturalist 50:1-8, 21-23, 36-50, 61-67, 85-92.

Hayne, D.W. 1949. Calculation of size of home range. Journal of Mammalogy 30:1-18.

Jenkins, S.H. 1981. Problems, progress, and prospects in studies of food selection by beavers. Proceedings of the Worldwide Furbearer Conference 1:559-579.

Lancia, R.A. 1979. Year-long activity patterns of radio-marked beaver (*Castor canadensis*). Ph.D. Dissertation, University of Massachusetts, Amherst, Massachusetts, 146 pp.

Lancia, R.A., W.E. Dodge and J.S. Larson. 1982. Winter activity patterns of two radio-marked beaver colonies. Journal of Mammalogy 63:598-606.

Miller, D.R. 1964. Colored plastic ear markers for beavers. Journal of Wildlife Management 28:859-861.

Potvin, C.L. and J. Bovet. 1975. Annual cycle of patterns of activity rhythms in beaver colonies (*Castor canadensis*). Journal of Comparative Physiology A 93:243-256.

Samuel, M.D., D.J. Pierce and E.O. Garton. 1985. Identifying areas of concentrated use within the home range. Journal of Animal Ecology 54:711-719.

SAS Institute Inc. 1988. SAS/STAT® User's Guide Release 6.03 Edition. Cary, N.C: SAS Institute.

Semyonoff, B.T. 1953. Beaver biology in winter in Archangel Province. In Biology of Furbearers Vol. 13. (In Russian) (In Translations of Russian Game Reports, Translated by J.M. MacLennan, 1957, Canadian Wildlife Service 1:1-109) pp. 71-92.

Smith, D.W. and R.O. Peterson. 1991. Behavior of beaver in lakes with varying water levels in northern Minnesota. Environmental Management 15:395-401.

Springer, J.T. 1982. Movement patterns of coyotes in south central Washington. Journal of Wildlife Management 46:191-200.

Swihart, R.K. and N.A. Slade. 1985a. Influence of sampling interval on estimates of home-range size. Journal of Wildlife Management 49:1019-1025.

Swihart, R.K. and N.A. Slade. 1985b. Testing for independence of observations in animal movements. Ecology 66:1176-1184.

Wheatley, M. 1989. Ecology of Beaver (*Castor canadensis*) in the Taiga of Southeastern Manitoba. M.Sc. Thesis, University of Manitoba, Winnipeg, Manitoba, 167 pp.

CHAPTER 6

ARE BEAVERS TERRITORIAL?

ABSTRACT

In 6 years and over 600 days of observing beavers, I never observed any evidence of aggressive behaviour among beavers. Some overlap of home ranges occurred, especially on the river, but most home ranges were almost exclusive to a family group. I found no evidence that scent mounds delineated territory and no evidence to prove the presence of territories. I hypothesize that mutual avoidance is more likely than territorialism.

INTRODUCTION

Burt (1943:351) defined home range as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" and territory as the "protected part of the home range". Brown and Orians (1970) have since listed 3 conditions which must all be met for an area to be considered a territory: 1) it must be a fixed area (which may change slightly with time); 2) it must be defended against conspecifics; 3) it must be used exclusively with respect to rivals. The home range, territory and exclusive areas may or may not be the same (Brown and Orians 1970). Territories are exclusive, but exclusive areas are not necessarily territories.

Beavers have long been thought to be territorial. Bradt (1938) wrote that beavers had long been known to be territorial. His basis for this assertion was the non-overlap of home ranges. However, non-overlap of home ranges does not necessarily equate with territoriality (Brown and Orians 1970). The presence of scent mounds is often cited as evidence of territories (Townsend 1953; Hay 1958; Aleksiuk 1968; Davis 1984). Some more recent works have examined the function of scent mounds and have questioned their role in territorial demarcation (Butler and Butler 1979; Walro 1980). Burt (1943) maintained that direct observation was necessary to determine the presence of territoriality.

My objective in this paper is to examine 6 years of data on beavers in the taiga, to determine if territorial behaviour exists in this population. The hypotheses were: H_o1) Beaver home ranges are randomly distributed and independent of the location of other beaver home ranges; H_o2) There is no territorial behaviour between beavers from different groups.

METHODS

I live-trapped beavers and marked each animal with uniquely numbered and coloured ear tags (Monel, Number 3) in both ears (Miller 1964). I also implanted radio transmitters in 29 of the 32 beavers discussed in this study. For tracking the beavers I used an H-shaped antenna and 24 channel receiver (Wildlife Materials Inc.). For beavers residing on the river or lake, I generally tracked and observed from a freighter canoe. When observing at ponds, I chose a high ridge or similar good vantage point from which to make observations. In general, I used the telemetry to locate the beaver and then, as much as possible, continued with visual observations of activities and movements.

For animals which remained in the study area for sufficient time for me to delineate their home ranges, I constructed home range maps as described in Chapters 3, 4 and 5. For known family groups I constructed composite maps of the family home range. Many beavers did not remain in the study area long enough for me to define their home range, or were not outfitted with transmitters so that I was unable to gather enough data to outline their home ranges. For these beavers I indicated on maps their sites of capture and an outline of areas they were known to use, if possible. I compiled maps on a yearly basis.

To separate different age classes, I used the classification system of Buckley and Libby (1955). "Kits" were any beavers less than 12 months of age. "Yearlings" were all beavers in their second year of life and "two-year-olds" were those in their third year of life. The term "adult" refers to any beaver older than 36 months of age. Within this paper, I use the term juvenile to denote any non-adult beaver.

For beavers where I was able to describe the home range, I identified all overlaps with any other delineated individual or family home range. Macdonald *et al.* (1979) provide a formula for determining spatial overlap of one beaver by another. The formula is:

$$S_{12} = \frac{A}{A_1} \quad \text{and} \quad S_{21} = \frac{A}{A_2}$$

where:
A_1 = home range area of beaver 1
A_2 = home range area of beaver 2
A = area of overlap of beavers 1 and 2
S_{12} = proportion of home range of beaver 1 overlapped by beaver 2
S_{21} = proportion of home range of beaver 2 overlapped by beaver 1

The calculations are based on over 37,000 observations of 32 different beavers. Number of observations per beaver per season was 45 to 2934 ($\bar{X}$ = 486 ± 69.1 ($\bar{X}$ ± 2SE)).

RESULTS

I live-trapped and ear-tagged 60 different beavers. I installed 45 transmitters on 42 of these animals. I had sufficient data to determine the home range for at least one season for 39 of these beavers.

During 6 years and over 600 days of observations, I never observed any overt signs of aggression between beavers. I observed scent mounds throughout the study area, but in greatest abundance on the banks of the Blind River, where they were scattered in great profusion. On one occasion in 1989 I observed an adult male beaver (BR1830) from the river re-marking an established scent mound near the river mouth. Another adult male (HB481) from an adjacent lake lodge observed the first beaver and then proceeded to remark the scent mound. At no time was there any aggressive behaviour between the two. Two other beavers, a juvenile female (BR1848) and an adult male (BR1844) who were never associated with one another, used a common bank burrow, though not at the same time.

There were overlaps of known beaver home ranges in 1987, 1989 and 1990 but not in 1986, 1988 or 1991 (Figures 1 - 6). The 1986 map includes only fall data. During these 6 years I recorded 38 other beaver captures for which I could not calculate accurate home ranges (Figures 1 - 6). These 38 other captures included 4 adult females, 16 juvenile males, 13 juvenile females, and 5 juveniles of undetermined sex. These numbers include duplicate captures of the same animal. Thirty-seven of these 38 captures occurred on the river, and one on an island in Twin Bays on the lake (Figures 1 - 6).

For the beavers whose home ranges overlapped, the proportion of the home range overlapped by another beaver ranged from 1.8 to 61 % (Table 1). The beavers BR1834 and BR1844 were not associated with each

Figure 1. Map of home range for beaver in 1986 (fall only). Known individual home range = ▦ ; ● = other adult female captures; ◆ = other juvenile, undetermined sex, captures.

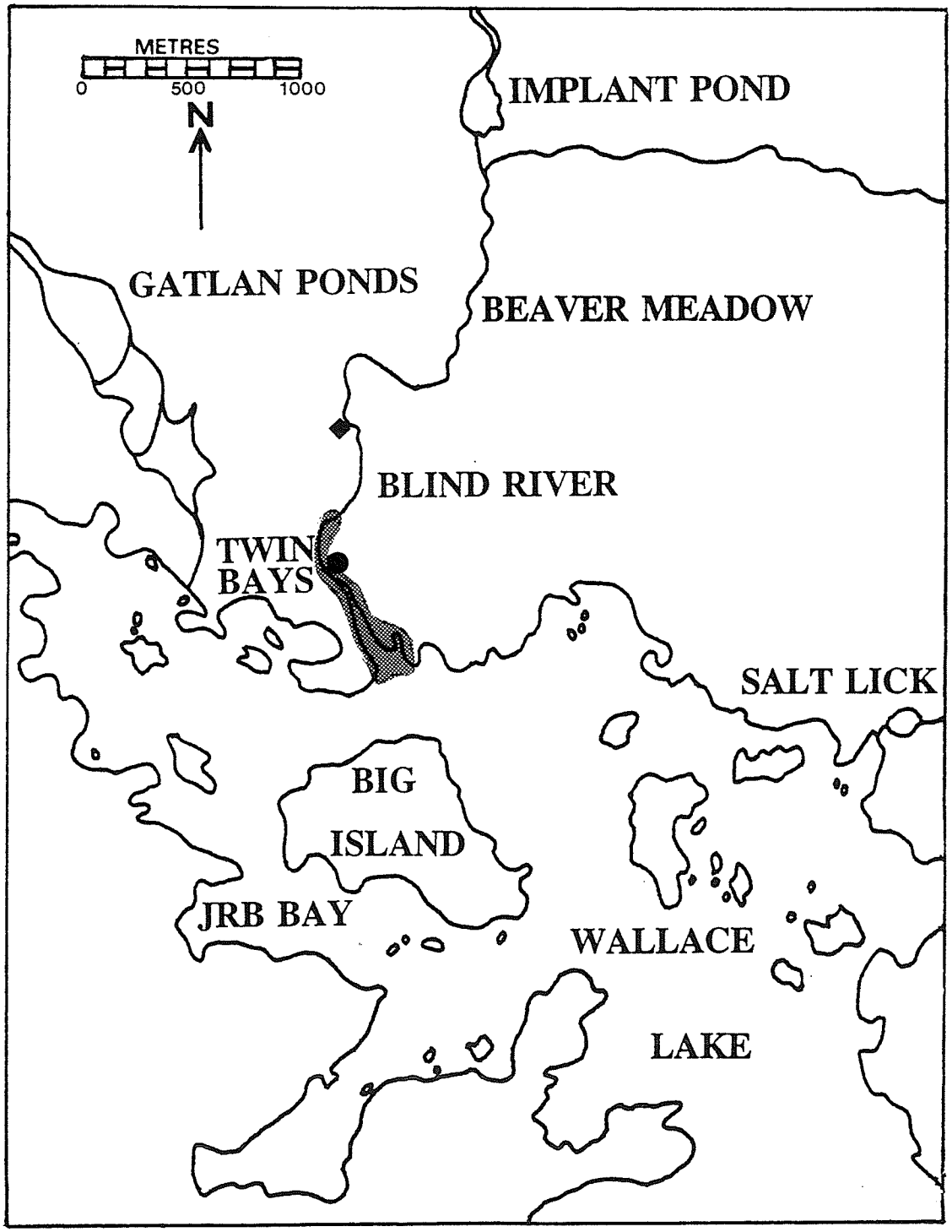

METRES
0
500
1000
N
IMPLANT POND
GATLAN PONDS
BEAVER MEADOW
BLIND RIVER
TWIN
BAYS
SALT LICK
BIG
ISLAND
JRB BAY
WALLACE
LAKE

Figure 2. Map of home ranges for beavers in 1987. Known individual home ranges = ▦ ; approximate individual home ranges = ⣿ ; ● = other adult female captures; ▼ = other juvenile male captures; ◆ = other juvenile, undetermined sex, captures.

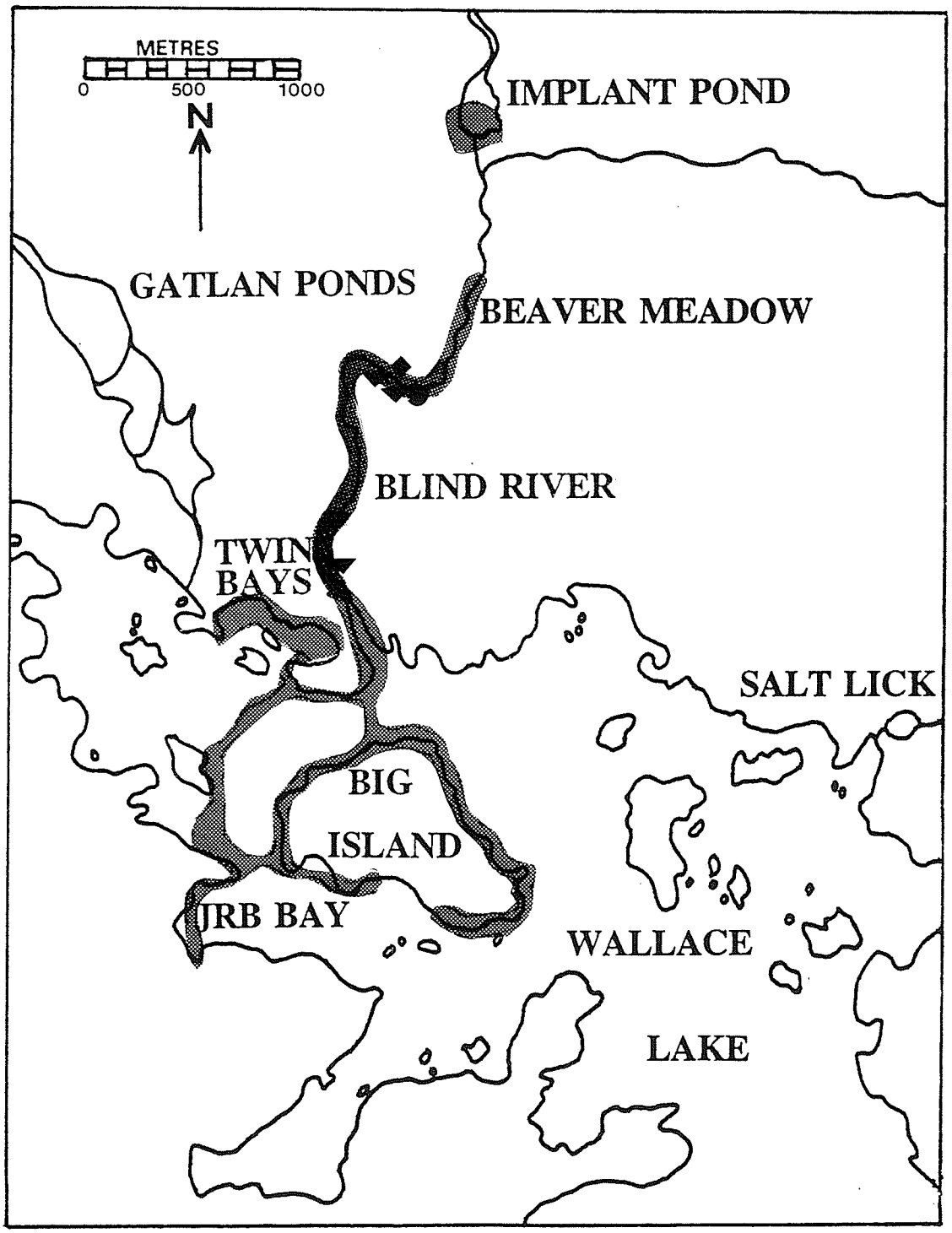

METRES
0
500
1000
N
IMPLANT POND
GATLAN PONDS
BEAVER MEADOW
BLIND RIVER
TWIN
BAYS
SALT LICK
BIG
ISLAND
JRB BAY
WALLACE
LAKE

Figure 3. Map of home ranges for beavers in 1988. Known individual home ranges = ▦ ; approximate individual home ranges = ⣿ ; ▼= other juvenile male captures;▲= other juvenile female captures; ◆ = other juvenile, undetermined sex, captures.

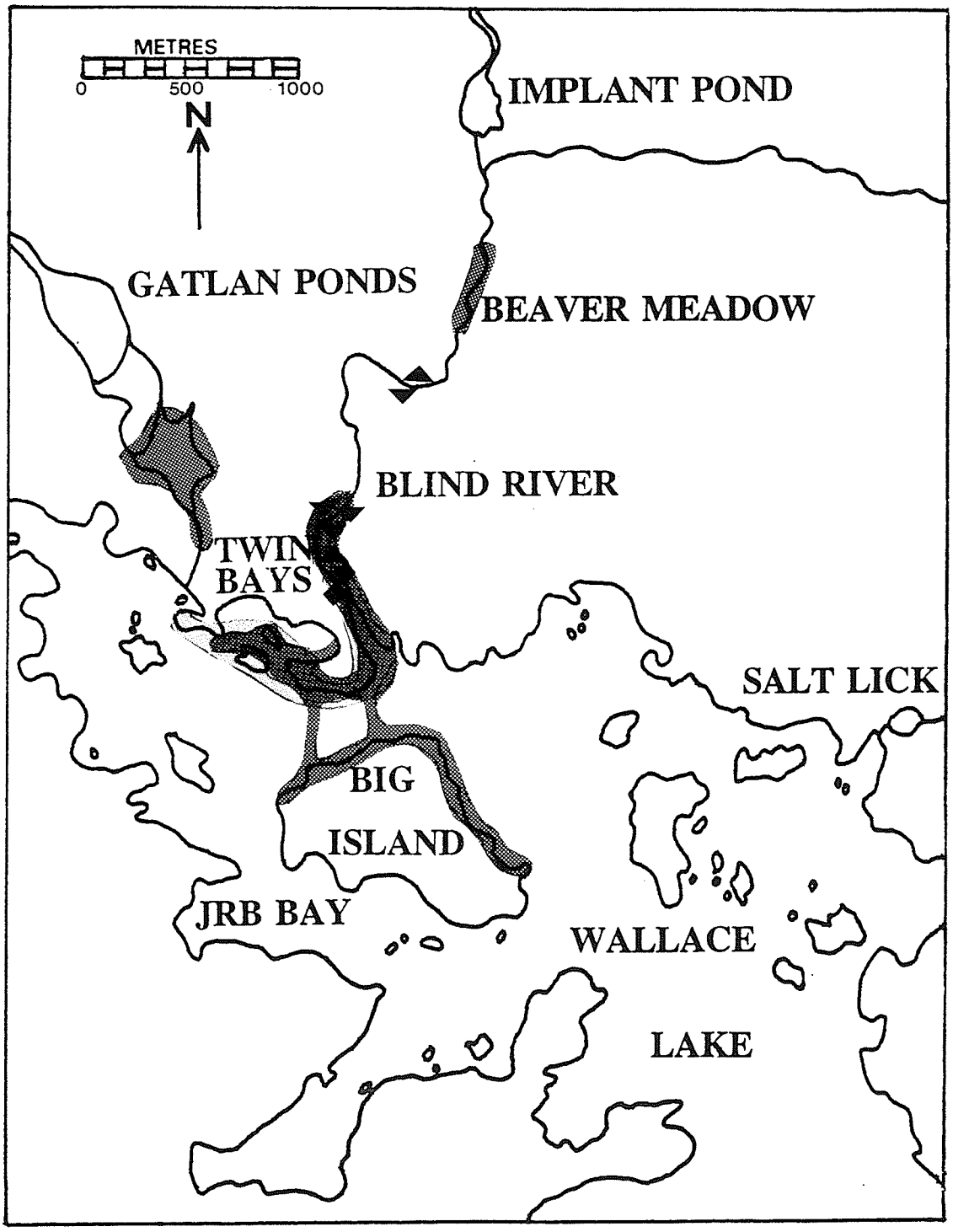

METRES
0
500
1000
N
IMPLANT POND
GATLAN PONDS
BEAVER MEADOW
BLIND RIVER
TWIN
BAYS
SALT LICK
BIG
ISLAND
JRB BAY
WALLACE
LAKE

Figure 4. Map of home ranges for beavers in 1989. Known family home ranges = ; known individual home ranges = ; approximate individual home ranges = ; = other adult female captures; = other juvenile male captures; = other juvenile female captures; = other juvenile, undetermined sex, captures.

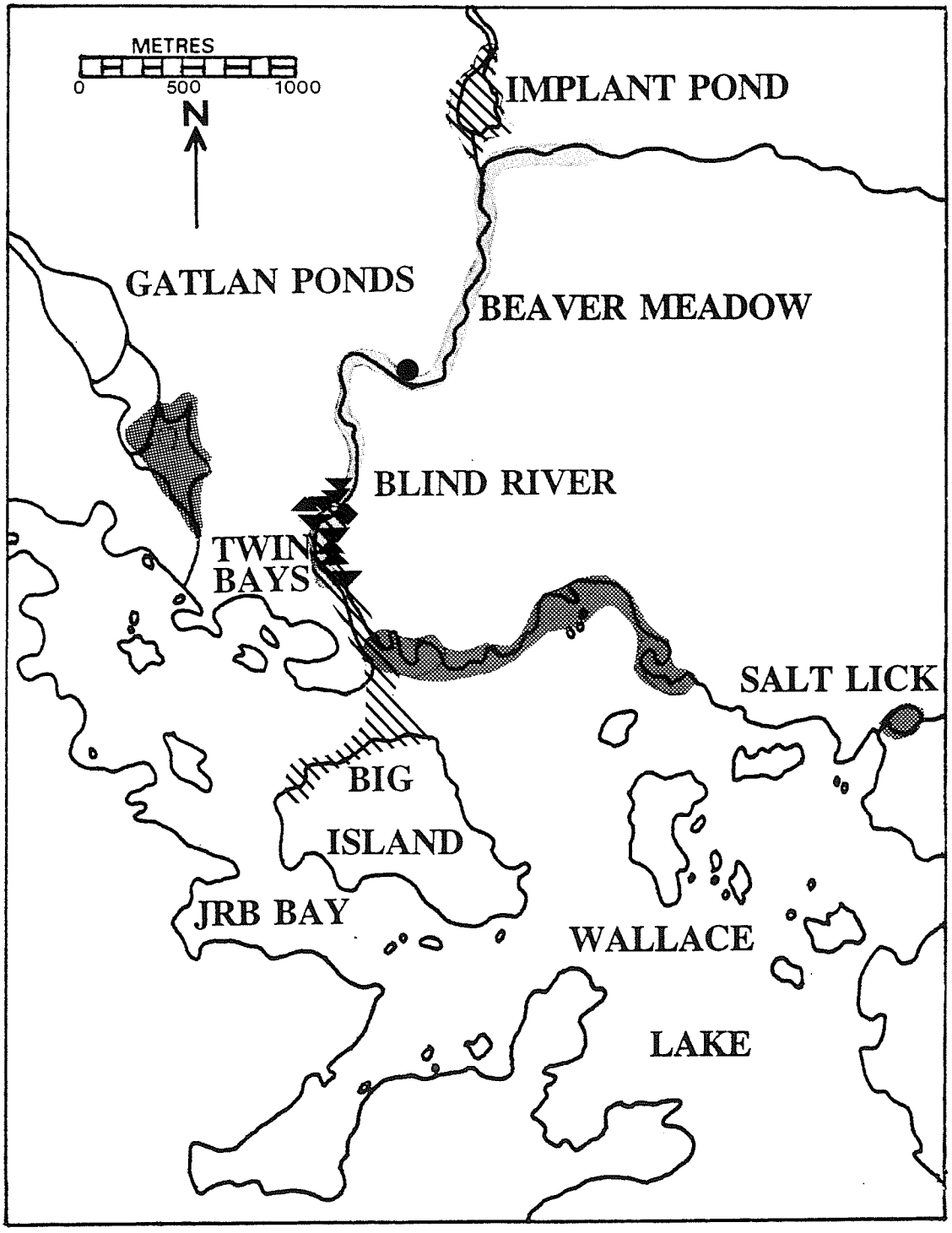

METRES
0
500
1000
N
IMPLANT POND
GATLAN PONDS
BEAVER MEADOW
BLIND RIVER
TWIN
BAYS
SALT LICK
BIG
ISLAND
JRB BAY
WALLACE
LAKE

Figure 5. Map of home ranges for beavers in 1990. Known family home ranges = ; known individual home ranges = ; approximate individual home ranges = ; = other adult female captures; = other juvenile male captures; = other juvenile female captures.

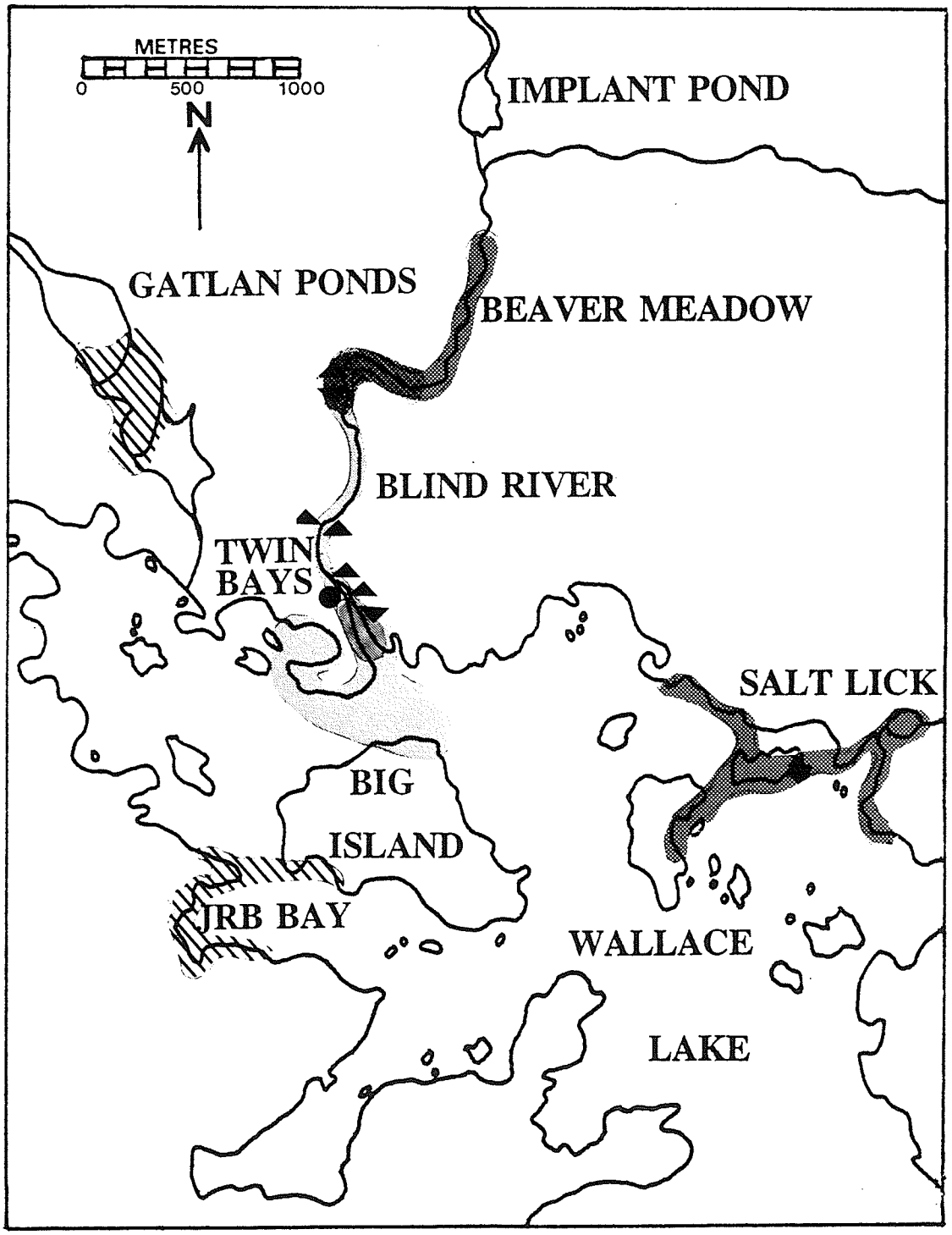

METRES
0
500
1000
N
IMPLANT POND
GATLAN PONDS
BEAVER MEADOW
BLIND RIVER
TWIN
BAYS
SALT LICK
BIG
ISLAND
JRB BAY
WALLACE
LAKE

Figure 6. Map of home ranges for beavers in 1991. Known family home ranges = \\ ; known individual home ranges = ▒ ; approximate individual home ranges = ⣿ ; ▼ = other juvenile male captures; ▲ = other juvenile female captures.

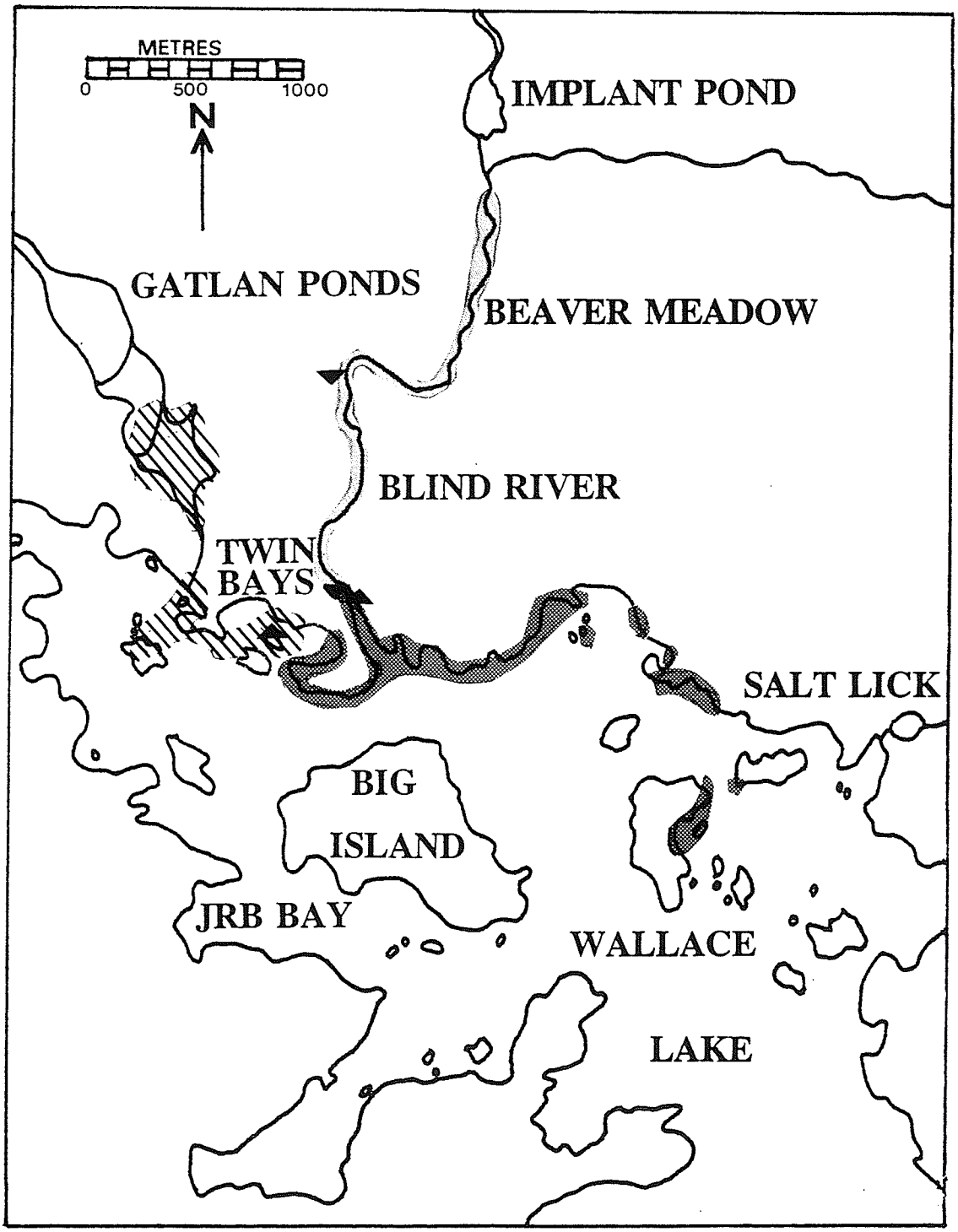

METRES
0
500
1000
N
IMPLANT POND
GATLAN PONDS
BEAVER MEADOW
BLIND RIVER
TWIN
BAYS
SALT LICK
BIG
ISLAND
JRB BAY
WALLACE
LAKE

Table 1. Overlap values (S) for beavers with overlapping home ranges in 1987, 1989 and 1990.

$$S_{12} = \frac{A}{A_1} \quad \text{and} \quad S_{21} = \frac{A}{A_2}$$

where:

A_1 = home range area of beaver 1
A_2 = home range area of beaver 2
A = area of overlap of beavers 1 and 2
S_{12} = proportion of home range of beaver 1 overlapped by beaver 2
S_{21} = proportion of home range of beaver 2 overlapped by beaver 1

1987

BEAVER 1	BEAVER 2	A_1 (HA)	A_2 (HA)	A (HA)	S_{12}	S_{21}
BR1834	BR1844	8.25	13.75	5.0	0.61	0.36
BR1834	BR1848	8.25	42.75	0.75	0.09	0.018
BR1844	BR1848	13.75	42.75	1.0	0.07	0.02

1989

BEAVER 1	BEAVER 2	A_1 (HA)	A_2 (HA)	A (HA)	S_{12}	S_{21}
HB481	BR1830	20.5	16.0	3.5	0.17	0.22
HB481	BR1848	20.5	9.5	2.0	0.10	0.21

1990

BEAVER 1	BEAVER 2	A_1 (HA)	A_2 (HA)	A (HA)	S_{12}	S_{21}
SL1682	SL1686	14.5	12.5	0.75	0.05	0.06

other in the summer, but did cohabit the following winter. If their overlaps are disregarded, the overlap values range from 1.8 to 22 %.

DISCUSSION

Scent Mounds

If scent mounds are intended to mark territory, they should be found at the periphery of the intended territory and be numerous enough to form a "fence". However, a study of the spatial distribution of scent mounds showed them to be too irregularly distributed to form a scent fence (Walro 1980). Walro concluded that the scent mounds could not serve to prevent movement of transients into colony areas (Walro 1980). Beaver scent mounds in my study area were most abundant on the river, and were spread along the length of the river. Brady and Svendsen (1981) also observed scent mounds throughout beavers' activity areas. Aleksiuk (1968; 1970) and Davis (1984) reported scent mounds to be located at the edge of the area of greatest activity and presumed they therefore delineated territory. Hay (1958) noted their location around inhabited sites. Butler and Butler (1979) also described scent mounds as being in areas of highest colony activity, primarily near trails, feeding areas and grooming areas.

In addition, if scent mounds are territorial markers, some response by strange beavers would be expected. I never observed any alarm response from beavers passing scent mounds constructed by other beavers. Butler and Butler (1979) also reported that, most commonly, strange beavers made no observable response to scent mounds of residents. Scent marking is common among carnivores as a mechanism of territorial maintenance. We must be careful not to infer from this that any animal that scent marks is marking territory.

The construction of scent mounds has been reported to be greatest in April to May (Butler and Butler 1979), May and June (Brady and Svendsen 1981) and July (Townsend 1953). Brenner (1964) believed that the period of scent mound construction indicated the breeding season,

and only observed scent mounds at that time. In most areas, breeding takes place during the ice-covered period, when scent mounds cannot be constructed. The April to July period, however, coincides with the time of year when 2-year olds are dispersing from their home colonies and looking for mates. Some scent mounds may be made by resident families, but some may also be made by dispersers "advertising" for a mate. Walro (1980) theorized that the ability to construct a scent mound may indicate sexual maturity, and may help in establishment of a pair-bond.

Butler and Butler (1979) and Walro (1980) have speculated that, as opposed to territory, the scent mounds may transmit information on sexual and reproductive status. Seton (1909) speculated a similar function many years earlier. Scent mounds may also reinforce intra-colony social bonds and provide transients with information on the colony, and may be used for individual and colony recognition (Butler and Butler 1979; Brady and Svendsen 1981).

I hypothesize that the scent mounds may also serve as some sort of sign post and supply information to resident and non-resident beavers. Many times I have released non-resident beavers on the Blind River, and less than 2 minutes later they were in a bank burrow. I speculate that the scent mounds may supply some information about food and shelter availability. This will require further study in order to be proven or disproven.

Mutual Avoidance

Even if scent mounds do not denote territory, it is still possible for beavers to be territorial. Territorial behaviour has been postulated to space colonies and delimit boundaries (Townsend 1953; Bergerud and Miller 1977; Davis 1984). Busher (1975) reported the presence of a "no-beaver's-land" between colony areas, into which only the adult male occasionally ventured. I never observed any territorial

or aggressive behaviour between beavers, but there was some overlap of home ranges. Similarly, Walro (1980) reported an absence of any overt aggression. Aleksiuk (1970), however, noted that transients avoided areas already occupied. This was not evident in my study.

The family home ranges in this study were generally separated by areas of little beaver activity. Busher *et al.* (1983) reported similar spaces between colonies, but also reported some intercolony movement when beaver densities were high. They reported no intercolony movement at low beaver densities. Davis (1984) reported overlap between 2 colonies at the river mouth, and consequent "territorial behaviour". Hay (1958) note that some colonies were isolated and others overlapped.

Territorial behaviour must be economically viable to a beaver. Time spent establishing and defending a territory is time unavailable for feeding and other activities. For beavers, the primary resources to be defended would be food gathering sites and lodge sites. Mates might be a defendable resource in areas where open water is the rule during breeding season. If food is plentiful, and numbers of potential lodge sites reasonable, then territorial behaviour may be unnecessary. In my study area, beaver food was in great abundance. Another consideration for beavers in the taiga is that they have only 6 months of the year for growth. Time away from feeding, for territorial defense, may reduce beaver growth and/or fat storage for winter. Most of my research animals were on the lake and river and most of the overlaps occurred on the river. I never saw any overlap in ponds. Ponds require a greater investment of energy for construction and maintenance. A greater degree of territorial behaviour might therefore be expected among pond beavers.

In contrast to territoriality, what may occur is mutual avoidance when possible (Brown and Orians 1970). Walro (1980) speculated that mutual avoidance may be the real separator of colonies. McIlroy (1973) working on wombats (*Vombatus ursinus*), which have similar scent marking

behaviour with some overlap of home ranges, also concluded that mutual avoidance was the rule rather than territoriality.

CONCLUSIONS

Neither H_o1 nor H_o2 were disproved. Territory requires exclusive use and defense of a fixed area. The beavers in my study had fixed home range areas, which in many cases were used predominately by the family group members. However, most home ranges were not completely exclusive, and were visited by transients. No evidence of defense of the area was ever observed. As opposed to territoriality, beavers may be practising mutual avoidance. In my study area, this may be partly due to an abundant food supply which makes territorial behaviour uneconomical.

LITERATURE CITED

Aleksiuk, M. 1968. Scent-mound communication, territoriality, and population regulation in beaver (*Castor canadensis* Kuhl). Journal of Mammalogy 49:759-762.

Aleksiuk, M. 1970. The seasonal food regime of arctic beavers. Ecology 51:264-270.

Bergerud, A.T. and D.R. Miller. 1977. Population dynamics of Newfoundland beaver. Canadian Journal of Zoology 55:1480-1492.

Bradt, G.W. 1938. A study of beaver colonies in Michigan. Journal of Mammalogy 19:139-162.

Brady, C.A. and G.E. Svendsen. 1981. Social behaviour in a family of beaver, *Castor canadensis*. Biology of Behaviour 6:99-114.

Brenner, F.J. 1964. Reproduction of the beaver in Crawford County, Pennsylvania. Journal of Wildlife Management 28:743-747.

Brown, J.L. and G.H. Orians. 1970. Spacing patterns in mobile animals. Annual Review of Ecology and Systematics 1:239-262.

Buckley, J.L. and W.L. Libby. 1955. Growth rates and age determination in Alaskan beaver. Transactions of the twentieth North American Wildlife Conference, Washington. pp.495-507.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346-352.

Busher, P.E. 1975. Movements and activities of beavers, *Castor canadensis*, on Sagehen Creek, California. M.A. Thesis, San Francisco State University, California, 86 pp.

Busher, P.E., R.J. Warner and S.H. Jenkins. 1983. Population density, colony composition, and local movements in two Sierra Nevadan beaver populations. Journal of Mammalogy 64:314-318.

Butler, R.G. and L.A. Butler. 1979. Toward a functional interpretation of scent marking in beaver (*Castor canadensis*). Behavioral and Neural Biology 26:442-454.

Davis, J.R. 1984. Movement and Behavior Patterns of Beaver in the Piedmont of South Carolina. M.Sc. Thesis, Clemson University, Clemson, South Carolina, 83pp.

Hay, K.G. 1958. Beaver census methods in the Rocky Mountain region. Journal of Wildlife Management 22:395-402.

Macdonald, D.W., F.G. Ball and N.G. Hough. 1979. The evaluation of home range size and configuration using radio tracking data. In C.J. Amlaner, Jr. and D.W. Macdonald (Eds.), A Handbook on Biotelemetry and Radio Tracking. Oxford, Pergamon Press, pp. 405-424.

McIlroy, J.C. 1973. Aspects of the ecology of the common wombat, *Vombatus ursinus* (Shaw 1800). Ph.D. Thesis, Australian National University.

Miller, D.R. 1964. Colored plastic ear markers for beavers. Journal of Wildlife Management 28:859-861.

Seton, E.T. 1909. Life Histories of Northern Animals. Charles Scribner's Sons, New York.

Townsend, J.E. 1953. Beaver ecology in western Montana with special reference to movements. Journal of Mammalogy 34:459-479.

Walro, J.M. 1980. Castor and anal glands of North American beaver (*Castor canadensis*): Histology and communicatory functions of secretions. Ph.D. Thesis, Ohio University.

CHAPTER 7

SEASONAL VARIATION IN FOOD PREFERENCES OF BEAVERS

ABSTRACT

Beavers in the taiga show a preference for *Populus tremuloides* as a primary food in both spring and summer. In spring *Pinus banksiana* is also consumed. *P. tremuloides* leaves are the preferred summer food and *P. tremuloides* bark and *P. banksiana* growing tips are preferred in spring. Beaver food choices appear to maximize protein intake and minimize potassium to sodium ratio. This strategy may serve to foster growth during the relatively short period of high protein availability.

INTRODUCTION

Beavers (*Castor canadensis*) are choosy generalist herbivores (Aleksiuk 1977; Jenkins and Busher 1979). They are opportunistic, adaptable to a wide range of foods and consume almost any species available (Atwood 1938; Aleksiuk 1977; Jenkins 1981). However, they show a strong preference for specific plant types under particular circumstances (Jenkins 1981). There is geographic variation in the species available for consumption, and often a corresponding variation in the species used and in preferences shown by beaver (Aleksiuk, 1977).

Numerous studies of beaver have included inventories of preferred foods (Seton 1909; Green 1936; Aldous 1938; Bradt 1938; Gese and Shadle 1943; Shadle *et al*. 1943; Tevis 1950; Hall 1960; Parovshchikov 1961; Brenner 1962; Novakowski 1967; Aleksiuk 1970; Northcott 1971; Slough 1978; Jenkins 1979; 1981; Svendsen 1980; Pinkowski 1983; Belovsky 1984; Doucet and Fryxell 1993; Fryxell and Doucet 1993). Most of the North American studies cited above have identified a preference for *Populus tremuloides* when available. In addition, several authors have identified preferences for herbaceous and/or aquatic vegetation when it is available (Green 1936; Tevis 1950; Parovshchikov 1961; Brenner 1962; Northcott 1971; Svendsen 1980; Jenkins 1981; Belovsky 1984). Jenkins (1980; 1981), Pinkowski (1983), Belovsky (1984), McGinley and Whitham (1985), Basey *et al*. (1988; 1990), Fryxell and Doucet (1991; 1993) and Fryxell (1992) have investigated changing preferences for specific tree species and sizes with increasing distance from the water.

A few studies have made attempts to identify some of the nutrient components of beaver foods (Cowan *et al*. 1950; 1955; Aleksiuk 1970; Vasilkov and Golodushko 1971; Belovsky 1984; Doucet and Fryxell 1993). However, the nutrient requirements for most wild animals, including beaver, have never been determined (Robbins 1993). The studies cited above have generally examined protein and energy content of foods, but

no analysis of individual mineral complements of different foods appears to have been made. Jenkins (1975; 1978) theorized that beavers may sample trees in order to asses their nutrient status as an economical method of determining variation in nutrients.

In this study I present some initial findings on the nutrient content of preferred and non-preferred foods in my area of study in the boreal forest. The purpose of this study was to identify the preferred species and types of foods, and then to determine the nutrient levels in the different types of vegetation.

The null hypotheses for this study were: H_o1) There is no preference for one type of vegetation over others for consumption; H_o2) Nutrient levels of the potential foods do not differ among different plant species or plant parts.

METHODS

During my observations of beaver activity described in Chapters 3 to 5, I observed the type of food beavers were consuming. I recorded the species and, if possible, the part of the plant being consumed. I collected samples of the various plant species and parts. I made these collections both at times when the beavers were apparently selecting a particular species or part, and again at a time when they were not using or using less of that species or part. Based on my observations, I classified the different vegetation as either primary food (the main food eaten), secondary food (eaten less frequently) or non-food (avoided).

The samples were analyzed at the Manitoba Agricultural Services Complex (later Norwest Labs) in Winnipeg. For all samples lab personnel determined dry matter (%), crude protein (%), sodium (%) and potassium (%) on both an "as fed" and "dry matter" basis (1991 samples). For 1992 and 1993 samples, additional analyses included sulphur (%), phosphorus(%), magnesium (%), calcium (%), copper (ppm), manganese (ppm), iron (ppm) and zinc (ppm), again both on an as fed and dry matter basis. I then made comparisons between nutrient content of food items and non-food items. I compared results based on the dry matter values.

RESULTS

SPECIES PREFERENCES

In spring, the period before leaf-out of deciduous trees, *Populus tremuloides* (PT) bark was one food of choice. Beavers also cut *Pinus banksiana* (PB), but only consumed the new growing tips from the tree leader and distal ends of branches. They did not consume the bark from *P. banksiana*.

In summer, beavers ate *P. tremuloides* almost exclusively. They ate the leaves first, avoiding the petioles, and then ate the bark in some instances. Other species available in abundance were *P. banksiana* and *Alnus crispa* (AC). I never observed beaver eating these species in summer.

In fall, beavers built foodpiles and repaired lodges. They were therefore cutting trees for construction, winter food consumption and immediate food consumption. They cut both *P. tremuloides* and *A. crispa*, but only used unpeeled stems of *A. crispa* for construction and the raft (the floating part) of the foodpile. Stems of *P. tremuloides* used in construction were always peeled (i.e. the bark was eaten) before being used as a building material. Aquatic plants occasionally appeared on the foodpile, but did not constitute a great proportion of the cache.

In summer, beavers usually fed at some distance from the lodge (see Chapter 3 and Appendix 1). In fall, tree stems were harvested in much closer proximity to the lodge than in summer.

NUTRIENT CONTENT

I collected 5 samples in spring and 15 samples in summer (Table 1). Based on the observations described above, I considered PB1, PB2, PT1 and PT2 to be primary food items and PB3 to be a non-food item in

Table 1. Summary of vegetation samples used for nutrient testing. Code numbers correlate with codes in Figures 1 to 12.

SAMPLE #	SPECIES	SAMPLE TYPE	SITE	DATE
PB1	Pinus banksiana	needles	TBS	1992-05-18
PB2	Pinus banksiana	needles	BR	1992-05-18
PB3	Pinus banksiana	bark	TBS	1992-05-18
PB4	Pinus banksiana	needles	BR	1991-07
PB5	Pinus banksiana	needles	CAVE	1991-07
PT1	Populus tremuloides	bark	TBS	1992-05-18
PT2	Populus tremuloides	bark	BI	1992-05-18
PT3	Populus tremuloides	petioles	TBS	1991-08
PT4	Populus tremuloides	bark	HB	1991-07
PT5	Populus tremuloides	bark	BI	1991-07
PT6	Populus tremuloides	bark	HB	1993-08
PT7	Populus tremuloides	leaves/petioles	HB	1991-07
PT8	Populus tremuloides	leaves/petioles	BI	1991-07
PT9	Populus tremuloides	twigs	HB	1991-07
PT10	Populus tremuloides	twigs	BI	1991-07
PT11	Populus tremuloides	leaves	HB	1991-07
PT12	Populus tremuloides	leaves	BI	1991-07
PT13	Populus tremuloides	leaves	HB	1993-08
AC1	Alnus crispa	bark	HB	1991-07
AC2	Alnus crispa	bark	CAVE	1991-07

spring. In summer, I considered primary food items to be PT11, PT12 and PT13, and secondary food items to be PT4, PT5, PT6, PT7, PT8, PT9 and PT10. Summer non-food items were PB4, PB5, PT3, AC1 and AC2.

Protein

In both spring and summer, protein levels were higher in primary foods than in non-food items (Figure 1). Some secondary food items were high in protein, but most were low in protein. For equivalent plant components, protein levels were higher in summer than in spring.

Macroelements

Sodium levels were low in all spring vegetation samples, and all summer samples except for two of the *P. tremuloides* leaf samples (the primary food) (Figure 2). Secondary foods were slightly higher in sodium than non-foods in summer. Potassium levels were highest in one non-food and the primary food in summer (Figure 3). Spring levels were similar in all items. The potassium to sodium ratio was higher in spring primary foods than summer primary foods (Figure 4). In summer it was lowest in primary foods, and highest in non-food items. In spring it was lower in the non-food item than in any of the primary food items.

Calcium levels were similar in all items in summer (Figure 5). In spring, *P. tremuloides* had a much higher level of calcium than the other primary food *P. banksiana*. Magnesium levels were higher in primary foods than secondary or non-foods in both spring and summer (Figure 6). Summer levels were slightly higher than spring. Phosphorus levels were similar in spring and summer primary foods, and in spring were much higher than the non-food item (Figure 7). In summer, the phosphorus level was lowest in the secondary food item. The summer primary food item had a higher sulphur level than the spring primary food item

Figure 1. Protein content (percent of dry matter) in vegetation samples. See Table 1 for codes.

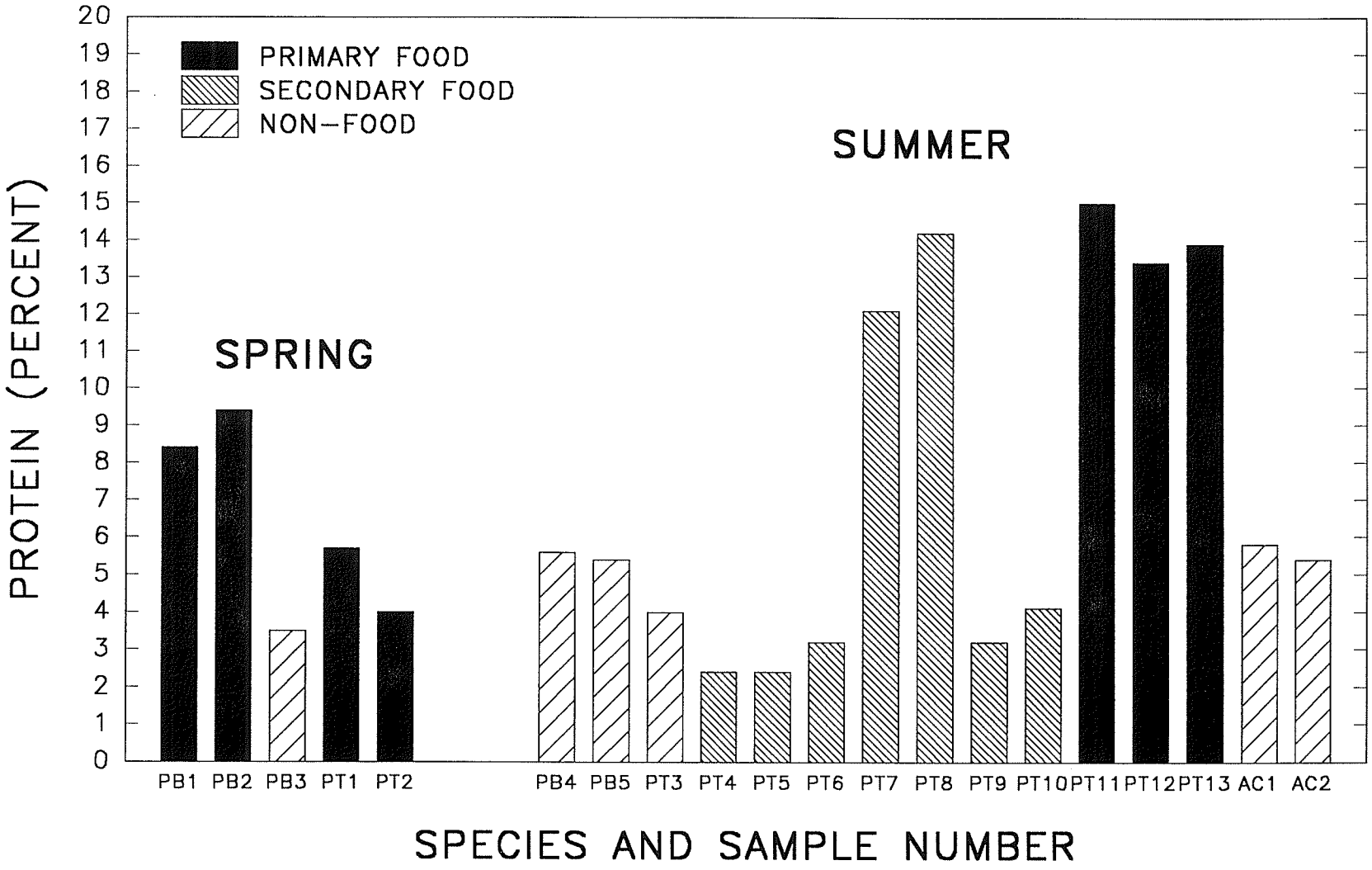

PRIMARY FOOD
SECONDARY FOOD
NON-FOOD
SUMMER
SPRING
PROTEIN (PERCENT)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
PB1 PB2 PB3 PT1 PT2 PB4 PB5 PT3 PT4 PT5 PT6 PT7 PT8 PT9 PT10 PT11 PT12 PT13 AC1 AC2
SPECIES AND SAMPLE NUMBER

Figure 2. Sodium content (percent of dry matter) in vegetation samples. See Table 1 for codes. ND = not discernible.

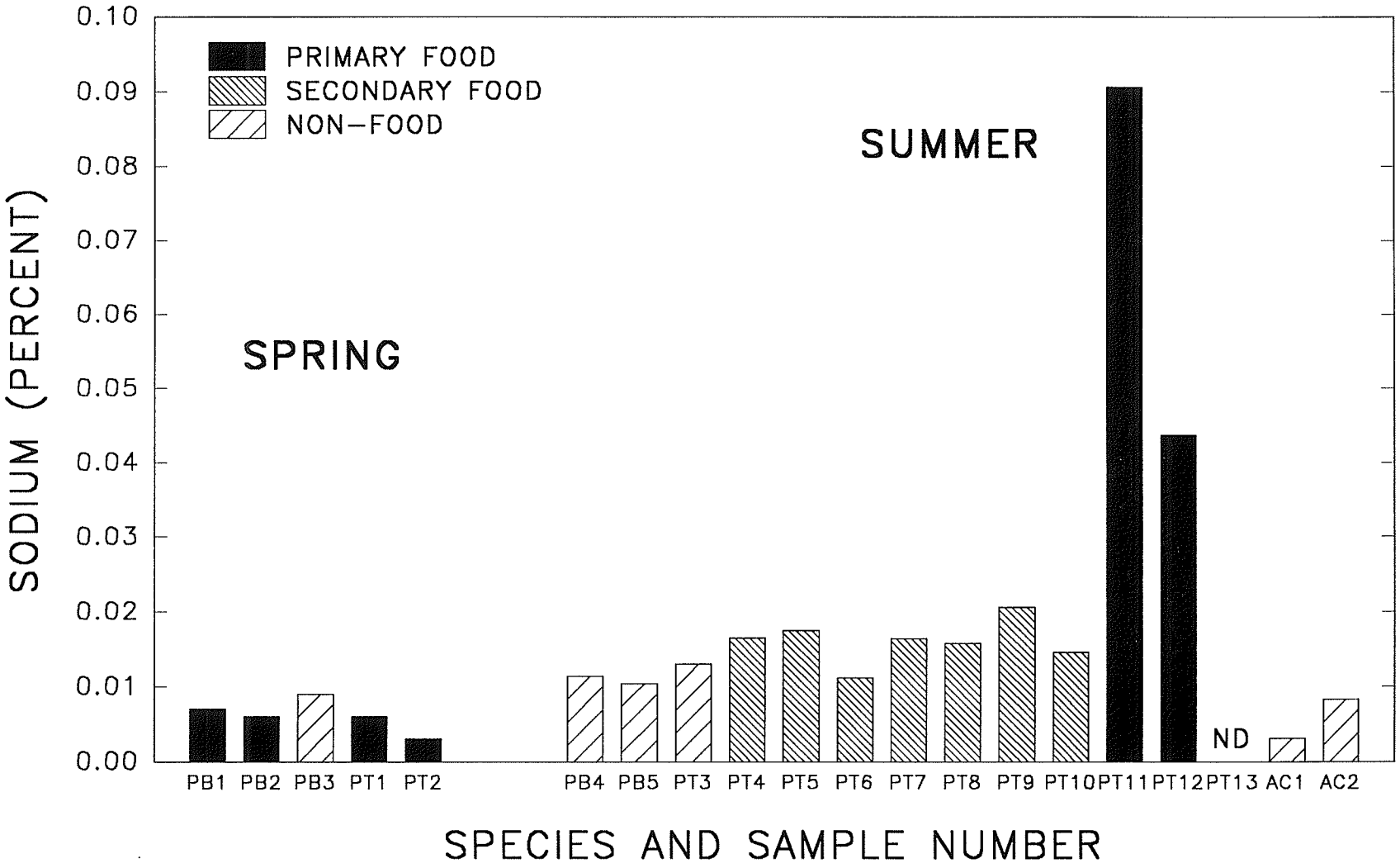

PRIMARY FOOD
SECONDARY FOOD
NON-FOOD
SUMMER
SPRING
SODIUM (PERCENT)
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
ND
PB1 PB2 PB3 PT1 PT2 PB4 PB5 PT3 PT4 PT5 PT6 PT7 PT8 PT9 PT10 PT11 PT12 PT13 AC1 AC2
SPECIES AND SAMPLE NUMBER

Figure 3 Potassium content (percent of dry matter) in vegetation samples. See Table 1 for codes.

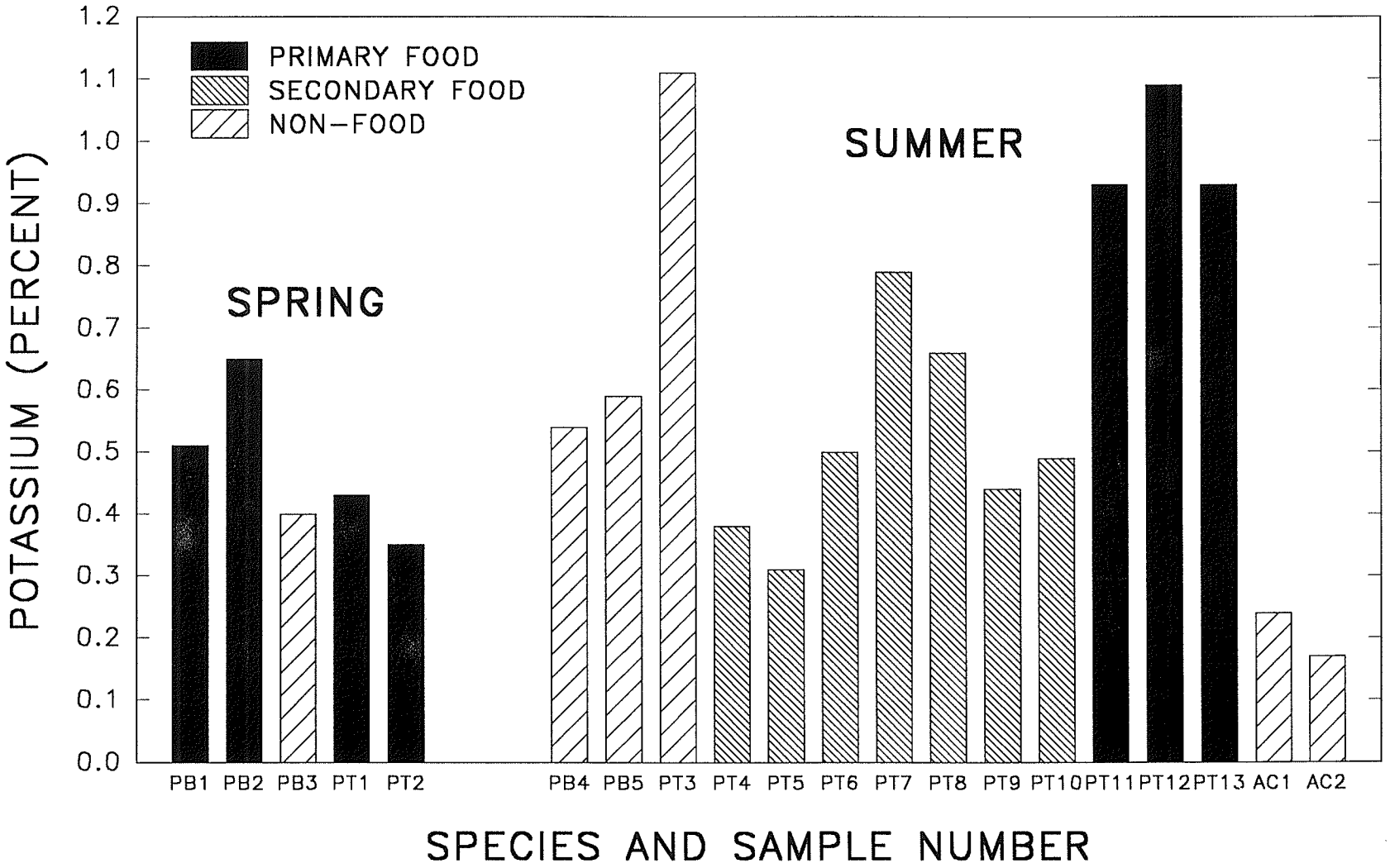

PRIMARY FOOD
SECONDARY FOOD
NON-FOOD
SPRING
SUMMER
POTASSIUM (PERCENT)
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
PB1 PB2 PB3 PT1 PT2 PB4 PB5 PT3 PT4 PT5 PT6 PT7 PT8 PT9 PT10 PT11 PT12 PT13 AC1 AC2
SPECIES AND SAMPLE NUMBER

Figure 4. Potassium to sodium ratio in vegetation samples. See Table 1 for codes. ND = not discernible due to sodium level not being discernible.

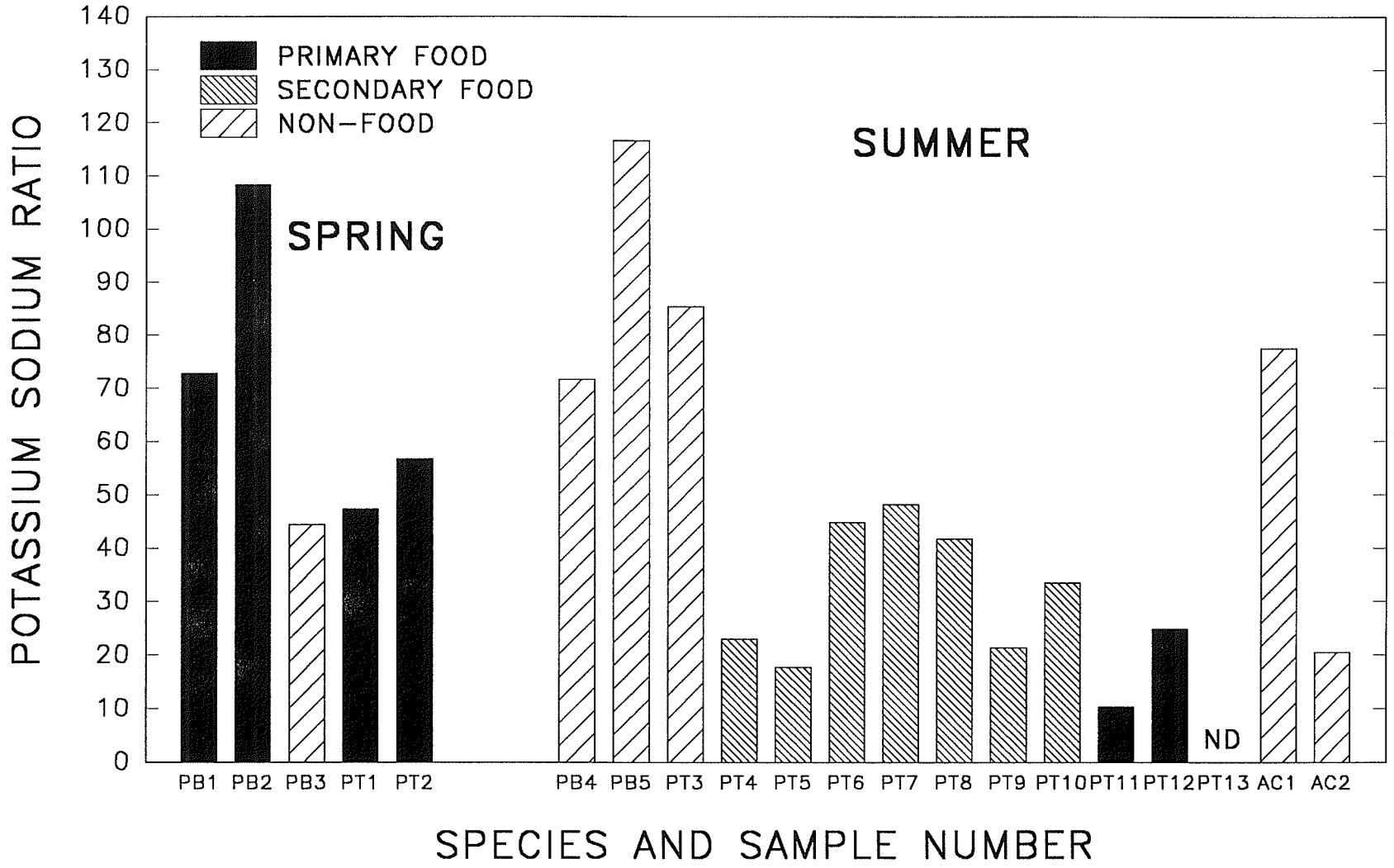

PRIMARY FOOD
SECONDARY FOOD
NON-FOOD
SPRING
SUMMER
POTASSIUM SODIUM RATIO
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
PB1 PB2 PB3 PT1 PT2 PB4 PB5 PT3 PT4 PT5 PT6 PT7 PT8 PT9 PT10 PT11 PT12 PT13 AC1 AC2
ND
SPECIES AND SAMPLE NUMBER

Figure 5. Calcium content (percent of dry matter) in vegetation samples. See Table 1 for codes.

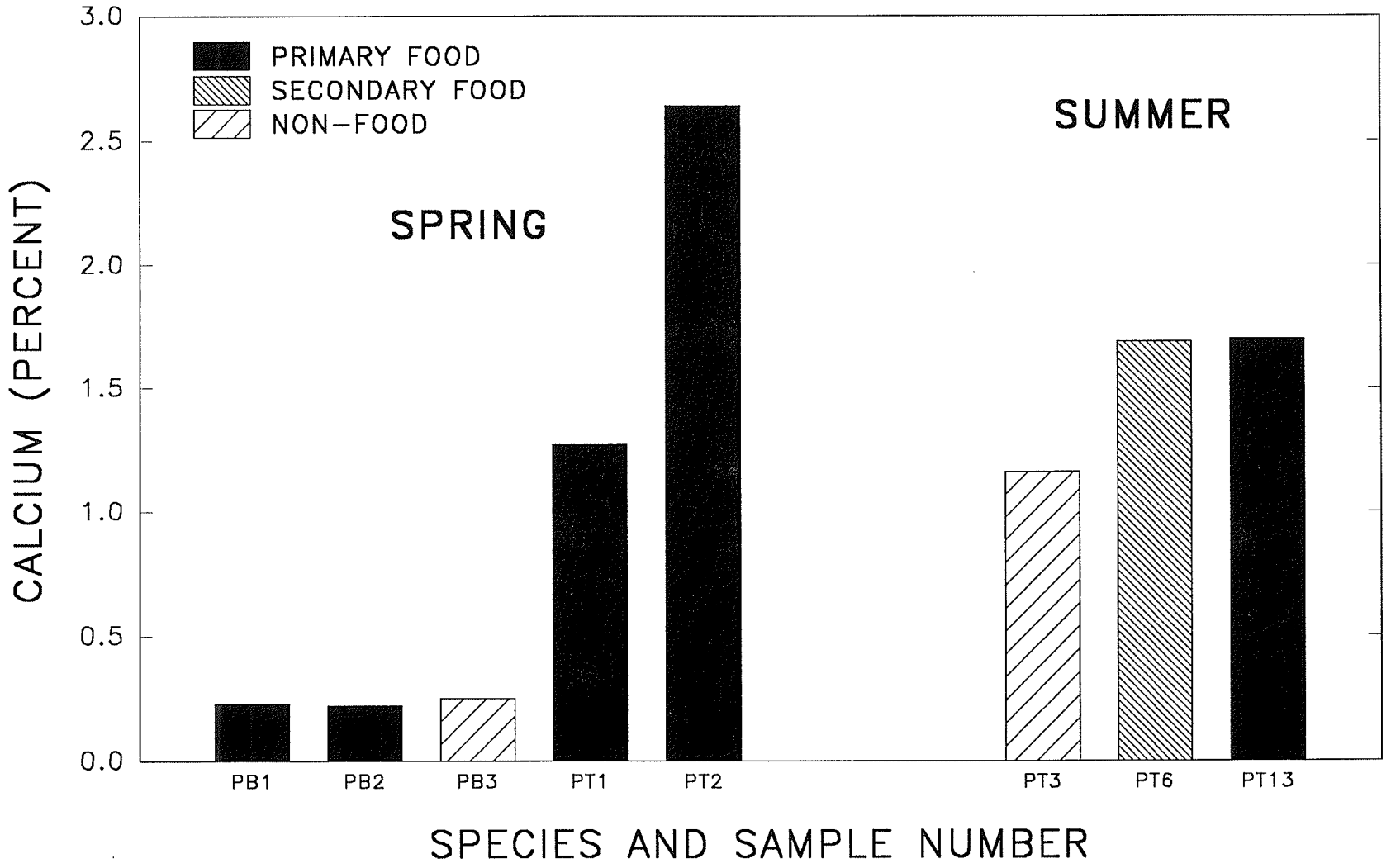

3.0
2.5
2.0
1.5
1.0
0.5
0.0
CALCIUM (PERCENT)
PRIMARY FOOD
SECONDARY FOOD
NON-FOOD
SPRING
SUMMER
PB1
PB2
PB3
PT1
PT2
PT3
PT6
PT13
SPECIES AND SAMPLE NUMBER

Figure 6. Magnesium content (percent of dry matter) in vegetation samples. See Table 1 for codes.

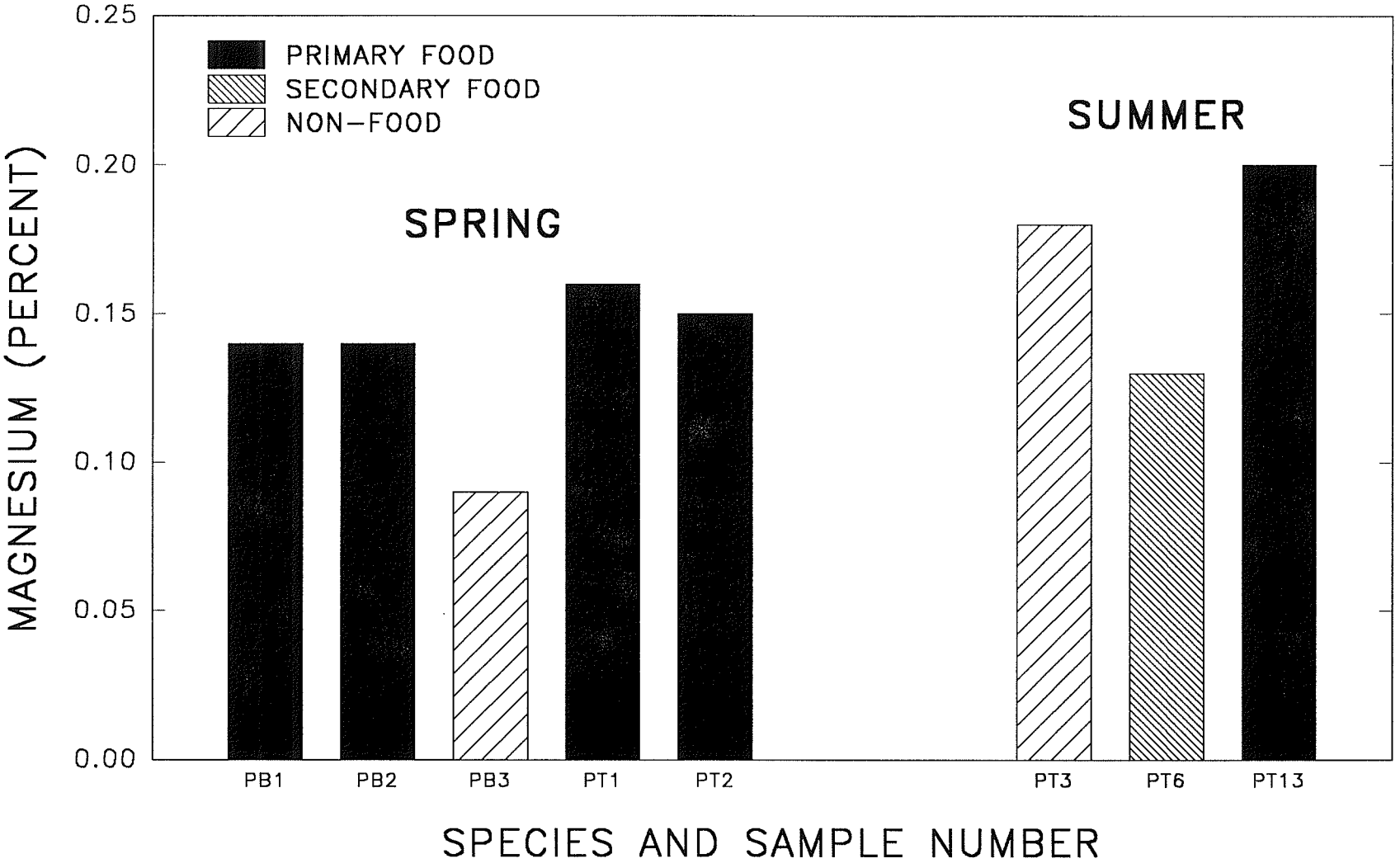
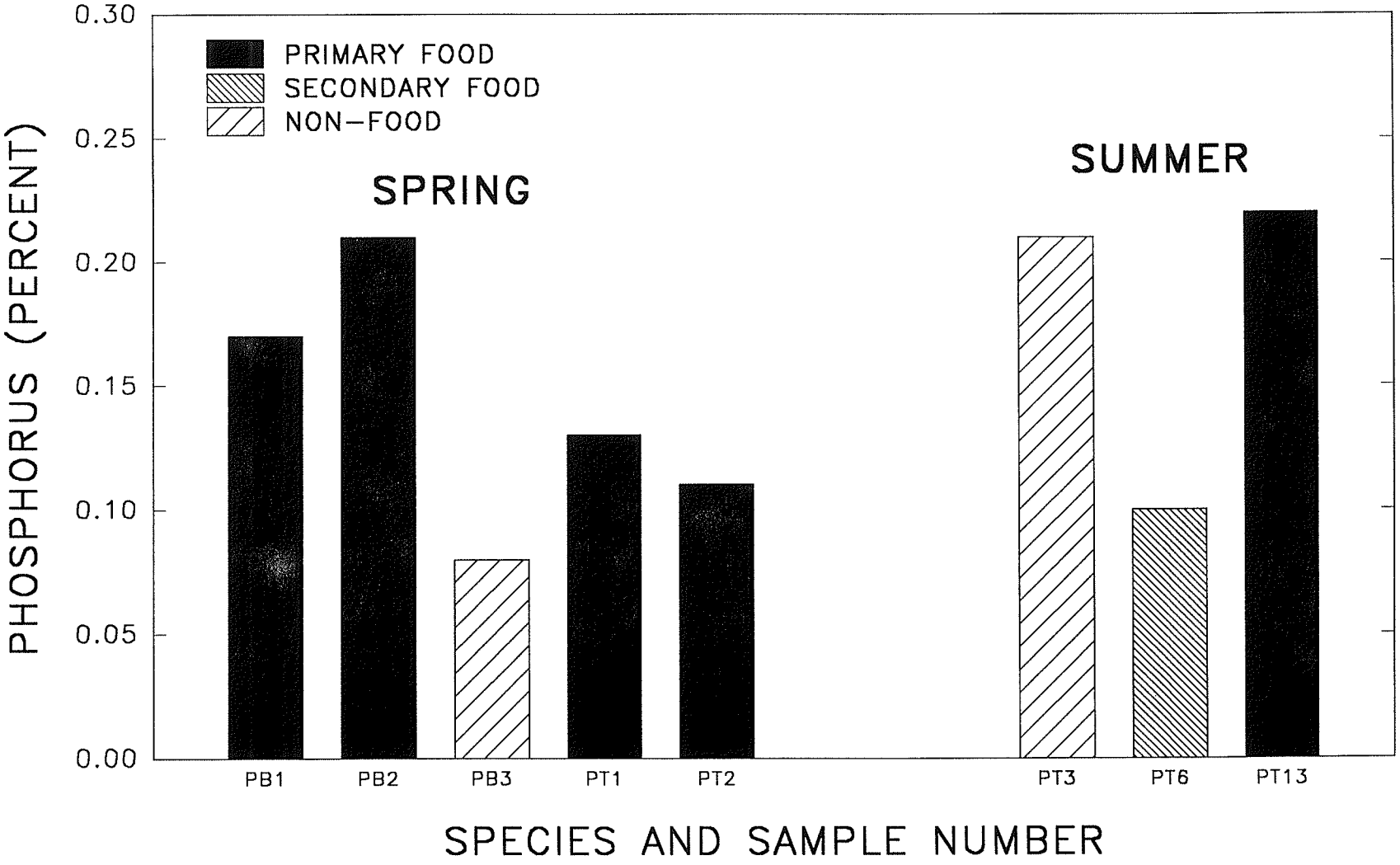

0.25
0.20
0.15
0.10
0.05
0.00
MAGNESIUM (PERCENT)
PRIMARY FOOD
SECONDARY FOOD
NON-FOOD
SPRING
SUMMER
PB1
PB2
PB3
PT1
PT2
PT3
PT6
PT13
SPECIES AND SAMPLE NUMBER

Figure 7. Phosphorus content (percent of dry matter) in vegetation samples. See Table 1 for codes.


PRIMARY FOOD
SECONDARY FOOD
NON–FOOD
SPRING
SUMMER
PHOSPHORUS (PERCENT)
0.30
0.25
0.20
0.15
0.10
0.05
0.00
PB1
PB2
PB3
PT1
PT2
PT3
PT6
PT13
SPECIES AND SAMPLE NUMBER

(Figure 8). In both seasons, primary food items had higher sulphur levels than secondary or non-food items.

Trace elements

Copper levels were higher in summer primary food items than spring primary food items (Figure 9). In spring, levels were similar in the primary food items to the non-food item. In summer, the level was higher in the primary food item than in the non-food or secondary food items. Iron levels were similar in spring and summer primary food items (Figure 10). In spring, the non-food item had higher levels of iron than the primary food items, whereas in summer they were similar, with the secondary food item being lower in iron.

Manganese levels were highest in the spring *P. banksiana* samples, and very low in the spring *P. tremuloides* samples (Figure 11). Summer levels were slightly higher in the non-food item than the primary food and lowest in the secondary food item. Zinc levels were highest in the spring *P. tremuloides* and lowest in the spring *P. banksiana* (Figure 12). Zinc levels were similar in all summer samples.

Figure 8. Sulfur content (percent of dry matter) in vegetation samples. See Table 1 for codes.

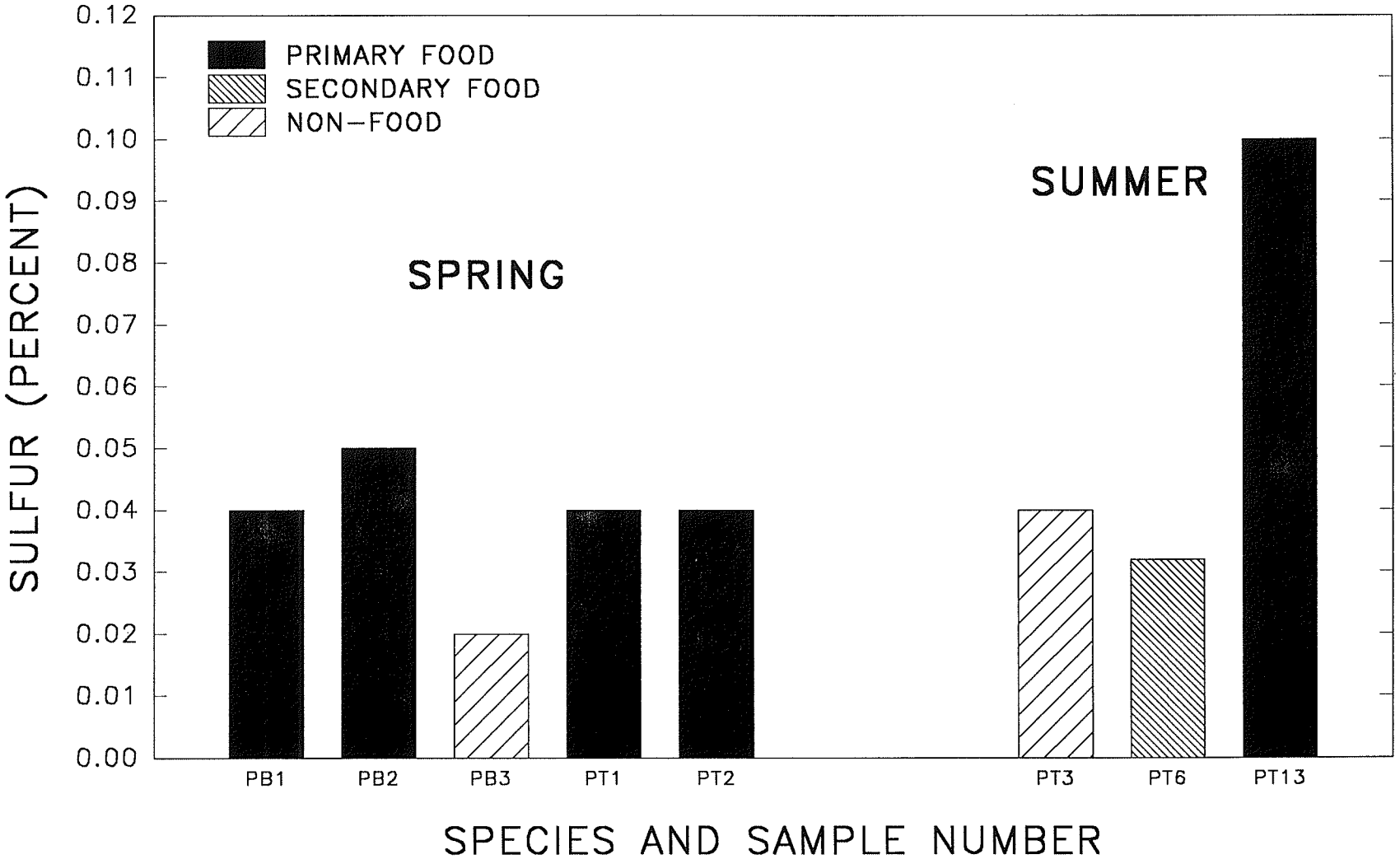

PRIMARY FOOD
SECONDARY FOOD
NON-FOOD
SUMMER
SPRING
SULFUR (PERCENT)
0.12
0.11
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
PB1
PB2
PB3
PT1
PT2
PT3
PT6
PT13
SPECIES AND SAMPLE NUMBER

Figure 9. Copper content (parts per million) in vegetation samples. See Table 1 for codes.

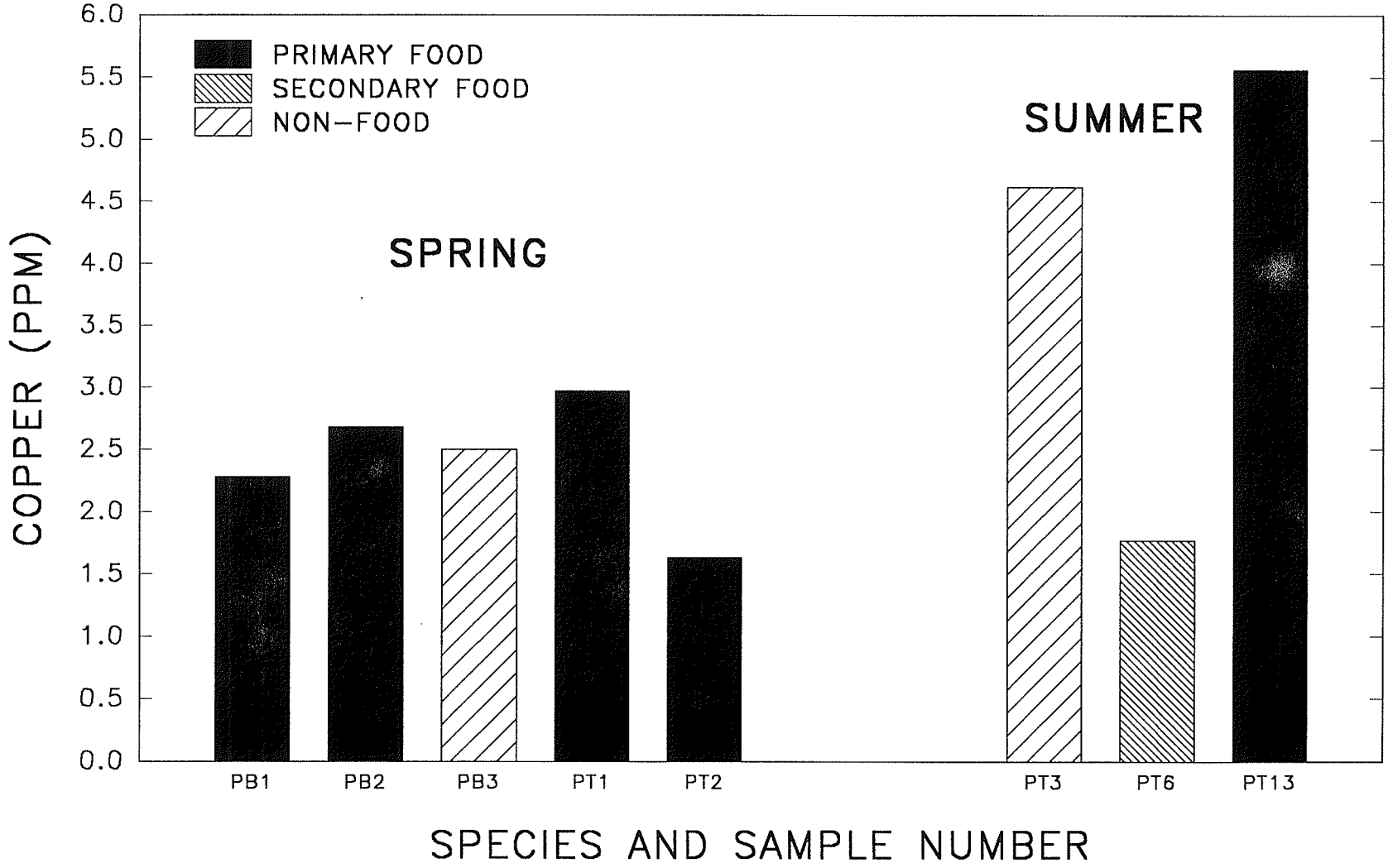

6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
COPPER (PPM)
PRIMARY FOOD
SECONDARY FOOD
NON–FOOD
SPRING
SUMMER
PB1
PB2
PB3
PT1
PT2
PT3
PT6
PT13
SPECIES AND SAMPLE NUMBER

Figure 10. Iron content (parts per million) in vegetation samples. See Table 1 for codes.

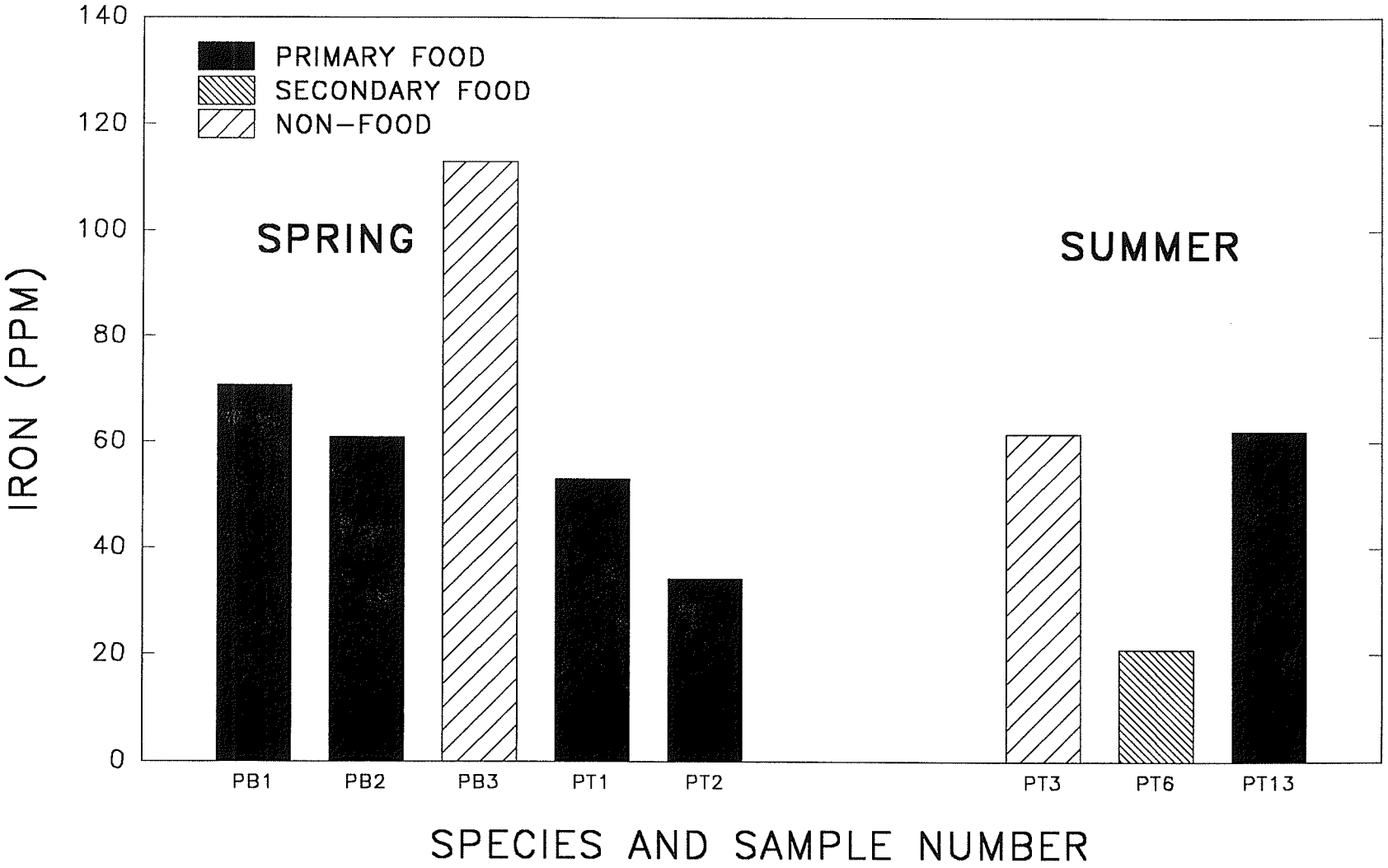

140
120
100
80
60
40
20
0
IRON (PPM)
PRIMARY FOOD
SECONDARY FOOD
NON–FOOD
SPRING
SUMMER
PB1
PB2
PB3
PT1
PT2
PT3
PT6
PT13
SPECIES AND SAMPLE NUMBER

Figure 11. Manganese content (parts per million) in vegetation samples. See Table 1 for codes.

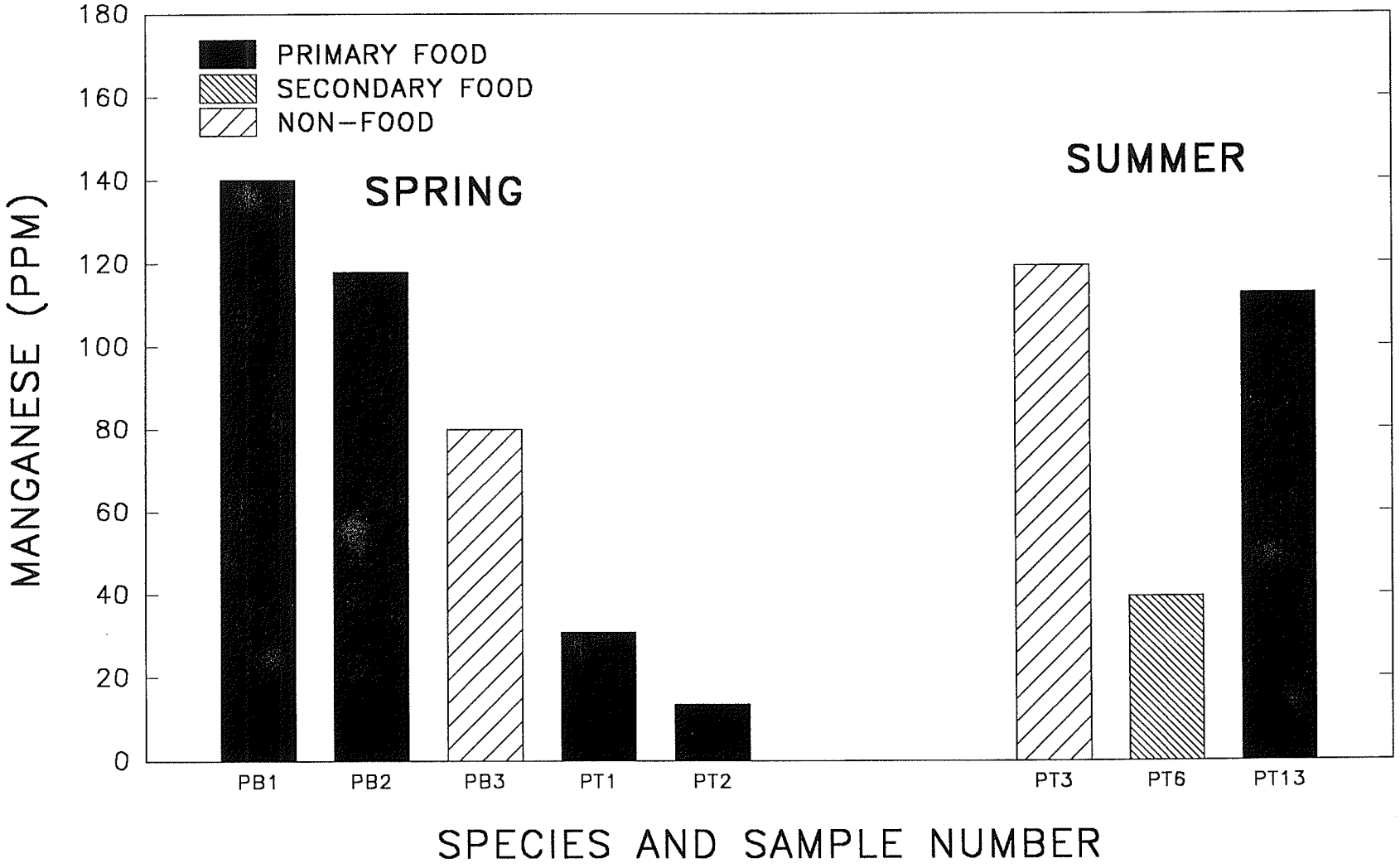
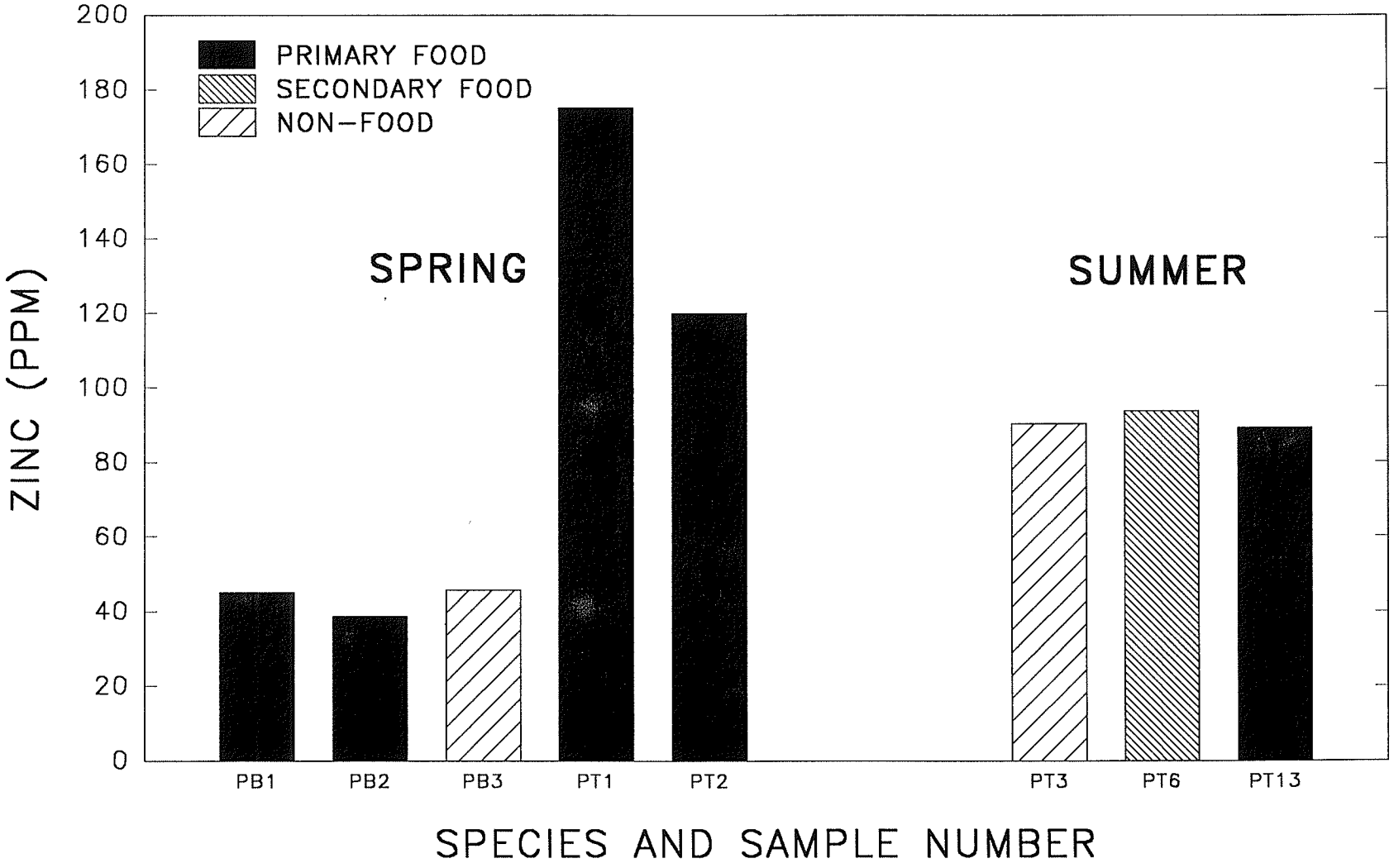

PRIMARY FOOD
SECONDARY FOOD
NON-FOOD
SPRING
SUMMER
MANGANESE (PPM)
180
160
140
120
100
80
60
40
20
0
PB1
PB2
PB3
PT1
PT2
PT3
PT6
PT13
SPECIES AND SAMPLE NUMBER

Figure 12. Zinc content (parts per million) in vegetation samples. See Table 1 for codes.


200
180
160
140
120
100
80
60
40
20
0
ZINC (PPM)
PRIMARY FOOD
SECONDARY FOOD
NON-FOOD
SPRING
SUMMER
PB1
PB2
PB3
PT1
PT2
PT3
PT6
PT13
SPECIES AND SAMPLE NUMBER

DISCUSSION

SEASONAL PREFERENCES

P. tremuloides was the food of choice when it was available. This was supplemented by *P. banksiana* in spring but not in summer. *P. tremuloides* is also the food of choice by beavers in other areas, but most authors report it being replaced by aquatic vegetation in the summer months. While Seton (1909) asserted that beavers never consumed any conifer species, Hall (1960) reported use of *Abies* spp. bark, and Northcott (1971) noted the use of conifers in the foodpile. Jenkins (1979; 1981) describes the use of *Pinus* sp. in spring and theorizes that it may be an important source of stored nutrients or a source of secondary compounds for castoreum. Since construction of scent mounds by beavers is much greater in spring (Butler and Butler 1979; Brady and Svendsen 1981), this may be a consideration. However, the protein level of *P. banksiana* is almost double that of *P. tremuloides*, the other food of choice in spring. Spring is a time of year when high protein intake would likely be sought as movement begins again after the winter. In summer, the equivalent parts of *P. banksiana* are much lower in protein than other choices available. Therefore, *P. banksiana* may be selected in spring because it is the highest source of protein for beavers at that time. However, it apparently cannot supply all requirements, since *P. tremuloides* is still consumed. *P. tremuloides* has a much higher level of calcium than the *P. banksiana* and also has a lower potassium to sodium ratio. Calcium may be an important requirement in spring especially for pregnant and lactating females.

Preference within *P. tremuloides* was for the leaves and secondarily the bark and twigs. The petioles were avoided. Roze (1989) similarly reported that porcupines (*Erethizon dorsatum*) eat only the leaves and avoid the petioles. Other authors have reported a preference

for the herbaceous parts of trees over the woody vegetation (Aleksiuk 1970; 1977; Svendsen 1980; Jenkins 1981). The petioles (PT3) are low in protein and sodium and high in potassium. Levels of other minerals are not widely disparate between the primary and secondary food items. The implications of the high potassium to sodium ratio will be discussed below.

Contrary to the results of many other studies (Green 1936; Tevis 1950; Parovshchikov 1961; Brenner 1962; Northcott 1971; Belovsky 1984), I did not find aquatic plants to be an important part of the diet of the beavers in my study area. Aleksiuk (1970) does not report any use of aquatic plants in the Mackenzie Delta region, so use of aquatic plants may be the result of latitudinal differences. Bradt (1938) reports use of aquatics but also the inclusion of some *Populus* spp. bark.

Food harvesting sites were located much closer to the lodge in the fall than in summer. In summer beaver cut trees on land and haul the stems back to the water's edge for consumption. Except when they are conveying food to kits in the lodge, food is not transported to the lodge. In fall, most of the items harvested are placed in the foodpile. Consequently, the habit of not cutting food near the lodge in summer, but harvesting from the lodge area in fall appears to be an energy conservation measure. Similar patterns of energy conservation have been demonstrated in studies of size distance relationships in beaver food choice (Schoener 1979; Jenkins 1980; Pinkowski 1983; Belovsky 1984; McGinley and Whitham 1985; Fryxell and Doucet 1991; 1993; Fryxell 1992). Jenkins (1981) also reported seasonal variation in feeding sites and linked this to different species preferences or to differences in seasonal accessibility of sites.

NUTRIENTS

Nutrient requirements of beavers are not known and probably vary with age, sex, season and reproductive condition (Robbins 1993). However, Robbins (1993) gives values for several members of the Rodentia. These ranges of values will be used as indicators of the adequacy of the beavers' diet. Many of the minerals interact and high levels of one mineral may impede the uptake of another mineral (Roze 1989; Robbins 1993). Water is one of the most important essential nutrients (Robbins 1993), but this is not a difficult requirement for a semi-aquatic animal to meet.

Protein

Browsers, in general, require about 6 % protein in their diet, the exact requirements depend on amino acid composition of the protein (Robbins 1993). In this study, the summer primary food and some summer secondary foods easily surpassed this level. In spring, the *P. tremuloides* samples were slightly below this level, but the *P. banksiana samples* exceeded the 6 % level. Preferred foods appeared to be generally higher in protein than less preferred or non-foods. These protein values are similar to values for comparable plant parts determined by Cowan *et al.* (1950) and Roze (1989). Protein is essential for growth and all other aspects of life and is the only nutrient in this study which is consistently more concentrated in primary foods than non-foods. Aleksiuk (1970) also found that beavers used higher protein foods such as *Salix* spp. leaves when available, which would lead to the most rapid growth possible. In my study area all growth must take place in less than six months of the year, therefore maximizing protein intake in summer in order to maximize growth would seem to be adaptive.

Macroelements

Macroelements are those which can be measured on a milligram per gram (or percent) basis. The requirements for sodium are 0.05 to 0.15 % of diet and for potassium are 0.3 to 0.6 % of diet. All primary foods surpassed these levels in summer but did not meet the sodium requirement in spring. The non-discernible sodium in sample PT13 was most likely the result of high rainfall in the summer of 1993 and consequent leaching of sodium from the leaves and soil (Roze 1989; Robbins 1993). While both sodium and potassium levels were high in preferred foods in summer, the potassium/sodium ratio was low. High levels of potassium may reduce the availability and retention of sodium (Robbins 1993). Beavers may select for a lower potassium to sodium ratio, which will in turn give them higher sodium intake. Spring is a time of sodium stress for most herbivores (Roze 1989; Robbins 1993). Aquatic vegetation has been shown to have much higher sodium levels than terrestrial vegetation (Belovsky and Jordan 1981; Roze 1989; Robbins 1993). The lack of use of aquatics may be due to lack of availability. Because of the length of winter in my study area, development of aquatic plants does not occur until about the same time as leaf-out of deciduous trees. Aquatics are therefore not available at the time when they would seem to be most needed. Other possible factors affecting selection of aquatics will be discussed later. However Schmidt-Nielsen and O'Dell (1961) showed that beaver urine is very low in solutes, and therefore beavers may have low sodium losses through excretion, and therefore lower requirements for sodium.

Requirements for the other macroelements I examined are given as 0.04 to 0.3 % magnesium (for rodents) and 0.4 t0 1.2 % calcium and 0.3 to 0.6 % phosphorus (generally for animals) (Robbins 1993). No values are given for requirements for sulphur. All foods and non-foods met or exceeded requirements for magnesium, while all were below the standard

for phosphorus, though primary foods tended to be higher than secondary or non-foods. Calcium levels were sufficient in all summer vegetation, but were only met by *P. tremuloides* in spring. Notably, there is a great deal of site variation in the calcium level for the spring *P. tremuloides* bark. Jenkins (1975; 1978) has also suggested variation in nutritional and chemical values between sites, and suggests that this is the reason for sampling behaviour he observed. Sulphur levels were higher in primary foods than secondary or non-foods.

Trace Elements

Trace elements are those that are required in only trace amounts and recorded in parts per million. Rodent requirements for trace elements are given by Robbins (1993) as: copper 1.6 to 6 ppm; iron 25 to 140 ppm; manganese 3.7 to 50 ppm; and zinc 9.2 to 30 ppm. Copper levels in primary foods just exceeded the minimum in spring, but easily met these requirements in summer. All primary food items surpassed the minimum iron levels, but none were extremely high in iron. Manganese levels were satisfactory in all the vegetation, but distinctly higher in *P. banksiana* in the spring. Conversely, zinc was found in much higher concentration in *P. tremuloides* in spring, although all vegetation met the minimum required levels. The values I found for copper and zinc are similar to those reported in foods of *Castor fiber* in Russia, but lower than values reported for manganese (Vasilkov and Golodushko 1971).

Energy and other aspects

One component of the vegetation that I did not specifically measure was energy content of the samples because facilities were not available to measure calorific content. Cowan *et al.* (1955) determined that beavers required 35 to 45 Calories of digestible energy per pound

of body weight per day. This equates to about 650 g of *P. tremuloides* or 775 g of *Salix* spp. for an 11.5 kg beaver (Cowan *et al.* 1955). In my study area vegetation was abundant, and it is doubtful that beavers had any difficulties meeting these requirements. As indicated earlier, beavers in an area with limited access to food for part of the year should be maximizing their protein intake to maximize growth. They would also be expected to maximize energy intake and deposit fat stores while energy is abundant (Aleksiuk and Cowan 1969; Aleksiuk 1970). Some of the secondary foods examined, while being low in most nutrients, may be higher in energy and therefore selected for this factor.

Approximately 93 % of energy available from *P. tremuloides* is digestible, while only 44 % of that available from water lilies (*Nuphar* spp.) is digestible (Doucet and Fryxell 1993). Similarly 100 % of protein in aspen is digestible, while only 42 % of that in water lilies is digestible (Doucet and Fryxell 1993). So although water lilies are much higher in protein and similar in energy to *P. tremuloides* (Doucet and Fryxell 1993), the much lower digestibility consequently lowers the real protein and energy content of the water lily. If protein intake is being maximized in order to maximize growth, as discussed earlier, then the water lily should be less favoured. In regions of North America where the open water season is longer, optimizing protein and energy intake over a short period of time is not so crucial. In those areas the advantages of using aquatic foods, including predator avoidance, may outweigh the lower digestibility.

Other factors may also play a role in determining which items are selected by beavers. Basey *et al.* (1988; 1990) discovered the presence of a phenolic compound in juvenile growth forms of *Populus* spp.. This compound was a response by the plants to beaver cutting, and was sufficient to deter beavers from selecting the juvenile growth. Plants frequently have chemical defenses which may reduce forage quality

(Lindroth and Batzli 1986), and Feeny (1970) has reported a similar interaction between moth caterpillars and oak leaves.

CONCLUSIONS

Both H_o1 and H_o2 were disproved. Beavers in the taiga appeared to have preferences for certain vegetation types which varied seasonally. Nutrient composition differed among vegetation types. Doucet and Fryxell (1993) found no correlation between the proportion of each forage species consumed and any single nutrient parameter. As discussed here, there are probably many interacting requirements that must be met for beavers. For beavers in the taiga, the essential food requirements appear to be protein, with a moderate potassium to sodium ratio in the food. Beavers appear to be selective in choosing the species and parts of trees they consume, selecting *P. tremuloides* in the spring and summer and supplementing with *P. banksiana* in the spring. This selection and the selection of leaves over other tree parts serves to maximize protein intake. Most other nutrients are in sufficient quantity in most of the vegetation available, and therefore do not appear to be selected for or against.

These results are the product of preliminary work. The samples have limited replication, and therefore no statistical analysis can be undertaken. However, they do provide us with an indicator of the levels of nutrients in beaver food in the taiga, and the types of nutrients beavers may be seeking in their food. More work is needed in my study area and in other areas to determine if beavers select foods differently in areas with different seasonal constraints.

LITERATURE CITED

Aldous, S.E. 1938. Beaver food utilization studies. Journal of Wildlife Management 2:215-222.

Aleksiuk, M. 1970. The seasonal food regime of arctic beavers. Ecology 51:264-270.

Aleksiuk, M. 1977. Diets (natural and synthetic): Castoridae. In M. Recheigl, Jr. (Ed.) Diets for Mammals, Vol. 1, CRC Press, Cleveland, pp.89-92.

Aleksiuk, M. and I.McT. Cowan. 1969. Aspects of seasonal energy expenditure in the beaver (*Castor canadensis* Kuhl) at the northern limit of its distribution. Canadian Journal of Zoology 47:471-481.

Atwood, E.L., Jr. 1938. Some observations on adaptability of Michigan beavers released in Missouri. Journal of Wildlife Management 2:165-166.

Basey, J.M., S.H. Jenkins and P.E. Busher. 1988. Optimal central-place foraging by beavers: Tree-size selection in relation to defensive chemicals of quaking aspen. Oecologia 76:278-282.

Basey, J.M., S.H. Jenkins and G.C. Miller. 1990. Food selection by beavers in relation to inducible defenses of *Populus tremuloides*. Oikos 59:57-62.

Belovsky, G.E. 1984. Summer diet optimization by beaver. American Midland Naturalist 111:209-222.

Belovsky, G.E. and P.A. Jordan. 1981. Sodium dynamics and adaptations of a moose population. Journal of Mammalogy 62:613-621.

Bradt, G.W. 1938. A study of beaver colonies in Michigan. Journal of Mammalogy 19:139-162.

Brady, C.A. and G.E. Svendsen. 1981. Social behaviour in a family of beaver, *Castor canadensis*. Biology of Behaviour 6:99-114.

Brenner, F.J. 1962. Foods consumed by beavers in Crawford County, Pennsylvania. Journal of Wildlife Management 26:104-107.

Butler, R.G. and L.A. Butler. 1979. Toward a functional interpretation of scent marking in beaver (*Castor canadensis*). Behavioral and Neural Biology 26:442-454.

Cowan, I.McT., W.S. Hoar and J. Hatter. 1950. The effect of forest succession upon the quantity and upon the nutritive values of woody plants used as food by moose. Canadian Journal of Research 28D:249-271.

Cowan, I.McT., A.J. Wood and W.D. Kitts. 1955. Feed requirements of deer, beaver, bear and mink for growth and maintenance. Twenty-second North American Wildlife Conference 179-188.

Doucet, C.M. and J.M. Fryxell. 1993. The effect of nutritional quality on forage preference by beavers. Oikos 67:201-208.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51:566-581.

Fryxell, J.M. 1992. Space use by beavers in relation to resource abundance. Oikos 64:474-478.

Fryxell, J.M. and C.M. Doucet. 1991. Provisioning time and central-place foraging in beavers. Canadian Journal of Zoology 69:1308-1313.

Fryxell, J.M. and C.M. Doucet. 1993. Diet choice and the functional response of beavers. Ecology 74:1297-1306.

Gese, E.C. and A.R. Shadle. 1943. Reforestation of aspen after complete cutting by beavers. Journal of Wildlife Management 7:223-228.

Green, H.U. 1936. The beaver of the Riding Mountain, Manitoba: An ecological study and commentary. Canadian Field-Naturalist 50:1-8, 21-23, 36-50, 61-67, 85-92.

Hall, J.G. 1960. Willow and aspen in the ecology of beaver on Sagehen Creek, California. Ecology 41:484-494.

Jenkins, S.H. 1975. Food selection by beavers: A multidimensional contingency table analysis. Oecologia 21:157-173.

Jenkins, S.H. 1978. Food selection by beavers: sampling behavior. Breviora 447:1-8.

Jenkins, S.H. 1979. Seasonal and year-to-year differences in food selection by beavers. Oecologia 44:112-116.

Jenkins, S.H. 1980. A size-distance relation in food selection by beavers. Ecology 61:740-746.

Jenkins, S.H. 1981. Problems, progress, and prospects in studies of food selection by beavers. Proceedings of the Worldwide Furbearer Conference 1:559-579.

Jenkins, S.H. and P.E. Busher. 1979. *Castor canadensis*. Mammalian Species 120:1-8.

Lindroth, R.L. and G.O. Batzli. 1986. Inducible plant chemical defences: a cause of vole population cycles? Journal of Animal Ecology 55:431-449.

McGinley, M.A. and T.G. Whitham. 1985. Central place foraging by beavers (*Castor canadensis*): a test of foraging predictions and the impact of selective feeding on the growth form of cottonwoods (*Populus fremontii*). Oecologia 66:558-562.

Northcott, T.H. 1971. Feeding habits of beaver in Newfoundland. Oikos 22:407-410.

Novakowski, N.S. 1967. The winter bioenergetics of a beaver population in northern latitudes. Canadian Journal of Zoology 45:1107-1118.

Parovshchikov, V.Ya. 1961. Foods of beavers near Archangelsk. (In Russian with English summary) Zoologicheski Zhurnal XL:623-624.

Pinkowski, B. 1983. Foraging behavior of beavers (*Castor canadensis*) in North Dakota. Journal of Mammalogy 64:312-314.

Robbins, C.T. 1993. Wildlife Feeding and Nutrition. San Diego, Academic Press.

Roze, U. 1989. The North American Porcupine. Washington D.C.: Smithsonian Institution Press.

Schmidt-Nielsen, B. and R. O'Dell. 1961. Structure and concentrating mechanism in the mammalian kidney. American Journal of Physiology 200:1119-1124.

Schoener, T.W. 1979. Generality of the size-distance relation in models of optimal feeding. American Naturalist 114:902-914.

Seton, E.T. 1909. Life Histories of Northern Animals. Charles Scribner's Sons, New York.

Shadle, A.R., A.M. Nauth, E.C. Gese and T.S. Austin. 1943. Comparison of tree cuttings of six beaver colonies in Allegany State Park, New York. Journal of Mammalogy 24:32-39.

Slough, B.G. 1978. Beaver food cache structure and utilization. Journal of Wildlife Management 42:644-646.

Svendsen, G.E. 1980. Seasonal change in feeding patterns of beaver in southeastern Ohio. Journal of Wildlife Management 44:285-290.

Tevis, L., Jr. 1950. Summer behavior of a family of beavers in New York State. Journal of Mammalogy 31:40-65.

Vasilkov, V.V. and B.Z. Golodushko. 1971. The contents of some microelements in the willow bark in beaver lands along the Dnieper. Doklady Akademii nauk BSSR 15:944-946. (In Russian)