1

of/de

1

PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT

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

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

Canada

VARIATION IN RACCOON AND SKUNK ABUNDANCE ALONG AN
AGRICULTURAL INTENSITY GRADIENT ACROSS TWO SPATIAL SCALES

JOHN H. PEDLAR, B.Sc.

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfilment
of the requirements for the degree of

Master of Science

Department of Biology
Carleton University
Ottawa, Ontario
January 16, 1995

©copyright
1995, John Harvey Pedlar

National Library
of Canada

Bibliothèque nationale
du Canada

Acquisitions and
Bibliographic Services Branch

Direction des acquisitions et
des services bibliographiques

395 Wellington Street
Ottawa, Ontario
K1A 0N4

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 0-315-98648-4

Canada

Name John Harvey PEDLAR

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.

Ecology

SUBJECT TERM

0329

U-M-I

SUBJECT CODE

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 0577
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
Polynology 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

The undersigned hereby recommend to
the Faculty of Graduate Studies and Research
acceptance of the thesis,

"Variation in raccoon and skunk abundance along an agricultural
intensity gradient across two spatial scales"

submitted by

JOHN HARVEY PEDLAR, B.Sc.

in partial fulfilment of the requirements
for the degree of Master of Science

Chair, Department of Biology

Thesis Supervisor

Thesis Supervisor

Carleton University

ABSTRACT

Raccoon and skunk abundance was monitored at tracking stations placed at 57 sites that fell along a gradient of agricultural intensity. Neither species exhibited a significant relationship with agricultural intensity when it was calculated as the amount of cultural energy input required to produce the crop mosaic in an agricultural landscape. However, raccoons exhibited a quadratic relationship when agricultural intensity was measured as percent wooded cover. Raccoon abundance was high in landscapes with mid to low amounts of wooded cover, particularly within wooded habitats. A more detailed cross-scale analysis of raccoon habitat use found that raccoons were most abundant: 1) in the near vicinity of woody vegetation species that are associated with fencerows and deciduous stands, 2) in landscapes with an extensive length of agricultural edge and 3) within wooded habitats in landscapes with extensive corn cover. Skunks showed a negative relationship with the amount of wooded cover in the landscape, and visited tracking stations located within open habitats and fencerows more often than stations located within wooded habitats. Both species appear to benefit from human alterations to the landscape. This phenomenon is discussed in the context of overabundant native species.

ACKNOWLEDGEMENTS

I would first like to thank my supervisors, Dr Lenore Fahrig and Dr Gray Merriam, for providing advice and guidance, and most importantly for encouraging me to think for myself. Thanks also go to my other committee member, Dr David Currie, who provided helpful suggestions when called upon. Dave Omond was a great help in preparing for my field season and Julie Cressman assisted in the 'dirty work' of animal tracking. Everyone in 'the lab' helped make my stay enjoyable - Ron Fritz, Brett Goodwin, Kringen Henein, Monica Mather, Andy McAllister, Shealagh Pope, Phil Taylor, Kurtis Trczinski, Lisa Venier and John Wegner provided useful advice at various stages in this project. Dr Leonard Lefkovitch provided statistical guidance. My work would not have been possible without the kind landowners who allowed me to use their property. Finally, I would like to thank my family and good friends in Meaford, Ontario, who were a constant source of support and inspiration.

Financial support was provided by Natural Sciences and Engineering Research Council (NSERC) operating grants to Dr H. G. Merriam and Dr L. Fahrig and an NSERC Postgraduate Scholarship to J. Pedlar.

TABLE OF CONTENTS

	<u>Page</u>
Abstract	ii
Acknowledgements	iii
Table of Contents	iv
List of Tables	v
List of Figures	vii
List of Appendices	viii
 GENERAL INTRODUCTION	 1
 CHAPTER 1: Variation in raccoon and skunk abundance along an agricultural intensity gradient	 4
Introduction	4
Methods	6
Results	14
Discussion	26
 CHAPTER 2: A scale-specific analysis of raccoon habitat use	 36
Introduction	36
Methods	38
Results	42
Discussion	48
 GENERAL DISCUSSION	 54
 APPENDICES	 58
 REFERENCES	 60

LIST OF TABLES

	Page
Table 1.1 Values used to convert areal crop measures to cultural energy measures.	11
Table 1.2 Data from 114 tracking stations placed into non-cultivated habitats along an agricultural intensity gradient.	15
Table 1.3 Poisson regression relating the number of weeks that raccoon and skunk tracks were identified at tracking stations to the amount of cultural energy required to produce the crops in a 1 km radius around the midpoint between the two stations at each site.	20
Table 1.4 Poisson regression relating the number of weeks that raccoon and skunk tracks were identified at tracking stations to percent wooded cover in a 1 km radius around the midpoint between the two stations at each site.	21
Table 1.5 Poisson regression relating the number of weeks that raccoon tracks were identified at tracking stations to percent wooded cover in 1 km radius around the midpoint between the two stations at each site and local habitat features measured in a 50 m radius around each station.	22
Table 1.6 Amount of deviance explained by the three best fit Poisson regression lines for the relationship between the number of raccoon track station visits and landscape level wooded cover when the data was broken down by local habitat type.	23
Table 1.7 Poisson regression relating the number of weeks that skunk tracks were identified at tracking stations to percent wooded cover in 1 km radius around the midpoint between the two stations at each site and local habitat features measured in a 50 m radius around each trap.	27
Table 2.1 Poisson regression relating the number of weeks that raccoon tracks were identified at tracking stations to woody vegetation features measured in a circle with 10 m radius around each station.	43

List of tables (continued)

	Page
Table 2.2 Poisson regression relating the number of weeks that raccoon tracks were identified at tracking stations to landscape features measured in a 1 km radius circle around the two stations at a site.	44
Table 2.3 Poisson regression relating the number of weeks that raccoon tracks were identified at tracking stations, to woody vegetation features measured in a circle with 10 m radius around each station and landscape features measured in a 1 km radius circle around the two stations at a site.	47

LIST OF FIGURES

	Page
Figure 1.1 Distribution of sites with respect to the percentage of wooded cover in a 1 km radius around the midpoint between the two tracking stations at a site. Sites were chosen in an attempt to obtain equal frequencies of a wide range of wooded cover.	16
Figure 1.2 Distribution of sites with respect to the percentage of cultural energy input required to produce the crops in a 1 km radius around the midpoint between the two tracking stations at a site. Sites were chosen in an attempt to obtain equal frequencies of a wide range of cultural energy inputs.	17
Figure 1.3 Relationship between the two measures of agricultural intensity. Cultural energy represents a human perspective of agricultural intensity, while wooded cover is a habitat element with which raccoons and skunks are associated historically.	18
Figure 1.4 Pattern in raccoon abundance, measured at tracking stations along an agricultural intensity gradient measured as the percent wooded cover in a 1 km radius around the two stations at a site. The best fit line is determined using iteratively reweighted least squares which minimizes the deviance in a Poisson regression.	24
Figure 1.5 Relationship between raccoon abundance and landscape level wooded cover from tracking stations placed in woods, wooded fencerows, and open habitats. Note that as landscape level wooded cover decreases, raccoon abundance remains high in woods and fencerows, but drops sharply in open habitats.	25
Figure 1.6 Pattern in skunk abundance, measured at tracking stations along an agricultural intensity gradient, measured as the percent wooded cover in a 1 km radius around the two stations at a site. The best fit line is determined using iteratively reweighted least squares which minimizes the deviance in a Poisson regression.	28
Figure 2.1 The relationship between number of weeks that raccoon tracks were identified at tracking stations and the length of edge in a circle with 1 km radius around the midpoint between the two stations at a site.	45

LIST OF APPENDICES

	<u>Page</u>
Appendix 1 Estimating the amount of cultural energy involved in pasture production.	58
Appendix 2 Independent variables included in the stepwise Poisson regression analyses used to determine the best set of local and landscape variables describing raccoon habitat use.	59

GENERAL INTRODUCTION

Human activity has a profound effect on the structure and functioning of many ecosystems. Direct human alterations generally affect both the composition and configuration of the native flora and fauna in an area (Dunning *et al.* 1992). The clearing of land for agricultural purposes has changed the configuration of wooded areas from large, relatively continuous tracts to linear strips and remnant fragments. Coincident with this change in configuration is a change in composition, due to the introduction of exotic species of crops, livestock and non-native vegetation. As a result of the altered composition and configuration, the connectivity of the landscape is changed. Connectivity refers to the ability of an organism to move between resource patches in a landscape (Merriam 1984, Taylor *et al.* 1993). Interpatch movements become increasingly important in landscapes that undergo rapid alteration, in which persistence depends upon modified movement behaviour to supplement the size of small populations and rapidly recolonize local extinctions (Merriam, in press).

Multi-species studies have shown that agricultural activities are detrimental to some indigenous species, while others respond with population increases (Hanski and Tiainen 1988, Estrada *et al.* 1993.). Less well documented in agricultural areas are the altered species interactions and cascading effects that can occur as a result of these altered abundance levels. Direct species interactions, such as predation (recent studies by Lindström *et al.* 1994, Suhonen *et al.* 1994, review by Sih *et al.* 1985), and indirect interactions such as competition (recent study by Christensen and

Whitham 1993, reviews by Connell 1983 and Schoener 1983) and higher order interactions (Wootton 1992, Lodge *et al.* 1994) can have strong influences on community structure. Species that have undergone population decline or expansion as a result of human activities can exert direct and/or indirect affects at a magnitude unparalleled in natural settings (*e.g.* Emmons 1984).

The raccoon (*Procyon lotor*) and the striped skunk (*Mephitis mephitis*) are two species that are generally considered to benefit from agricultural activity (Garrot *et al.* 1993). The present study attempts to determine how raccoons and skunks respond to varying levels of agricultural activity and to gain insight into the mechanisms driving changes in abundance. This is an important first step in understanding the effect these animals have on the diversity and abundance of species in agroecosystems.

Underlying all ecological studies is the concept of spatial scale. The extent of an investigation (O'Neill *et al.* 1986) refers to the entire study area that was sampled. This defines the upper limit of resolution in a study; generalizations beyond this require potentially inaccurate extrapolations. Conversely, the grain of a study (O'Neill *et al.* 1986) refers to the size of the individual sampling units, below which patterns cannot be discerned. The spatial scale used in a study is important because ecological patterns are often scale dependent (review in Wiens 1989). For instance, Niemelä and Spence (1994) studied the distribution and abundance of forest dwelling carabids (Coleoptera) across several spatial scales in Alberta, Canada. At the scale of a beetle's range of movement, they found that abundance was strongly affected by several features of plant cover. However, differences in abundance at sites separated

by several kilometres were not related to plant cover features. They suggested that these larger scale patterns in distribution and abundance were determined by regional and historical events such as patterns of disturbance and migration.

Historically, ecologists have paid little attention to spatial scale when designing and carrying out experiments. Recently there has been an increased awareness of scale effects and numerous calls for scale-specific studies (Wiens *et al.* 1986, Addicott *et al.* 1987, and Levin 1992). The present study works toward this end by carrying out a scale-specific analysis of raccoon habitat use.

Chapter 1: Variation in Raccoon and Skunk Abundance along an Agricultural Intensity Gradient

INTRODUCTION

Urban and agricultural expansion are massive, unplanned experiments that offer the opportunity to study how ecological processes are affected by changes in: species composition, spatial distribution of resources, disturbance regimes, and physiological stress (McDonnell and Pickett 1990). The present study focuses on a gradient of agricultural intensity, however there is no *ipso facto* measure for agricultural intensity. Potential measures can be placed into two general categories: those representing a human perspective of agricultural intensity and those that are more directly related to the organisms under study. I used two measures, one from each of these perspectives.

There are two main concepts that define agricultural intensity from a human perspective. The first is the *amount* of land in an area that has been altered for agricultural purposes. The other involves the specific *agricultural activities* that are carried out on that altered land. For instance, a 500 ha block of land with 200 ha of cleared land would be considered more intensely farmed than a similar block with only 100 ha cleared. Furthermore, if two areas had similar amounts of cleared land and one was predominantly pasture land while the other was mostly corn cropping, the corn growing area would be considered more intensely farmed. Anderson (1991) presents a measure for quantifying naturalness, which he calls cultural energy, that

can be used to quantify agricultural intensity from a human perspective. Cultural energy is the amount of human-derived energy input that is required to produce and maintain an altered landscape. Pimentel (1980) has estimated the average amount of energy required to produce one hectare of various agricultural crops. These values can be used to convert areal crop measures to a measure of the cultural energy required to produce the crop mosaic in an agricultural landscape. Such a measure takes into account both the amount of cleared land and the specific cropping activities occurring on that land.

An alternative view of agricultural intensity is the amount of natural or historical habitat remaining in an agricultural landscape. Wooded cover is a habitat feature with which raccoons and skunks have been historically associated, and it was anticipated that they would respond to the amount of wooded cover in the present landscape. Therefore, percent wooded cover was used as a second measure of agricultural intensity.

There were two specific objectives to the present study. The first was to determine if raccoon and skunk abundance varied along an agricultural intensity gradient measured by cultural energy input and percent wooded cover at the landscape level. In the case where there was a significant relationship between agricultural intensity and animal abundance, I was interested in examining how this relationship varied within the various local habitats that were sampled. This second step provided more detailed information on raccoon and skunk populations along the gradient.

Raccoons and skunks are omnivorous and represent top predators in many

agricultural areas. Variation in raccoon and skunk abundance has the potential to exert strong effects on the abundance and diversity of species in agroecosystems.

METHODS AND MATERIALS

Study Area

The study was conducted on a 150 km x 100 km block of land extending to the east, west and south of Ottawa, Ontario, Canada. Areas with varying levels of agricultural intensity were coarsely defined on topographic maps, based on the amount of treed cover at the 1:50 000 scale. On the same maps, primary and secondary roads that provided a relatively equal sampling of a full range of agricultural intensities were identified. Sites were chosen by driving these roads, stopping at 5 km intervals, and asking permission to use the land of the nearest landowner. If access was denied the next landowner was approached. A distance of 5 km between sites was chosen as a trade-off between the spatial independence of samples and the logistical constraints of monitoring a large number of sites. Based on home range estimates (review in Lotze and Anderson 1979), a 5 km spacing between sites should minimize the chance of sampling the same individual or small group of individuals at two different sites. A total of 57 sites was obtained. Sites varied from densely wooded areas to areas of intense cultivation.

Measuring Animal Activity

Tracking plates were used to detect the presence of mammal species. The plates were constructed from 1.6 mm thick white plastic cut into 0.6 m x 0.5 m sheets. Carbon decolorizing powder suspended in paraffin oil (20 g/100 ml) was painted in a 10 cm wide band around the outside of the sheet, leaving the central area available to accept track imprints from visiting animals. A 0.5 m x 0.4 m sheet of butcher paper was taped over the central area of the tracking plate. Butcher paper accepted and retained tracks better than the white plastic base. A 10 cm long piece of 4 cm diameter PVC pipe was attached at one end of the plastic sheet. A small piece of sardine was placed in the pipe as bait. The pipe was closed at one end so animals had to walk over the sheet in order to get to the bait.

Two tracking plates were randomly placed at least 100 m, but not more than 400 m apart into non-cultivated areas at each site. In order to place the tracking plates randomly at a site, I drew a rough map of the property and overlaid it with a numbered grid. A random number was chosen to determine which grid the first tracking plate would be placed in. The second tracking plate was similarly located, with the constraint that it fall between 100 m and 400 m from the first station. The tracking plates were placed more than 100 m apart to increase the likelihood that they were sampling the variation in the landscape; the closer two tracking plates are, the more likely they are to be affected by the same local conditions. The upper limit of 400 m was employed to reduce the amount of time spent at each site, which was

necessary given the time constraints of checking 57 sites.

There were logistical constraints on placing the tracking stations in crop fields, so I was limited to sampling in non-cultivated areas, which included woods, wooded and non-wooded fencerows, fallow fields, and oldfields. Raccoons (Ellis 1964, and Fritzell 1978) and skunks (Storm 1972) have been shown to move extensively through agricultural landscapes and therefore I assumed that abundance indices obtained in non-cultivated areas were indicative of population changes in the landscape. Analysis of raccoon and skunk abundance within the habitats sampled was a further check on this assumption.

Tracking stations were checked once a week from August 31 to October 10, 1993, for a total of 6 checks. During weekly checks the butcher paper was collected and replaced and the tracking stations were repainted and rebaited. Tracks were identified using Murie (1954).

I used the number of weeks that raccoon or skunk tracks were identified at a tracking station as response variables. While this is not a direct measure of abundance, it is an index that should be consistent between sites along the gradient.

Measuring Agricultural Intensity

In an agricultural context, cultural energy refers to the amount of auxiliary energy in the form of fertilizers, herbicides, farm machinery, labour, and various other chemical inputs that is required to produce a particular agricultural landscape

(Anderson 1991). In order to measure this, maps of the crops at and around each site were made during the field season. The information on these maps was transposed onto air photos and the amount of each crop type in a 1 km radius circle around the midpoint between the two traps at a site was measured using a digital planimeter. Forty of the sites had air photo coverage from 1993, 7 were from 1986 and 10 were from 1975. Sites with coverage from 1986 and 1975 were groundtruthed and inaccuracies in field boundaries and treed cover were corrected on the air photos. The crops measured included: corn, barley, oats, soybeans, alfalfa, hay and pasture. Pimentel (1980) provides estimates of the amount of energy required to produce 1 ha of each of these crops. These estimates were used to convert the areal crop measures to an energy value for each crop. These energy values were summed to obtain an estimate of the total cultural energy required to produce the crops in the agricultural landscape surrounding each site.

The estimates provided by Pimentel (1980) for pasture production did not reflect pasture production in the Ottawa area. Based on personal observations and interviews with farmers (n=10), I modified Pimentel's estimate for hay production to describe pasture production in this region (Appendix 1). Barley and oats, as well as alfalfa and hay had not been consistently differentiated in the field. Therefore Pimentel's (1980) value for barley was used for barley and oats, and his value for hay was used for hay and alfalfa. There is considerable regional variation in the energy required to produce crops. Pimentel (1980) often provided estimates for a particular crop from a number of different areas in the United States. I used the estimate from

the location that was closest to Ottawa. The final conversion factors are shown in Table 1.1.

The percentage of treed cover in a 1 km radius circle around the two traps at a site was measured from air photos as described above for crops.

Defining Local Habitat Types

I was interested in determining whether skunk and raccoon abundance varied depending on the habitat in which the tracking station was located. For raccoons, which have a well documented affinity for corn (Stuewer 1943, Turkowski and Mech 1968, Sonenshine and Winslow 1972), I also anticipated that local variability in tracking results could be related to whether the trap was placed in the near vicinity of corn or not.

In order to classify the local habitat that a tracking station was placed into, a circle with a 50 m radius was delineated around each tracking station and the main habitat type in that circle was classified as: wooded, wooded fencerow, or open. Wooded habitat was defined as an aggregation of trees over 4 m in height. Wooded fencerows were defined as linear elements having an essentially continuous string of trees or shrubs over 2 m in height. Open areas included fallow fields, oldfields, and non-wooded fencerows. Proximity to corn was a binary classification; traps were classified as either falling within 50 m of a corn field or not.

Table 1.1 Values used to convert areal crop measures to cultural energy measures. All values were taken from Pimentel (1980) except for pasture which was derived from observations of local pasture production practices and Pimentel's estimate for hay.

Crop	Locality of Estimate	Kcal/ha
corn	New York	4 381 864
soybeans	Ohio	2 273 883
barley	Minnesota	1 990 000
hay	New York	631 992
pasture	Ottawa/New York	53 920

Statistical Analysis

My response variables were the number of weeks that raccoon or skunk tracks were identified at each tracking station. These variables consisted of a limited range (i.e. 0 to 6) of discrete numbers. Data with these characteristics are often referred to as count data (McCullagh and Nelder 1989). The variance of count data has been shown to change with the mean, and therefore, count data often require a transformation to meet the assumptions of classical regression (McCullagh and Nelder 1989). Poisson regression uses a deviance formula (in place of classical sums of squares) that allows non-constant variance to be directly incorporated into the analysis (Hastie and Pregiborn 1992). Therefore, Poisson regression in Spls (Hastie and Pregiborn 1992) was used to model the relationship between the track frequencies of skunks and raccoons and the two measures of agricultural intensity. Plots of deviance residuals exhibited homogeneity of variance, indicating that this was an appropriate approach for analyzing the data.

The two tracking stations at a site were not spatially independent as they were well within the daily activity range of a raccoon. Including each trap result as an independent data point would result in an inflated number of degrees of freedom and consequently an increased chance of Type I error. To remedy this, I included a class variable (SITES) in the analysis that had a level for each of the 57 sites. This variable effectively nested traps within sites, such that the two traps at a site were considered subsamples from one experimental unit.

In a random effects model, the error associated with the nested term represents the error between experimental units, while the model error term represents the error within experimental units (Neter *et al.* 1985). In the present study, the experimental units are each of the 57 agricultural landscapes and the two traps at each site are subsamples within each experimental unit. Since the sites in this study represent a random sample of all possible sites (i.e. a random effects model) the correct error term for detecting differences between sites along the gradient was that associated with the variable SITES.

The default significance test for Poisson regression is the chi-square test. However if the deviance associated with the error term is high, an F-test, based on a ratio of deviances has been found to be more accurate (Hastie and Pregiborn, 1992). In the present study, the F-test was used if the deviance associated with SITES was significant using a chi-square test and $\alpha=0.05$.

To examine the relationship of animal abundance to agricultural intensity in different local habitats, I re-ran the original analysis with the significant measure of agricultural intensity and the class variables for habitat and corn proximity (raccoons only) included in the model. Interaction terms between the local variables and the landscape level intensity measure were included to determine if the effect of the landscape level intensity measure was dependent on the local placement of the tracking station. This was investigated by plotting separate Poisson regression lines of the relationship between animal abundance and agricultural intensity for the different habitat types.

RESULTS

Tracking Station Results

One hundred and fourteen tracking stations were checked once a week for six weeks, resulting in a total of 684 station-weeks. Raccoon tracks were identified on 274 station-weeks at 80 stations and skunk tracks were identified on 56 station-weeks at 35 stations. Sample sizes and animal counts within each habitat are shown in Table 1.2.

Agricultural Intensity Measures

Sites were chosen in an attempt to provide an equal frequency of a range of agricultural intensities. A full range of wooded cover was sampled, but there was a high representation of sites with a low percentage of wooded cover (Fig. 1.1). There was also a wide range of cultural energy values, with an over-representation at the low intensity end (Fig. 1.2). As expected, the two measures of agricultural intensity were negatively correlated ($R=-0.803$, $P<0.0001$). There is considerable variation in this relationship, indicating that the two measures are not simply mirror images of one another, but represent different aspects of agricultural intensity (Fig. 1.3).

Table 1.2 Data from 114 tracking stations placed into non-cultivated habitats at 57 sites along an agricultural intensity gradient.

Habitat Type	No. Tracking Stations	Station-Weeks	Weeks with Raccoon Tracks	Weeks with Skunk Tracks
woods	44	264	132	6
wooded fencerows	35	210	106	21
open	35	210	36	29
Total	114	684	274	56

Figure 1.1 Distribution of sites with respect to the percentage of wooded cover in a 1 km radius around the midpoint between the two tracking stations at a site. Sites were chosen in an attempt to obtain equal frequencies of a wide range of wooded cover.

Figure 1.2 Distribution of sites with respect to the amount of cultural energy input required to produce the crops in a 1 km radius around the midpoint between the two tracking stations at a site. Sites were chosen in an attempt to obtain equal frequencies of a wide range of cultural energy inputs.

Figure 1.3 Relationship between the two measures of agricultural intensity. Cultural energy represents a human perspective of agricultural intensity, while wooded cover is a habitat element that raccoons and skunks have developed with historically.

Raccoons

The number of raccoon track station visits was not significantly related to the amount of cultural energy required to produce the crops in an agricultural landscape (Table 1.3). Polynomial relationships were examined but none were significant. There was a significant quadratic relationship between raccoon trap visits and percent treed cover (Table 1.4, Fig. 1.4). When this relationship was considered with local habitat features, proximity to corn and the habitat type that the trap was placed into both explained a significant amount of the variation in raccoon abundance (Table 1.5). Contrasts were examined using dummy variables in a Poisson regression analysis. Tracking stations within 50 m of corn had more raccoon visits than stations more than 50 m from corn ($F_{1,54}=5.257$, $P<0.025$). Raccoon tracks were identified more times at stations in woods and wooded fencerows than at stations in open areas ($F_{1,54}=18.905$, $P<0.001$). There was a significant interaction between habitat type and landscape level wooded cover (Table 1.5). A plot of the interaction indicated that in landscapes with mid to low amounts of wooded cover, raccoon abundance remained relatively high in woods and wooded fencerows, but dropped sharply in open areas (Fig. 1.5). The amount of deviance explained by the best fit line in each of the habitats is given in Table 1.6. In each of these analyses, some traps were from the same site and consequently p-values were invalid because of lack of independence. The deviance is provided solely to give an idea of how well each of the lines fits the data.

Table 1.3 Poisson regression relating the number of weeks that raccoon and skunk tracks were identified at tracking stations to the amount of cultural energy required to produce the crops in a 1 km radius around the midpoint between the two stations at each site.

Model term	df	Deviance	F	P
Raccoons				
cultural energy	1	3.85	1.15	>0.100
sites	55	184.15		
error	57	74.74		
Skunks				
cultural energy	1	2.30	1.20	>0.100
sites	55	105.23		
error	57	41.08		

Table 1.4 Poisson regression relating the number of weeks that raccoon and skunk tracks were identified at tracking stations to percent wooded cover in 1 km radius around the midpoint between the two stations at each site.

Model term	df	Deviance	F	P
Raccoons				
% wooded cover	1	18.70	6.68	<0.025
(%wooded cover) ²	1	25.47	9.10	<0.005
sites	54	151.06		
error	57	83.06		
Skunks				
% wooded cover	1	21.02	13.36	<0.001
sites	55	86.51		
error	57	41.08		

Table 1.5 Poisson regression relating the number of weeks that raccoon tracks were identified at tracking stations to percent wooded cover in 1 km radius around the midpoint between the two stations at each site and local habitat features measured in a 50 m radius around each station.

Model term	df	Deviance	F	P
habitat type	2	46.42	12.14	<0.001
within 50 m of corn	1	10.03	5.25	<0.050
% wooded cover	1	15.46	8.09	<0.010
(%wooded cover) ²	1	23.80	12.45	<0.001
habitat x wooded cover	2	13.96	3.65	<0.050
corn proximity x wooded cover	1	1.42	0.74	>0.100
sites	54	103.21		
error	51	59.25		

Table 1.6 Amount of deviance explained by the three best fit Poisson regression lines for the relationship between the number of raccoon track station visits and landscape level wooded cover when the data were broken down by local habitat type.

Habitat Type	Number of Traps	Explained Deviance	Total Deviance
wooded	44	35.092	82.107
wooded fencerow	35	3.746	44.350
open	35	26.223	86.887

Figure 1.4 Pattern in raccoon abundance (ra), measured at tracking stations, along an agricultural intensity gradient, measured as the percentage of wooded cover (pwc) in a 1 km radius around the two tracking stations at a site. The best fit line is determined using iteratively reweighted least squares which minimizes the deviance in a Poisson regression. The equation of the line is: $ra = e^{(0.5907 + 0.0355pwc - 0.0005pwc^2)}$

Figure 1.5 Relationship between raccoon abundance and landscape level wooded cover from tracking stations placed in woods (symbol=W, solid line), wooded fencerows (symbol=F, dotted line), and open habitats (symbol=O, dashed line). Note that as landscape level wooded cover decreases, raccoon abundance remains relatively high in woods and fencerows, but drops sharply in open habitats.

Skunks

The number of skunk trap visits was not significantly related to cultural energy (Table 1.3). There was significant negative relationship between skunk trap visits and percent wooded cover (Table 1.4, Fig. 1.6). When local habitat features were included in the analysis, habitat type was found to explain a significant proportion of skunk abundance (Table 1.7). Tracking stations in wooded fencerows and uncultivated open areas had more skunk visits than stations in wooded habitats ($t_{1,55}=15.305$, $P<0.001$). The interaction between habitat and wooded cover was not significant (Table 1.7).

DISCUSSION

Neither skunks nor raccoons showed a significant relationship with agricultural intensity measured as cultural energy. Essentially this measure combined all of the agricultural activity in a landscape and produced a single value to estimate its intensity. While this may be a reasonable way to measure agricultural intensity from a human perspective, it has the potential to mask the effect of particular landscape elements that animals may be responding to. The significant relationship between skunks and raccoons and wooded cover is evidence of this. The different results obtained from the two measures of agricultural intensity demonstrates the importance of considering ecological problems from less anthropocentric perspectives.

Table 1.7 Poisson regression relating the number of weeks that skunk tracks were identified at tracking stations to percent wooded cover in 1 km radius around the midpoint between the two stations at each site and local habitat features measured in a 50 m radius around each trap.

Model term	df	Deviance	F	P
habitat type	2	23.34	8.10	<0.005
% wooded cover	1	10.59	7.35	<0.010
habitat x wooded cover	2	2.42	1.68	<0.100
sites	55	79.27		
error	53	33.00

Figure 1.6 Pattern in skunk abundance (sa), measured using tracking plates, along an agricultural intensity gradient, measured as the percentage of wooded cover (pwc) in a 1 km radius around the two tracking stations at a site. The best fit line is determined using iteratively reweighted least squares which minimizes the deviance in a Poisson regression. The equation of the line is: $sa = e^{(-0.0796 - 0.0267pwc)}$

In agricultural landscapes with intermediate amounts of wooded cover, raccoons reached relatively high abundances in all habitats sampled. The increased numbers of raccoons is due in part to their ability to make use of human-derived energy sources. In the present study, raccoon tracks were identified more often at stations located within 50 m of a cornfield. This is in agreement with numerous studies that have documented raccoons supplementing their diets with corn (Stuewer 1943, Hamilton 1951, Tester 1953, Dorney 1954, Turkowski and Mech 1968, and Sonenshine and Winslow 1972).

Raccoon tracks were identified more often at tracking stations located in woods and wooded fencerows. Wooded cover is important to raccoons in several ways. Trees with adequately sized cavities are used extensively for natal and winter dens (Stuewer 1943, Stains 1961, Shirer and Fitch 1970 and Urban 1970). Wooded cover also provides raccoons with a means of escape from predation. Humans are the major predator, although the red fox, coyote and several species of owl are reported to occasionally prey on raccoons (Lotze and Anderson 1979).

In agricultural landscapes with intermediate amounts of wooded cover, raccoons are seldom far from wooded cover and appear to frequently venture into uncultivated open habitats. As the amount of wooded cover in the landscape decreases, raccoons increasingly avoid uncultivated open areas; probably because these areas are increasingly isolated from the protection and denning sites offered by wooded cover. This provides some evidence that raccoons move less extensively through high intensity agricultural landscapes with little wooded cover. However,

since there were no tracking stations in crop fields, this finding is tentative.

Raccoon abundance remained high in wooded habitats as landscape level wooded cover decreased. This suggests that the density of raccoons in wooded habitats increases in high agricultural intensity landscapes. Matthiae and Stearns (1981) studied mammal populations in forest islands in Wisconsin. Based on a combination of live-trapping, trail use, and scat frequency, they determined that raccoons often reach abnormally high densities in forest islands in urban areas. They suggested that raccoons used the forest islands for daytime cover and utilized sewers and garbage for night foraging.

This has implications concerning the limiting resources of raccoon populations. If, as is likely the case, increased raccoon densities are supported by the surfeit of corn in high agricultural intensity areas, then raccoon populations in wooded habitats are limited by food, rather than other resources. The number of den trees has been suggested as a limiting resource for raccoon populations (Stuewer 1943). However, Dorney (1954) found that 90 percent of raccoons in a highly productive marsh in Wisconsin used underground dens for overwintering. Fritzell (1978) radiotracked raccoons in the Prairies of North Dakota and found that seven of ten litter sites were in farm buildings. Raccoons appear to be able to make use of novel den sites when abundant food resources are available. It is not known where raccoons in high agricultural intensity areas in Ontario overwinter or give birth.

Skunks exhibited a negative relationship with percent wooded cover, reaching highest activity levels in open, high intensity areas. This is in agreement with Verts

(1967) who studied skunk populations on a 1338 km² study area in Illinois. He divided the study area into 259 ha grids which he classified according to the amount of wooded cover each grid contained. Using livetrapping as an index of abundance, he found that skunks were more abundant in grids with little or no treed cover.

A similar pattern was found in the present study for local habitats where skunk track frequencies were highest in uncultivated open areas and wooded fencerows. Wooded fencerows offer food in the form of fruit, and high numbers of insects (Thomas *et al.* 1992), birds (Best 1983) and small mammals (J. Wegner, pers. comm.), while still allowing skunks to locate in relatively open landscapes. In landscapes with little or no wooded cover, fencerows were scarce or non-existent and yet skunks continued to increase in abundance. It appears that skunks can make use of wooded fencerows when they are available, but can also thrive without them.

The reason why skunks preferentially locate in open areas (at either scale) is not clear. Natal and overwintering dens are exclusively underground (Verts 1967, Storm 1972 Houseknecht and Tester 1978) but can be excavated in both wooded (Allen and Shapton 1942) and grassy (Verts 1967) areas. Skunks have few predators, which they deter by expelling musk. This method of defence should be effective in both wooded and open areas. Unlike raccoons, skunks do not appear to heavily supplement their diet with agricultural grain crops. Several studies have reported skunks eating corn (Hamilton 1936, and Llewellyn and Uhler 1952), yet it was neither consistently nor heavily taken. Furthermore, Storm (1972) radiotracked skunks on an extensively cultivated study area in Illinois and found that skunks

foraged less than expected in corn fields based on the proportionate area of land planted to corn in the study area.

Several studies have found skunks to be primarily insectivorous (Dixon 1925, Selko 1937, and Llewellyn and Uhler 1952). However, Ryszkowski (1985) has documented a 12-30 times reduction in soil invertebrate biomass in arable fields and a 6 to 15 times reduction in soil invertebrate biomass in meadows as compared to mixed forests. It may be that, while soil insect biomass in general decreases in open areas, certain insect species that provide high energy return to skunks increase. Skunks feed heavily on Orthopterans and Coleopterans (Llewellyn and Uhler, 1952). Beetles, such as scarabid larvae and Orthopterans such as grasshoppers and crickets are primarily found in open, grassy areas. Whether the rate of energy intake is higher by hunting these insects in open areas than by hunting in wooded areas is not known.

Population explosions of small and mid-sized omnivores and predators have been documented in tropical areas (Terborgh and Winter 1980, and Emmons 1984). Soulé *et al.* (1988) termed this phenomenon meso-predator release, referring to the fact that the population explosions seemed to be a result of large predators being removed from the system. It is unlikely that lack of large predators is playing a part in the high abundance of raccoons and skunks in mid and high intensity agricultural areas. There are relatively few natural predators on skunks and raccoons, and most of the potential predators (e.g. coyotes, foxes, and owls) are present in mid and high intensity agricultural areas (pers. obs.).

Garrot *et al.* (1993) raise the question "is overabundance an issue for conservation biologists?". They point out that while invading exotic species have received much attention, little has been paid to expanding or overabundant native species, despite studies that have documented deleterious effects to flora and fauna due to overabundant native species (e.g. Alverson *et al.* 1988). They suggest that one of the reasons why scientists are reticent to tackle this issue is that it is difficult to determine when a species is overabundant. I propose that one instance of overabundance occurs when densities are higher than those that occur in areas with little or no human disturbance. By such a definition, the present study provides evidence that raccoons and skunks are overabundant at mid and high agricultural intensities.

Not all species that occur at higher than natural abundances require management action. Garrot *et al.* (1993) outline two specific instances (as defined by Caughley 1981) in which overabundance becomes a problem. The first involves species that cause a threat to human life or livelihood. Striped skunks are reported to have the highest incidence of rabies infection among North American carriers (Parker 1975). Raccoons carry canine distemper, a rabies-like disease, and at least 13 other pathogens known to cause disease in humans (Lotze and Anderson 1979). Raccoon rabies is steadily moving northward and has reached the Canada-US border. Focal points for rabies outbreaks have been related to areas of high host density (Smith and Harris 1991). The high numbers of skunks and raccoons in high and mid-intensity agricultural areas represent potential outbreak points. In rural areas, this threat may

be highest for raccoon populations that have been squeezed into small woodlots in high intensity agricultural areas.

Garrot *et al.* (1993) state that a second instance of problematic overabundance "involves common species that depress the densities of favoured species". While I agree in principle with this statement, the term "favoured species" leaves me uneasy. This terminology is reminiscent of a style of management that attempted to promote game species, at the expense of "less valuable", non-game species. The examples provided by Garrot *et al.* (1993) suggest that this is clearly not their intention, but I would suggest exchanging "favoured species" with "native species" to avoid any possible misinterpretation. The extremely broad diet of raccoons (see Lotze and Anderson 1979, for review) and skunks (see Wade-Smith and Verts 1982, for review) creates the potential for them to affect the abundance and survival of many species in agroecosystems. For instance, numerous studies have identified raccoons and skunks as nest predators (Wilcove 1985, Small and Hunter 1988, and Picman 1988). However, the specific effect of skunks and raccoons has often not been quantified. Raccoons have been reported to severely reduce waterfowl (Urban 1970) and gull (Kadlec 1971) nesting success, while other studies report little effect (Dorney 1954). Chessness *et al.* (1968) identified skunks and raccoons as major quail nest predators and documented a significant increase in nest success as a result of predator removal. Despite varying results, it is clear that raccoons and skunks do prey on nests and can strongly influence nest success. Angelstam (1986) found that nests in Sweden were preyed on in proportion to the densities of mammalian and avian predators. High

numbers of skunks and raccoons in high and mid intensity agricultural areas may be problematic for nesting success. Again, this effect may be felt most strongly in small woodlots in high agricultural intensity areas, where raccoons reach high densities. In these areas, corn would not be available until August and raccoons probably rely heavily on food of animal origin before then.

Raccoons and skunks meet both criteria that have been outlined for defining overabundant species. Native species, such as raccoons and skunks, are often not considered overabundant because they are viewed as a natural part of the biological system. However, when the abundance of native species has been inflated by human-derived resources, they can exert pressure on other species at a level that is unparalleled in natural settings. If the goal of management is to reduce human impacts on ecosystems, reducing the numbers of overabundant native species should be considered a valid management approach.

Chapter 2: A Scale Specific Analysis of Raccoon Habitat Use

INTRODUCTION

Habitat selection is the process by which organisms distribute themselves throughout the environment. It is reasonable to expect that this is often achieved based on choices made at several spatial scales (Orians and Wittenberger 1991, Ward and Saltz 1994). At the scale of a home range, an animal will preferentially locate in a landscape that offers a high frequency of encounter with the various resources necessary for survival. Within its home range, an animal will make fine scale land use choices based on factors such as food availability, predation risk, and competitive interactions. Several hierarchical levels of resource aggregation may be distinguished by an animal between its finest scale of perception and its home range (Kotliar and Wiens 1990).

Cross-scale habitat studies are important because they provide scale-specific information on habitat preference (Morris 1987), and the scale chosen for study provides a basis for comparison of habitat use patterns within and between species (Addicott *et al.* 1987). The present study examined raccoon habitat use in rural areas of eastern Ontario at a landscape scale (measured as a circle with a 1 km radius) and a local scale (circle with 10 m radius). Raccoons have been reported to have home ranges from less than 10 ha to over 4000 ha (review in Lotze and Anderson 1979), and typical values vary between 50 ha and 250 ha (Stuewer 1943, Ellis 1964, and

Shirer and Fitch 1970). Therefore, the landscape scale used in this study (*i.e.* 314 ha) is slightly larger than the upper end of the typical operating range of an individual raccoon. Densities of raccoons typically range from one raccoon per 5 ha to one per 43 ha (review in Lotze and Anderson 1979), so it is also reasonable to expect that interacting groups of raccoons will be found at this scale. Raccoons can distinguish resources, such as den sites and food items, at the scale of several metres, therefore the local scale used in this study represents fine-scale choices made by raccoons in carrying out activities necessary for survival.

There are several possible outcomes to cross-scale habitat studies. Probably the least common result is to find significant effects at the landscape level only. This situation would require an organism that needed a large expanse of a habitat type that was relatively homogeneous internally. Hansen *et al.* (1993) have suggested that landscape level habitat features describing old growth forest would be the best predictor of spotted owl (*Strix occidentalis*) abundance. Conversely, some organisms may respond solely or primarily to local habitat features. Pearson (1993) studied wintering bird populations in Georgia and found that the abundance of generalist species was strongly related to local vegetation features and only weakly related to landscape features. He suggested that this was due to the fact that generalists could make use of locally distributed resources in a variety of landscapes. Probably the most common outcome is that animals respond to both local and landscape attributes. This outcome can be further subdivided based on the information provided by the different scales. Similar patterns may be reflected across the two scales. In this case

local features often provide insight into the mechanisms driving landscape level patterns. However, differentiating local and landscape effects can be difficult because of cross-scale correlations between habitat variables (Pearson 1993). Finally, different patterns can be found at the two scales. In this case the information provided by the two scales is complementary and both are needed to understand the distribution and abundance of the species (Orians and Wittenberger 1991).

Raccoons have benefitted from agricultural activity, and have responded with elevated abundance in agricultural areas (see first chapter). Detailed knowledge of habitat use is important for identifying areas that may be adversely affected by raccoon overabundance. Furthermore, raccoon rabies has reached the Canada-US border and control programs involving trapping and vaccinating animals and distributing vaccinated baits will be more efficient with this information.

METHODS AND MATERIALS

The study area and sampling design is the same as that described in Chapter 1. The large number of sites and considerable variation in landscape features was amenable to studying the relationship between raccoon abundance and landscape level features. An index of raccoon abundance was obtained using two tracking stations at each site, as described in Chapter 1.

Landscape Level Habitat Features

On air photos, a circle with a 1 km radius was delineated around the midpoint between the two traps at each site. The percent coverage of corn, grain (barley and oats), hay (alfalfa and hay) and woods in the 1 km radius circle around each site was measured using a digital planimeter. Raccoons are generally associated with edge situations (*e.g.* Bider 1968), and it was anticipated that raccoons would respond to the amount of agricultural edge in a landscape. I measured agricultural edge as the length (km) of interface between land used for agricultural purposes and wooded cover in the 1 km radius circle around each site.

Local Habitat Features

Raccoons make use of wooded cover for denning, predator avoidance and food. Therefore I anticipated that the composition and structure of woody vegetation would be an important determinant of local habitat use. Local woody vegetation was sampled by walking a 10 m transect in a north, south, east, and west direction from each trap. At 2 m intervals along each transect a 2 m long wooden pole with markings at 0.5 m and 1 m was held upright. All woody species touching the pole in each vertical stratum (0.0m-0.5m, 0.5m-1.0m, 1.0m-2.0m) were identified. Two additional vertical strata (2.0m-6.0m, over 6.0m) were recorded by looking directly up the pole and estimating the height of intercepting vegetation.

Vegetation sampling resulted in 62 variables. The frequency of encountering woody vegetation in each of the five vertical strata was calculated as the number of times that woody vegetation was encountered in a particular layer, divided by the number of possible encounters (i.e. 20). The remaining 57 variables were the frequency of occurrence of each tree and shrub species at each trap. This was calculated as the number of times that a particular tree or shrub was encountered divided by the number of sampling points, regardless of vertical stratum (i.e. 20).

Statistical Analysis

The general analytical approach was to produce one statistical model with the set of landscape level features that best predicted raccoon abundance and another model with the best set of local features. The two models were then combined in one analysis to determine if there were unique effects attributable to either scale. Local and landscape effects can be difficult to distinguish because of correlations between the two scales (Pearson 1993). If all the variables (local and landscape) were included in the same analysis and chosen by a stepwise procedure, variables from one scale could be predominantly chosen, but important variables from the other scale could simply be masked by correlations. By building the models separately at each scale, and then combining them, I was able to observe how this correlation structure affected the important variables at each scale.

Before examining the relationship between raccoon abundance and local woody

vegetation, I needed to pare down the 62 local woody vegetation variables to those that were most likely to be important to raccoons. The raccoon is a common species, and it is unlikely that its distribution and abundance are dictated by rare or uncommon plant species. From a pragmatic perspective, uncommon plant species are unlikely to be found significant because of the large number of zeroes that they introduce into an analysis. Therefore, I removed all tree and shrub species that occurred at less than 10 percent of the traps. This left 22 species variables and 5 structural variables.

Due to the "count" nature of the data (McCullagh and Nelder 1989), Poisson regression was used to model the relationship between raccoon abundance and the local and landscape habitat features. Since some variables may have non-linear relationships with raccoon abundance, I looked for polynomial terms between each remaining local vegetation variable and raccoon abundance using separate Poisson regressions (Hastie and Pregiborn 1992). I also looked for polynomial relationships between each of the five landscape level variables and raccoon abundance.

Significant polynomial terms at each scale were included in subsequent analyses. The final set of local and landscape variables used for analysis is listed in Appendix 2.

In order to determine the best local and the best landscape models, stepwise Poisson regression (SAS 1990, Vol. 2, p. 1120) was used. Poisson regression in SAS is actually an approximation to Poisson regression, derived from logistic regression, but was used because of the efficiency of the stepwise routine in SAS. Final models, chosen by the stepwise procedure in SAS, were run using Poisson regression in Spls (Hastie and Pregiborn 1992) so that correct Poisson deviances could be reported. The

best local and landscape variables were included together in a final Poisson regression to determine if either scale had unique effects on raccoon abundance. For all analyses I report both order-dependent and order-independent (also called sigma-restricted or type three) deviances to provide insight into the correlation structure within and across scales.

As in the previous chapter, a class variable which nests traps within sites was included in the analysis to account for the inflated degrees of freedom that come about when each trap is used as an independent data point. Significance tests are based on the deviance associated with this nested variable. A significance level of $\alpha=0.05$ was used for all analyses.

RESULTS

At the local scale, the frequency of occurrence of white ash (*Fraxinus americana*), wild red raspberry (*Rubus idaeus*), sugar maple (*Acer saccharum*), white spruce (*Picea glauca*), and woody vegetation between 1 m and 2 m in height were included in the best stepwise model describing raccoon activity at track stations (Table 2.1). At the landscape scale, the first and second order terms for the length of agricultural edge and the second order term for the percent cover of corn were included in the model (Table 2.2).

I did not anticipate the quadratic relationship between raccoon abundance and edge; four data points caused the inclusion of the second order term (Fig. 2.1). The

Table 2.1 Poisson regression relating the number of weeks that raccoon tracks were identified at tracking stations to woody vegetation features measured in a circle with 10 m radius around each station. These variables were chosen from a set of 31 local woody vegetation measures using a stepwise Poisson regression.

Model term	df	Sequential Deviance	Sigma-restricted Deviance	F*	P	slope
white ash	1	18.738	15.050	7.005	<0.025	0.676
white spruce	1	12.488	10.158	4.728	<0.050	-1.500
wild red raspberry	1	13.179	9.338	4.346	<0.050	0.584
woody veg. 1-2 m	1	20.791	19.015	8.850	<0.010	1.186
sugar maple	1	12.288	12.288	5.719	<0.025	0.700
sites	56	120.315				
error	52	64.937				

*F-value is based on sigma-restricted deviance

Table 2.2 Poisson regression relating the number of weeks that raccoon tracks were identified at tracking stations to landscape features measured in a 1 km radius circle around the two stations at a site. These variables were chosen from a set of 8 landscape measures using stepwise Poisson regression.

Model term	df	Sequential Deviance	Sigma-restricted Deviance	F*	P	slope
length of edge	1	31.087	38.104	13.340	<0.001	0.4420
(length of edge) ²	1	18.269	19.197	8.238	<0.010	-0.0280
(percent cover of corn) ²	1	15.132	15.132	6.494	<0.025	0.0003
sites	53	123.507				
error	57	74.740				

*F-value is based on sigma-restricted deviance

Figure 2.1 The relationship between the number of weeks that raccoon tracks were identified at tracking stations and the length of edge in a circle with 1 km radius around the midpoint between the two stations at a site. The solid line represents the best Poisson fit when the four solid symbols are included in the analysis and the dotted line shows the best Poisson fit with these points removed.

only apparent similarity between these tracking stations was their proximity to pasture. Two tracking stations were located in a field that was actually used periodically for pasturing and the other two were in small wooded areas surrounded by pasture. In order to determine if pasture had a negative effect at other tracking stations, I classified each station in the study as either falling within 10 m of pasture or not. A Poisson regression with pasture proximity as a dummy variable indicated that there were significantly fewer raccoon visits to track stations that were located within 10 m of pasture ($F_{1,56}=4.03, P<0.05$). The amount of pasture in the landscape did not increase in landscapes with high amounts of edge, and generally varied between 5 and 10 percent coverage. Taken together, these findings suggest that the low number of raccoon visits to the four track stations in question is due to their proximity to pasture, and that the preponderance of tracking stations near pasture in landscapes with high amounts of edge is simply due to chance or unintended sampling bias. I suggest that the best fit line with these points removed gives the most realistic picture of the relationship between raccoons and edge.

When local and landscape features were included in the same analysis, edge remained significant at the landscape level (Table 2.3). Frequency of occurrence of sugar maple, and woody vegetation between 1 m and 2 m in height remained significant at the local scale, while white ash was marginally significant (Table 2.3).

Table 2.3 Poisson regression relating the number of weeks that raccoon tracks were identified at tracking stations, to woody vegetation features measured in a circle with 10 m radius around each station and landscape features measured in a 1 km radius circle around the two stations at each site.

Model term	df	Sequential Deviance	Sigma-restricted Deviance	F*	P	slope
white ash	1	18.738	7.222	3.894	<0.100	0.5027
white spruce	1	12.488	0.205	0.111	>0.500	-0.2619
wild red raspberry	1	13.179	3.342	1.802	>0.100	0.4530
vegetation 1-2 m	1	20.791	13.007	7.012	<0.025	1.0400
sugar maple	1	12.288	7.645	4.121	<0.050	0.5672
length of edge	1	14.637	8.871	4.782	<0.050	0.2597
(length of edge) ²	1	2.357	3.158	1.702	>0.100	-0.0133
(percent cover of corn) ²	1	5.008	5.008	2.700	>0.100	0.0002
sites	53	98.312				
error	52	64.937				

*F-value is based on sigma-restricted deviance

DISCUSSION

Relating the results of the present study to those found in the literature is difficult because past studies have not been scale specific. At times it was necessary to extrapolate local results to higher scales and landscape results to lower scales in order to relate them to previous findings. This, in itself, is an indication of the resolution at which certain patterns can be detected, or at least understood and explained, given the present understanding of raccoon habitat use.

At the local scale, white ash, wild red raspberry, and woody vegetation between 1 m and 2 m in height were positively related to raccoon track station visits. These variables were commonly associated with wooded fencerows. Wild red raspberry is one of several fruit-bearing fencerow species from which raccoons obtain food (Schoonover and Marshall 1951). Food of animal origin may also be obtained from the high abundance of insects (Thomas *et al.* 1992), birds (Best 1983) and mammals (J. Wegner, pers. comm.) associated with fencerows. Many of the trees found in fencerows are not mature enough to provide den sites (pers. obs.), however they would provide escape cover for raccoons while in transit.

Raccoon activity was positively related to the frequency of occurrence of sugar maple in the near vicinity of each track station. This result can be interpreted at two scales. On a fine scale, maple trees provide raccoons with daytime rest sites and cavities for natal and overwinter denning (Stuewer 1943). At a coarser scale, sugar maples are one of several hardwood species that form deciduous stands, which have

been identified as good raccoon habitat in previous studies (Stuewer 1943 and Twitchell and Dill 1949). As a quick check on this possibility, I ran the stepwise selection process with sugar maple removed and red oak (*Quercus rubra*), another hardwood species, was chosen in its place. This result suggests that sugar maple is acting as a surrogate for deciduous stands.

Raccoon activity was negatively related to frequency of occurrence of white spruce. Within the study area, white spruce occurred almost solely as part of mixed forests growing on poorly drained, acidic soil. These areas have low secondary productivity and probably offer little food to raccoons. Furthermore, the trees are often too small to provide den sites.

At the landscape scale, the relationship between raccoons and agricultural edge is most accurately described by a positive relationship. The loss of significance of the second order edge term when local features were included in the analysis provides more evidence that this term was generated by local features. Agricultural edge truly offers the raccoon the best of all worlds. Within the wooded side of the edge, raccoons obtain den sites and protective cover. At the habitat boundary, raccoons forage on the increased density and diversity of prey items (Odum 1971). For instance, raccoons have been implicated in the increased levels of nest predation that occur at forest edges (Gates and Gysel 1978, Wilcove 1985, and Small and Hunter 1988). Finally, on the non-wooded side of the habitat boundary, raccoons can make use of agricultural grain crops. For instance, the present study found a positive relationship between the amount of corn in the landscape and raccoon abundance.

Other studies have documented raccoons making use of corn at the scale of specific corn fields (Dorney 1954, Turkowski and Mech 1968, and Sonenshine and Winslow 1972).

Before discussing the cross-scale analysis, the implications of the variables included in the study should be considered. It could be argued that the outcome of cross-scale habitat studies is entirely dependent on the variables that are included at each scale. However, it would be impossible to include every potentially important environmental variable at each scale, and the present study made no attempt to do so. In fact, potentially important local (e.g. pasture proximity) and landscape (e.g. coniferous versus deciduous woods) variables were discovered in the process of interpreting the results of the variables that were used. However, the fact remains that reasonable variables were measured at each scale, and the interrelated effects of these variables are real, and can be used to gain insight into how spatial scale mediates raccoon habitat selection. Caution should be used in making general statements concerning the relative importance of landscape and local effects to a species unless one is confident that the majority of important variables at each scale have been considered (Morris 1987).

When local and landscape features were included in the same analysis, the length of edge in the landscape had an effect above and beyond local features. This indicates that, as the amount of edge in the landscape increased, raccoon activity was higher across all local habitats sampled, not just in areas with local edge features. For instance, tracking stations in non-wooded fencerows and oldfields also received a

high frequency of raccoon visits. This increased activity across the landscape apparently did not extend to tracking stations in or near pasture, which still had a low frequency of raccoon visits, even in landscapes with extensive edge.

The landscape scale measure of corn became non-significant when local features were included in the same model. As the amount of corn in the landscape increases, wooded cover is reduced to wooded fencerows and small woodlots that often contain species such as white ash and sugar maple. This result reflects the fact that in landscapes with large amounts of corn, raccoons seldom visited tracking stations that were not in fencerows or woodlots. In these landscapes, raccoons may be limiting their activities to wooded areas and the crops in the near vicinity of the wooded cover. However, raccoons may be moving through crops, and since there were no tracking stations in crops, this finding is tentative.

At the local scale, vegetation between 1 m and 2 m in height had effects above and beyond landscape features. As noted, these features are commonly found in fencerows and this result suggests that raccoons frequent fencerow and edge situations, regardless of the landscape they are in. Frequency of occurrence of sugar maple also remained significant with landscape features in the analysis. Interpreted at a local scale, this suggests that, regardless of the landscape, raccoons frequent maple trees, probably for daytime rest sites and denning purposes. I have suggested that sugar maple may also be interpreted as a surrogate for deciduous woods. Landscapes with extensive coverage of deciduous woods, and consequently low amounts of edge, often had relatively high numbers of raccoon track station visits. This phenomenon

was poorly described by the relationship between raccoons and landscape level edge and may be another reason for the continued significance of sugar maple.

Conversely, the local effect of white spruce was subsumed by the landscape level edge effect. Spruce occurred almost solely as part of large tracts of mixed forest, with little agricultural edge. The low number of raccoon track station visits in such situations was well described by the relationship with landscape level edge.

As noted, there are several possible outcomes to a cross scale habitat study. In the present study, many of the patterns at the local scale were reflected at the landscape scale. Local woody plant species and structural features that were indicative of fencerows were frequented by raccoons, and landscapes with more of this preferred local habitat had more raccoon activity. I have also suggested that the effect of sugar maple and white spruce, measured locally, can be scaled up to explain coarser patterns. Local variables did provide some insight into the mechanism behind these patterns: fruit bearing species, such as wild red raspberry, provide food to raccoons, and sugar maples provide den sites in wooded areas. The inclusion of more local variables, such as bird or small mammal abundance and local crop types, would undoubtedly provide more mechanistic insight.

The effect of landscape level corn does not appear to scale down directly. Raccoons preferentially locate in landscapes with increasing cover of corn; however they appear to distribute themselves within the landscape based on more locally distributed woody vegetation features. Orians and Wittenberger (1991) found that female yellow headed blackbirds in Washington State preferentially nested on marshes

with high populations of Odonates, but established nest sites within the marsh based on local vegetation density. Adult birds often moved away from the nest sites to forage in the most Odonate-rich areas of the marsh. Different results at local and landscape scales appear to be most common when preferred resources are spatially separated.

Pearson (1993) studied overwintering bird populations in Georgia and found that 60 percent of the variability in the abundance of generalist species was related to local vegetation features, while only 13 percent was attributed to landscape features. He hypothesized that habitat generalists were less likely to be affected by the landscape they were in and more likely to be driven by fine scale discrimination of food and cover sites. This finds tentative support in the present study where raccoons did show a unique landscape level edge effect, but significant local variables were more numerous and explained more deviance.

GENERAL DISCUSSION

This study established that raccoons and skunks vary in abundance in areas with different levels of agricultural intensity, measured as percent wooded cover. In particular, skunks increased in abundance as the amount of wooded cover in the landscape decreased. Raccoons increased in landscapes with intermediate amounts of wooded cover. These landscapes often contain an extensive length of interface between wooded cover and land used for agricultural purposes (i.e. agricultural edge) which raccoons were shown to frequent at both local and landscape scales. Raccoons also maintained high abundance within woodlots and wooded fencerows in high intensity agricultural areas with extensive corn cover.

Raccoons and skunks are not the only native North American species to reach high abundances in agricultural areas. Other species generally considered to benefit from agricultural activity include: red fox (*Vulpes vulpes*), opossum (*Didelphis virginiana*), coyote (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*), and gulls (*Larus* spp.) (Garrott *et al.* 1993). All of these species can make use of a variety of food types including both agricultural produce and native flora and fauna. The overabundance scenario outlined for raccoons and skunks may more realistically involve a guild of overabundant generalists that collectively exerts an intense selective force on species attempting to coexist in these agroecosystems.

In order to build on the findings in the present study, future studies should attempt to quantify the effect that raccoons, skunks, and other overabundant species

have on native flora and fauna. Experiments that measure the response of target prey species to the removal or exclosure of specific overabundant species would help to meet this end (*e.g.* Alverson *et al.* 1988). When possible, these experiments should be spatially explicit, as the effect of predation is likely to be scale dependent. For instance, raccoon predation in forest fragments may be much more intense in landscapes with little wooded cover and extensive corn cover, than in landscapes with more extensive wooded cover.

The prey species chosen for study will depend on the food sources and feeding patterns of the overabundant species in a particular geographic region. As discussed in the first chapter, reduced bird nesting success is well recognized as a potentially negative effect of raccoon and skunk overabundance. Other groups also have the potential to show adverse effects and should be considered for further study. Several turtle species have been reported to suffer heavy egg loss, generally between 50 and 100 percent, due to predation (Christen and Bider 1987, Congdon *et al.* 1987, and Temple 1987). Raccoons were identified as a major predator in each of these studies, while skunks were implicated to a lesser extent. Although less well studied, heavy predation on anurans has also been reported for raccoons (Schaaf and Garton 1970) and skunks (Groves 1980). In areas with increasing amounts of agricultural activity there is less and less aquatic habitat for these amphibious groups. Heavy predation, coupled with this loss in habitat could result in reduced herpetofaunal diversity in agricultural areas.

One potential indirect interaction involves skunks, raccoons, and small

mammal trophic specialists, such as the short-tailed weasel (*Mustela erminea*). In southern Scandinavia, a guild of mammalian and avian generalists make use of the rich array of resources that result from the mixed farming that is carried out in that region (Erlinge *et al.* 1983, Korpimäki 1986). These generalist species also account for about 80 percent of the predation on small mammals in this region, while specialists in the weasel family account for only 20 percent (Erlinge *et al.* 1983). In northern Scandinavia, where there is little or no farming, microtine rodents exhibit 4-5 year population cycles (Hansson 1984); this pattern is not found in southern Scandinavia. It has been suggested that the generalist species prevent microtine population cycles from developing in this region by switching to alternative prey sources when microtine populations are low and switching back when populations begin to increase (Erlinge *et al.* 1983, Angelstam *et al.* 1984). These studies do not report how these alterations affect the trophic specialists in the weasel family, but it seems likely that their abundance would also be affected. Skunks (Hamilton 1936, and Llewellyn and Uhler 1952) and, to a lesser extent, raccoons (Hamilton 1951, and Schoonover and Marshall, 1951) are reported to feed on mice. These species, in combination with other common generalists, such as the red fox, coyote, and ring-billed gull, may affect the abundance and persistence of weasels in North American agroecosystems through competition for prey species.

It has been suggested that predation generates diversity by limiting the ability of a select few competitors to monopolize resources (Paine, 1966). However, when alternative, human-generated resources are available, predators can maintain high

populations independent of fluctuations in natural prey populations. Under such circumstances, predators have the potential to reduce the abundance and diversity of prey species. This study is not intended as a "call to arms" against raccoons and skunks in agricultural areas. However, it is intended to alert ecologists to a potentially important conservation issue and provide empirical evidence for a justified and educated management response.

Appendix 1 Estimating the amount of cultural energy involved in pasture production.

Based on interviews (n=10) and personal observations, a common approach to pasture production in the Ottawa area is to establish a pasture field and leave it with little or no maintenance for approximately 5 years. Pimentel (1980) provides an estimate of the amount of cultural energy required to establish and harvest hay. By modifying this estimate such that it represents only the amount of energy used to establish the hay, and then prorating it over the average 5 year life span of a pasture field, I was able to produce a reasonable measure for the average energy input/ha/year for pasture. The specifics of the estimate are shown below.

Item	Quantity/ha	Kcal/ha
Machinery ¹	9.16 kg	161 420
Fuel ²	5.26 l	49 856
Nitrogen	3.18 kg	46 746
Phosphorus	3.18 kg	3 498
Potassium	13.62 kg	21 792
herbicide	0.09 kg	9 092
seed	1.14 kg	23 940
Total input for establishment		269 598
Average energy input per year		53 920

¹ based on use of 1 tractor, 1 set of tandem discs, 1 harrow, and 1 seed drill

² half the value given by Pimentel (1980) to produce and harvest hay

Appendix 2 Independent variables included in the stepwise Poisson regression analyses used to determine the best set of local and landscape variables describing raccoon habitat use.

Local Woody Vegetation Variables:

red maple (*Acer rubrum*)
 white ash (*Fraxinus americana*)
 red pine (*Pinus resinosa*)
 white elm (*Ulmus americana*)
 trembling aspen (*Populus tremuloides*)*
 wild red raspberry (*Rubus idaeus*)
 willow (*Salix* sp.)*
 basswood (*Tilia americana*)*
 ironwood (*Carpinus caroliniana*)
 white cedar (*Thuja occidentalis*)
 sugar maple (*Acer saccharum*)
 common buckthorn (*Rhamnus cathartica*)
 red oak (*Quercus rubra*)
 yellow birch (*Betula lutea*)
 red osier dogwood (*Cornus stolonifera*)
 riverbank grape (*Vitis riparia*)*
 Canada plum (*Prunus nigra*)
 prickly ash (*Xanthoxylum americanum*)
 pin cherry (*Prunus pensylvanica*)
 Manitoba maple (*Acer negundo*)
 narrowleaf meadowsweet (*Spiraea alba*)
 white spruce (*Picea glauca*)
 vegetation 0.0-0.5 m in height
 vegetation 0.5-1.0 m in height
 vegetation 1.0-2.0 m in height
 vegetation 2.0-6.0 m in height
 vegetation over 6.0 m in height

Landscape level Variables:

percent cover of corn*
 percent cover of grain
 percent cover of hay
 percent wooded cover*
 length of agricultural edge*

*linear and quadratic terms included in analysis

REFERENCES

- Addicott, J.F., J.M. Aho, M.F. Antolin, D.K. Padilla, J.S. Richardson, and D.A. Soluk. 1987. Ecological neighbourhoods: scaling environmental patterns. *Oikos* 49:340-346.
- Allen, D.L., and W.W. Shapton. 1942. An ecological study of winter dens with special reference to the eastern skunk. *Ecology* 23:59-68.
- Alverson, W.S., D.M. Waller, and S.L. Solheim. 1988. Forests too deer: Edge effects in northern Wisconsin. *Conservation Biology* 2:348-358.
- Anderson, J.E. 1991. A conceptual framework for evaluating and quantifying naturalness. *Conservation Biology* 5:347-352.
- Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. *Oikos* 47:365-373.
- Angelstam, P., E. Lindström, and P. Widén. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia (Berlin)* 62:199-208.
- Best, L.B. 1983. Bird use of fencerows: implications of contemporary fencerow management practices. *Wildlife Society Bulletin* 11:343-347.
- Bider, J.R. 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. *Ecological Monographs* 38:269-308.
- Caughley, G. 1981. Overpopulation. Pages 7-9 *In* P.A. Jewell, and S. Holt, eds. *Problems of management of locally abundant wild animals*. Academic Press, New York.
- Chessness, R.A., M.M. Nelson, and W.H. Longley. 1968. The effect of predator removal on pheasant reproductive success. *Journal of Wildlife Management* 32:683-697.
- Christens, E., and J.R. Bider. 1987. Nesting activity and hatching success of the painted turtle (*Chrysemys picta marginata*) in southwestern Quebec. *Herpetologica* 43:55-65.
- Christensen, K.M., and T.G. Whitham. 1993. Impact of insect herbivores on competition between birds and mammals for pinyon pine seeds. *Ecology* 74:2270-2278.

- Congdon, J.D., G.L. Breitenbach, R.C. van Loben Sels, and D.W. Tinkle. 1987. Reproduction and nesting ecology of snapping turtles (*Chelydra serpentina*) in southeastern Michigan. *Herpetologica* 43:39-54.
- Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122:81-116.
- Dixon, J. 1925. Food predilections of predatory and fur-bearing mammals. *Journal of Mammalogy* 6:34-46.
- Dorney, R.S. 1954. Ecology of marsh raccoons. *Journal of Wildlife Management* 18:217-225.
- Dunning, J.B., B.J. Danielson, and H.R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169-175.
- Ellis, R.J. 1964. Tracking raccoons by radio. *Journal of Wildlife Management* 28:363-368.
- Emmons, L.E. 1984. Geographic variation in densities and diversities of non-flying mammals in Amazonia. *Biotropica* 16:210-222.
- Erlinge, S., G. Göansson, L. Hansson, G. Högstedt, O. Liberg, I.N. Nilsson, T. Nilsson, T. von Schantz, and M. Sylvén. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. *Oikos* 40:36-52.
- Estrada, A., R. Coates-Estrada, and D. Meritt, Jr. 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. *Ecography* 16:309-318.
- Fritzell, E.K. 1978. Habitat use by prairie raccoons during the waterfowl breeding season. *Journal of Wildlife Management* 42:118-127.
- Garrot, R.A., P.J. White, and C.A. Vanderbilt White. 1993. Overabundance: an issue for conservation biologists. *Conservation Biology* 7:946-949.
- Gates, J.E., and L.W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871-883.
- Groves, J.D. 1980. Mass predation on a population of the American toad, *Bufo americanus*. *The American Midland Naturalist* 103:202-203.

- Hamilton, W.J., Jr. 1936. Seasonal food of skunks in New York. *Journal of Mammalogy* 17:240-246.
- Hamilton, W.J., Jr. 1951. Warm weather foods of the raccoon in New York State. *Journal of Mammalogy* 32:341-344.
- Hansen, J.A., S.L. Garman, B. Marks and D.L. Urban. 1993. An approach for managing vertebrate diversity across multiple-use landscapes. *Ecological Applications* 3:481-496.
- Hansson, L. 1984. Predation as a factor causing extended low densities in microtine cycles. *Oikos* 43:255-256.
- Hanski, I., and J. Tiainen. 1988. Populations and communities in changing agro-ecosystems in Finland. *Ecological Bulletins* 39:159-168.
- Hastie, T.J., and D. Pregiborn. 1992. Generalized linear models. Pages 195-247 *In* J.M. Chambers and T.J. Hastie, eds. *Statistical Models in S*. Wadsworth and Brooks/Cole Advanced Books and Software, Pacific Grove, California.
- Houseknecht, C.T., and J.R. Tester. 1978. Denning habits of striped skunks (*Memphitis memphitis*). *American Midland Naturalist* 100:424-430.
- Kadlec, J.A. 1971. Effects of introducing foxes and raccoons on herring gull colonies. *Journal of Wildlife Management* 35:625-636.
- Kotliar, N.B., and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253-260.
- Korpimäki, E. 1986. Predation causing synchronous decline phases in microtine and shrew populations in western Finland. *Oikos* 46:124-127.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943-1947.
- Lindström, E.R., H. Andrén, P. Angelstam, G. Cederlund, B. Hörnfeldt, L. Jäderberg, P. Lemnell, B. Martinsson, K. Sköld, and J.E. Swenson. 1994. Disease reveals the predator: Sarcoptic mange, red fox predation, and prey populations. *Ecology* 75:1042-1049.
- Llewellyn, L.M., and F.M. Uhler. 1952. The foods of fur animals of the Patuxent Research Refuge, Maryland. *American Midland Naturalist* 48:193-203.

- Lodge, D.M., M.W. Kershner, J.E. Aloï, and A.P. Covich. 1994. Effects of an omnivorous crayfish (*Oronectes rusticus*) on a freshwater littoral food web. *Ecology* 75:1265-1281.
- Lorze, J. and S. Anderson. 1979. *Procyon lotor*. *Mammalian Species* 119:1-8.
- Matthiae, P.E., and F. Stearns. 1981. Mammals in forest islands in southeastern Wisconsin. Pages 55-66 *In* R.L. Burgess, and D.M. Sharpe eds. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag Inc., New York.
- McCullagh, P., and J.A. Nelder. 1989. *Generalized linear models* (2nd edition). Chapman and Hall, London.
- McDonnell, M.J., and S.T.A. Pickett. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology* 71:1232-1237.
- Merriam, H.G. 1984. Connectivity: a fundamental ecological characteristic of landscape pattern. Pages 5-15 *In* J. Brandt and P. Agger eds. *Proceedings of the 1st international seminar on methodology in landscape ecological research and planning*. International Association for Landscape Ecology, Roskilde, Denmark.
- Merriam, H.G. in press. Movement in spatially-divided populations: responses to landscape structure. *In* W.Z. Lidicker ed. *Landscape approaches in mammalian ecology and conservation*, in press. University of Minnesota Press, Minneapolis, USA.
- Morris, D.W. 1987. Ecological scale and habitat use. *Ecology* 68:362-369.
- Murie, O.J. 1954. *A field guide to animal tracks*. Houghton Mifflin Company, Boston, Mass.
- Neter, J.W., W. Wasserman, and M.H. Kutner. 1985. *Applied Linear Statistical Models*. Richard D. Irwin Inc., Homewood, Illinois.
- Niemalä, J.K., and J.R. Spence. 1994. Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. *Ecography* 17:166-175.
- Odum, E.P. 1971. *Fundamentals of ecology*. W.B. Saunders Company, Philadelphia, Pennsylvania, USA.

- O'Neill, R.V., D.L. DeAngelis, J.B. Waide, and T.F.H. Allen. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey.
- Orians, G.H., and J.F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137:S29-S49.
- Paine, R.T. 1966. Food web complexity and species diversity. *The American Naturalist* 100: 65-75.
- Parker, R.L. 1975. Rabies in skunks. Pages 41-51 *In* G.M. Baer ed. The natural history of rabies. Academic Press, New York.
- Pearson, S.M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. *Landscape Ecology* 8:3-18.
- Picman, J. 1988. Experimental study of predation on eggs of ground-nesting birds: effects of habitat and nest distribution. *The Condor* 90:124-131.
- Pimentel, D. 1980. Handbook of energy utilization in agriculture. CRC Press, Boca Raton, Florida.
- Ryszkowski, L. 1985. Impoverishment of soil fauna due to agriculture. *Intecol Bulletin* 12:6-17.
- SAS. 1990. SAS/STAT Users Guide, Version 6, Fourth Edition, Volume 2. SAS Institute Inc., Cary, NC, USA.
- Schaff, R.T., and J.S. Garton. 1970. Raccoon predation on the American toad, *Bufo americanus*. *Herpetologica* 26:334-335.
- Schoener, T.W. 1983. Field experiments on interspecific competition. *American Naturalist* 122:240-285.
- Schoonover, L.J., and W.H. Marshall. 1951. Food habits of the raccoon (*Procyon lotor*) in north-central Minnesota. *Journal of Mammalogy* 32:422-428.
- Selko, L.F. 1937. Food habits of Iowa skunks in the fall of 1936. *Journal of Wildlife Management* 1:70-76.
- Shirer, H.W., and H.S. Fitch. 1970. Comparison from radio-tracking of movements and denning habits of the raccoon, striped skunk, and opossum in northeastern Kansas. *Journal of Mammalogy* 51 '91-503.

- Sih, A., P. Crowley, M. McPeck, J. Petrenka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16:269-311.
- Small, M.F., and M.L. Hunter. 1988. Forest fragmentation and avian nest predation in forested landscapes. *Oecologia* 76:62-64.
- Smith, G.C., and S. Harris. 1991. Rabies in urban foxes (*Vulpes vulpes*) in Britain: the use of a spatial stochastic simulation model to examine the pattern of spread and evaluate the efficacy of different control regimes. *Philosophical Transactions of the Royal Society of London B* 334:459-479.
- Sonenshine, D.E., and E.L. Winslow. 1972. Contrasts in distribution of raccoons in two Virginia localities. *Journal of Wildlife Management* 36:838-847.
- Soulé, M.E., D.T. Bolger, A.C. Alberts, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2:75-92.
- Stains, H.J. 1961. Comparison of temperatures inside and outside two tree dens used by raccoons. *Ecology* 42:410-413.
- Storm, G.L. 1972. Daytime retreats and movements of skunks on farmlands in Illinois. *Journal of Wildlife Management* 36:31-45.
- Stuewer, F.W. 1943. Raccoons: their habits and management in Michigan. *Ecological Monographs* 13:203-257.
- Suhonen, J., K. Norrdahl, and E. Korpimäki. 1994. Avian predation risk modifies breeding bird community on a farmland area. *Ecology* 75:1626-1634.
- Taylor, P.D., L. Fahrig, K. Henein, and H.G. Merriam. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68:571-573.
- Temple, S.A. 1987. Predation on turtle nests increases near ecological edges. *Copeia* 1987:250-252.
- Terborgh, J., and B.G. Winter. 1980. Some causes of extinction. Pages 119-131 *In* M.E. Soulé and B.A. Wilcox, eds. *Conservation Biology: an ecological-evolutionary perspective*. Sinauer Associates, Sunderland, Massachusetts, USA.

- Thomas, M.B., S.D. Wratten, and N.W. Sothorn. 1992. Creation of 'island' habitats in farmland to manipulate populations of beneficial arthropods: predator densities and species composition. *Journal of Applied Ecology* 29:524-531.
- Tester, J.R. 1953. Fall food habits of the raccoon in the South Platte Valley of northeastern Colorado. *Journal of Mammalogy* 34:500-502.
- Turkowski, J.F., and L.D. Mech. 1968. Radio-tracking the movements of a young male raccoon. *Journal of the Minnesota Academy of Science* 35:33-38.
- Twitchell, A.R., and H.H. Dill. 1949. One hundred raccoons from one hundred and two acres. *Journal of Mammalogy* 30:130-133.
- Urban, D. 1970. Raccoon populations, movement patterns, and predation on a managed waterfowl marsh. *Journal of Wildlife Management* 34:372-382.
- Verts, B.J. 1967. The biology of the striped skunk. University of Illinois Press, Urbana.
- Wade-Smith, J., and B.J. Verts. 1982. *Memphitis memphitis*. *Mammalian Species* 173:1-7.
- Ward, D., and D. Saltz. 1994. Foraging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev Desert. *Ecology*:48-58.
- Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Wiens, J.A., J.F. Addicott, T.J. Case, and J. Diamond. 1986. Overview: The importance of spatial and temporal scale in ecological investigations. Pages 145-153 *In* J. Diamond and T.J. Case eds. *Community Ecology*. Harper and Row, New York.
- Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211-1214.
- Wootton, J.T. 1992. Indirect effects, prey susceptibility and habitat selection: impacts of birds on limpets and algae. *Ecology* 73:981-991.

END

0 5 - 0 6 - 9 5

FIN