

Life on the Edge: The Eastern Screech-Owl in Winnipeg

by

Christian Artuso

A Thesis submitted to the Faculty of Graduate Studies of
The University of Manitoba
in partial fulfilment of the requirements of the degree of

Doctor of Philosophy

Department of Environment and Geography

University of Manitoba

Winnipeg

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FACULTY OF GRADUATE STUDIES

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**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of
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Of

Doctor of Philosophy

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ABSTRACT

Cavity-nesting birds may be sensitive to urbanization due to changes in the availability of breeding resources. Nonetheless, the Eastern Screech-Owl has higher productivity and survival in suburbs than rural areas in the southern portion of its range (Texas). Densities and life-history traits of birds may differ in range peripheral areas, rendering generalization about the effect of urbanization difficult. I examined the population density, reproduction, habitat selection, and diet of Eastern Screech-Owls in Manitoba to test whether the patterns observed in Texas held at the northern periphery of the range, and whether such patterns would be more or less pronounced. I conducted a random-stratified survey across a rural to urban gradient and monitored nests in natural cavities and nest boxes. I collected data on diet and measured variables related to the cavity tree and at the habitat level at nests and unused cavities.

Eastern Screech-Owl density was positively correlated with human density, peaking in medium to high-density suburbs. Screech-owls preferred riparian habitat but densities and breeding in residential areas versus greenspace did not differ. Brood sizes peaked in suburban areas, where fledging averaged five days in advance of rural areas. Owls selected habitat where canopy cover was relatively high, and with sufficient potential nest-sites close to some coniferous trees. They selected nest sites in taller trees, closer to water and with lower shrub density below the nest than unused cavities. They avoided potential nest sites with more buildings and higher domestic cat activity. Screech-owls had a more diverse diet with more vertebrate prey in low-density suburban areas as opposed to rural and high-density suburban areas. The mechanisms behind this pattern

appear to be the urban heat island, reduced predation, greater diversity of prey, and favorable habitat alteration including planted conifers and buildings for roosting and more open vegetation. The percentage of rufous morph screech-owls in Manitoba has fallen from 6-11% in the 1920s to <1% today, whereas no decline has occurred in Minnesota or North Dakota. I argue that, based on differences in survival rates between color morphs in extreme cold, this is evidence of a northward range expansion facilitated by the anthropogenic influences noted above.

The differences in density, reproductivity, and breeding phenology between suburban and rural areas, as well as the mechanisms involved, are similar to those found in Texas, suggesting that, at least in this case, the influence of urbanization is not strongly mitigated by latitude.

ACKNOWLEDGEMENTS

I would like to thank my funding sources: The University of Manitoba Graduate Fellowship, The Special Conservation Fund of Manitoba Conservation, Manitoba Hydro, The Winnipeg Foundation, and the Great Gray Owl Fund administered by R. W. Nero, as well as a kind donation by Pat Cooper.

I wish to thank the members of my committee, Merlin W. Shoesmith, Richard K. Baydack, James R. Duncan, Nicola Koper for their support and guidance throughout the degree process. I also thank other faculty members of the University of Manitoba whose instruction and assistance have been invaluable to me including Stéphane McLachlan, Spenser G. Sealy, David Walker, and James F. Hare. These chapters were greatly improved by the thoughtful comments of Richard K. Baydack, Robert P. Berger, Brigitte De March, Larry De March, James R. Duncan, John M. Eadie, Frederick R. Gehlbach, C. Stuart Houston, Karla Kinstler, Nicola Koper, Erkki Korpimäki, Robert W. Nero, Spenser G. Sealy, Peter Taylor, Merlin W. Shoesmith, and various anonymous reviewers. I thank Brigitte De March, Nicola Koper, and David Walker for their help with the various statistical applications used. I thank Robert P. Berger, James R. Duncan, Terry Galloway, Randy Mooi, Justin Rasmussen, Rob Roughly, and Spenser G. Sealy for assistance in identifying prey remains. I am grateful to Dale Marciski, the Outreach Officer at the Meteorological Service of Environment Canada, for his assistance in gathering climate data.

The following people submitted observations of Eastern Screech-Owl and Great Horned Owl in Manitoba, participated by listening for owls in their area, contributed sight records for the historical database (even indirectly, e.g. by taking birds found injured to rehabilitation), helped collecting pellets, helped to monitor roost sites, gave me permission to enter their property, or otherwise assisted me in various aspects of fieldwork or preparing manuscripts. I thank them all immensely: Linda Anderson, Nancy Anderson, Leslie Andrews, Nadine Andrusiak, Terry Angus, Alfred Aug, Ron Austin, Melissa Baer, Ken Baker, David Barnes, Pat Barnes, Mary Barrett, Derek Bartray, Nathalie Bays, Barny Beaulieu, Kurt Belton, Leane Belton, Gloria Benhem, Keith Benson, Keith Benson, Ballie Berger, Henry Berger, Ron Berglund, Jim Bertwhistle, Patty Best, Brad Bird, Marcia Blair, Murray Blair, Luc Blanchette, Frank Boileau, Jim Boulton, Chris Boumford, David Bowles, Erl Braaten, James Bradley, Joy Bradley, Louise Brisebois, Jack Brown, Paul Buchanan, Bill Buhler, Gary Budyck, Greg Buzza, Tim Byers, Alison Campbell, Kevin Campbell, Brad Carey, Leslie Carignan, Brendan Carruthers, Silvio E. Cascino, Michelle Caughy, David Chevalier, Dan Chranowski, Phil Christianson, Ward Christianson, Dave Christie, John Christie, Jamie Chuback, Ed Chudrick, Redmond Clarke, Steve Clubb, Michael Cobus, Colin Conrad, Kyle Conrad, Michael Conrad, Pat Cooper, Andy Courcelles, Lea Craig, Jack Crolley, John Cunningham, Charles Curtis, Cal Cuthbert, Edgar Dandridge, Steve Davidge, Rob de Graaf, Brigitte De March, Larry de March, Chris De Ruyck, Ben DeBeer, Angel Delorme, Steve Demmings, Ken De Smet, Paul Desrosiers, Nick Devine, Wil DeWit, Jeddich Doerksen, Cindy Dowse, Ronald Dueck, James R. Duncan, Patsy Duncan, Alvin Dyck, Bill Eaton, Estelle Eaton, Kyle Elliott, Richard Ellis, Adolf Ens, Kristen Erikson,

Dennis Fast, Debi Forlanski, Margaret Frederikson, Paul Friesen, Maureen Frolick, Barbara Fuller, Vern Gaddows, Ian Gagnon, Wendy Garson, Corinna Gascho, Margaret Gibson, Randy Giesbrech, Doreen Giesbrecht, Mary Giesbrecht, Marlene Gifford, Mike Gigian, Ed Gilroy, Micheline Girard, Miles Goolie, Paul Goossen, Gordon Grieff, Jaye Grieff, Paula Grieff, Susan Grieff, Jim Gyselinck, Keith Hamblin, Cary Hamel, Derrick Hampton, Lavin Hanke, Hao He, Bob Hart, David Hatch, Jerry Hayes, John Hays, Carolyn Hernandez, Ruth Hiebert, Jeff Higdon, Chris Higgs, Leane Hill, Heather Hinam, Frank Hinings, Debbie Hobbs, Janice Hobbs, George Holland, Jean Horton, Ray Iverson, Jang Byoung-Soon, Liesel Jansson, Reinhard Jansson, Maricia Johnson, Paul Jones, Bernice Kennedy, Janet Kennedy, Fawad Khan, Mark King, Sally King, Todd King, Janis Klapecki, Lorne Klassen, Rudolf Koes, Hilton Kotyk, Brenda Kroeker, Roy Laham, Linda Laham, Heather Laird, Bill Lapuck, Georgina Larson, Raymond Larson, Betty Lavender, Anne Layman, Lew Layman, Kathleen Leathers, Yun-Kyoung Lee, Gladys Legal, Nick Leone, Sid Leverick, Michael Lewyc, Pat Lewyc, Li Chunxiao, Cory Lindgren, Alain Louer, Dean MacDonald, Frank Machovec, Irene Magnuson, Nia Massey, Brenda Maxwell, Christian McBride, Les McCann, Hope McGaha, Stéphane McLachlan, Ted McLachlan, Ardylle McMaster, Dan McMaster, Glen McMaster, Laura McMaster, Dean Medeiros, Sarah Medill, Norm Melnychuk, Gwen Mewendorss, Al Mickey, Don Middleton, Kim Middleton, Corey Millar, Lucille Miller, Marthat Moffat, R. Moodie, Fred Mooi, Randy Mooi, Janet Moore, Liz Morash, Ian Morrow, John Murray, Joan Murray, Shirley Murray, Gwen Mwenendorf, Wayne P. Neilly, John Neils, Robert W. Nero, Darrel Neufeld, Harry Neufeld, Lori Nichols, Robb Nicholl, Kevin Nixon, Bruce Norvey, George Nykuleik, Gerry Oliver, Cheryl Orr, Phil Ould, Rachel Panteau, Brian Parkers, Robert Parsons, Terry Pastrick, Fred Pawlyszyn, Monica Pazerniuk, Linda Pearn, Carole Penner, Jake E. Peters, Jennifer Pollock, Barry Pomeroy, Ryan Porteous, Angelé Pradaehi, Susan Procner, Gordon Prouse, Mike Quigley, Justin Rasmussen, Jacklyn Regehn, Don Reimer, Mary Reimer, Elvira Roberge, Amber Robinson, Robert Robinson, Rong Rong, Sherri Routly, Alex Sanderson, Chris Sands, Linda Sands, Linda Scarrow, Wayne Scarrow, Allan Scarth, Al Schirtt, Dorothy Schirtt, Inara Schwartz, Gerald Scott, Sue Scott, Jean Scriven, Spenser G. Sealy, Bob Sellars, Bud Shadholt, Bill Shestopalka, Courtenay Shultz, Richard Silverman, Dawn Simmons, Ken Simonite, Bob Sinclair, Lynn Sinclair, Rob Sinclair, Janet Skavinski, John Skene, Jeff Sleno, Mike Slobodian, Alex Small, Borden Smid, Monica Smith, Penny Smith, Rick Smith, Sheila Smith, Shirley Snyder, Richard Sobkowich, Grace Sommerholder, Marlene Sommerville, Doug Southam, Barbara Staciewicz, Diana Staniforth, Richard Staniforth, Bob Stewart, Bill Stokes, Bob Stokes, Angela Stoppa, Thaila Stoppa, Brian Straub, Glen Suggett, Jo Swartz, Dennis Swayze, Eugene Szach, George Taylor, Peter Taylor, Robert Taylor, Yvette Taylor, Ruby Tekhaus, Catherine Thexton, Susan Thomas, Beth Thompson, Ken Tilling, Peter Tkachuk, Teo Tkachuk, Paul Tougas, Jeff Turner, Bob Tyler, Todd Underwood, David Unger, Jakon Unger, Donald Unruh, Marg Unruh, Hersh Upadhyay, Katrine Van den Meulen, Fran Vandermeuten, Liis Veelma, Audrey Veitch, Annette Verniest, Sherrie Versluis, Marlene Waldron, William J. Walley, Adam Walley, Glen Walley, Gene Walz, Ralph Wang, Dave Warrenchuk, Sigrid Warrenchuk, Barb Watson, Emmy Weibe, Ron Weibe, John Weier, Jerry Weshnoweski, Zena White, James Whitelaw, James Whitman, David Wiebe, Ron Wiebe, Jonathan Wiens, Diane Wilks,

Judy Winslow, Larry Winslow, Brent Young, Reto Zach, Laurie Zaporzan, Tom Zaporzan, Jerry Zaste, Sigrid Zueff, and George Zulich.

I also thank the following people who submitted observations of Eastern Screech-Owls from Minnesota, North Dakota and South Dakota: Phil Alban, Lowell Anderson, Deric Andol, Ruth Audbery, Doug Backland, Dave Bartkey, Betsy Batstone-Cunningham, Patrick Beauzay, Gayle Beecher, Ruth Beecher, Robert P. Berger, Judd Brink, David Cahlander, Elizabeth Campbell, Mark S. Citsay, Kathy Connelly, Keith Corliss, Hugh Curtler, Linda Curtler, Jeff Dankert, Rob Daves, Alyssa DeRubeis, Roger Dietrich, Herb Dingman, Terry Dorsey, Tim Driscoll, Bob Dunlap, Wayne Easley, Kim Eckert, Paul Egeland, Corey Ellingson, Laura Erikson, Ronald Erpelding, Lowell Fahani, Ben Fritchman, Rick Gjervold, Mark A. Gonzalez, Ray Greenwood, Anne Hanley, Peder Svingen, Paul Hertzell, Craig Hultberg, Gary Huschle, Larry Igl, Robert Janssen, Mike A. Johnson, Karla Kinstler, Jack Knoll, Gary Kuyava, David O. Lambeth, Leo Lantz, Jack Lefor, Fred Leshner, Dodie Logue, Craig Mandel, William Marengo, Ron Martin, Janelle Masters, Michelle McDowell, Michael Melius, Scott Meyer, Warren Nelson, Frank Nicoletti, Gary Nielsen, Robert Nordgren, Connie Norheim, Ricky Olsen, Gary Otnes, Marion Otnes, Keith Pulles, Patricia Quyle, Robert N. Randall, Dean Reimer, Kim Risén, Paulette Scherr, Al Schirmacher, Nathan Schirmacher, George Skinner, Terry Sohl, Marsha Sovada, Don Starkweather, Daniel Streifel, Dan Svingen, Anthony Hertzell, Clark Talkington, Dan Thimgan, Sandy Thimgan, Doug Thompson, Billy Joe Unzen, Tom Warwa, Steve Watson, Sherry Watson, Steve Weston, and Jim Williams.

The following museums provided information on Eastern Screech-Owl specimens in their collections or sightings from record card schemes: The American Museum of Natural History, The Bell Museum of Natural History, The Carnegie Museum of Natural History, The Cornell University Museum of vertebrates, The Field Museum of Natural History, The Harvard University Museum of Comparative Zoology, The Heritage North Museum (Dauphin, Manitoba), The Manitoba Museum, The Michigan State University Museum, The Provincial Museum of Alberta, The Royal Ontario Museum, The Royal Saskatchewan Museum, The Science Museum of Minnesota, The Smithsonian National Museum of Natural History, The Stewart Hay Memorial Museum in the University of Manitoba's Department of Biological Sciences, The University of Michigan Museum of Zoology, and The Yale Peabody Museum.

To Youn-Young Park
for her extraordinary patience
and continual vision and support,
without which i could never have risked such change
and without which this project would never have even got off the ground,
let alone bear fruit.

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ABBREVIATIONS

Av	average (also \bar{x})
Br	breeding season*
Can1, Can2	canonical axis 1 and 2 (from multiple discriminant function analyses)
DBH	diameter at breast height (of trees)
Dist. bldg	distance to nearest building
Dist. road	distance to nearest road
Dist. water	distance to nearest river or creek
DmCavH	diameter of trunk or branch at the height of the cavity
EASO	Eastern Screech-Owl (<i>Megascops asio</i>)
GHOW	Great Horned Owl (<i>Bubo virginianus</i>)
GHOW_Av	average detections of Great Horned Owl per survey transect*
GLM	general linear model
H.	height
HDcat	human density category*
High	bird species that tolerate high anthropogenic disturbance
MDA	multiple discriminant function analyses
Mig	passage migrants and winter visiting bird species
Min	bird species that tolerate only minimal anthropogenic disturbance
Minflpath	minimum flight path from cavity*
Mod	bird species that tolerate moderate anthropogenic disturbance
m.s	morph specified*
n.d	no date
Non-br	non-breeding season*
Non-p	non-passerines
NRCT	native riparian cavity trees (American elm, green ash, Manitoba maple, bur oak, basswood, and eastern cottonwood)
other dec	other deciduous tree (species other than those in NRCT)
open ugr	open understory (ground layer)
% candense	% canopy density above nest tree*
Pass	passerines
p/ha	number of people per hectare
Relcanheight	relative canopy height*
Res	resident and locally breeding bird species
Rip	riparian*
sp / spp	species (singular / plural)
tr	trees
W	wildlands areas (<1 p/ha)
R	rural areas (1 – 10 p/ha)
S1	low-density suburban areas (>10 – 20 p/ha)
S2	moderate density suburban areas (>20 – 30 p/ha)
S3	high-density suburban and urban areas (>30 p/ha)
S-h	high-density suburban and urban areas (>30 p/ha)
S-l	low-density and medium-density suburban areas (>10 – 30 p/ha)

* See text for operational definition used in this thesis

1. Introduction

BACKGROUND:

Avian Preadaptations to the Process of Urbanization

Birds react to the dramatic changes wrought on the landscape by urbanization in a great variety of ways. Birds are sometimes classified into broad categories depending on their tolerance for human activity, e.g. predevelopment species which tolerate little or no anthropogenic disturbance, suburban-adapted species which can benefit from some level of anthropogenic habitat change and human activity, and urban exploiters which benefit greatly from urbanization and which are either human commensals or near-obligate human symbionts (Blair 1996). Some of the best known examples of symbiotic avian/human relationships include the European Starling (*Sturnus vulgaris*), the House Sparrow (*Passer domesticus*) and the Chimney Swift (*Chaetura pelagica*), which formerly roosted and nested in large hollow trees but which subsequent to broad scale habitat change in North America now relies almost exclusively on human structures (Johnston 2001).

Such flexibility in the way birds respond to human activities makes summarizing the effects of urbanization on the world's avifauna a challenge; however, some general trends have been reported. Urban areas are sponsored environments for many species, e.g. certain corvids, at least in part because of the prevalence of anthropogenic food sources. Therefore, despite their lower avian biodiversity, urban areas often have greater avian abundance (Emlen 1974, Walcott 1974, Gavareski 1976, Lancaster and Rees 1979,

Beissinger and Osborne 1982, Cicero 1989, Blair 1996, Jokimäki et al. 1996, Bolger 1997, Germaine et al. 1998, Cam et al. 2000, Blair 2001, Marzluff 2001, McKinney 2006, Palomino and Carrascal 2006, Smith and Wachob 2006). Peak biodiversity, at least on a local scale in North America, may occur at intermediate levels of human disturbance. This is perhaps because intermediate human disturbance levels appear to create conditions where the gain of suburban-adapted avian species exceeds the loss of predevelopment species (Batten 1972, Jokimäki and Suhonen 1993, Blair 1996, Blair 1999, Blair 2001, Adams 2005, Marzluff 2005, Donnelly and Marzluff 2006, Palomino and Carrascal 2006). Some have related this pattern to a theoretical relationship between net primary productivity (highest in urbanized environments) and species richness with species richness peaking at intermediate levels of productivity (Morin 1999, Mittelbach et al. 2001, Shochat et al. 2006). The relationship between net primary productivity and urbanization seems counterintuitive since impervious surfaces reduce primary productivity to near zero; however, this is compensated for by the above average primary productivity in several urban environments, in particular urban parks and greenspaces (Imhoff et al. 2000, Kaye et al. 2005, Shochat et al. 2006). In Europe and Africa, at least on a regional level, evidence for the association between intermediate human disturbance and avian biodiversity is lacking. Instead regions with high avian diversity correspond to relatively dense human populations, perhaps due to the distribution of resources and continental climatic patterns (Balmford et al. 2001, Chown et al. 2003, Gaston and Evans 2004, Norris and Harper 2004, Pidgeon et al. 2007). These observed differences illustrate the need to consider multiple spatial scales when seeking generalizations about urban environments (Clergeau et al. 2006).

Even if avian biodiversity does peak at intermediate levels of disturbance, this does not represent the whole picture, as the suite of species occupying heavily impacted areas tend to be very similar, whereas the species excluded from developing areas may be threatened or limited in their distribution. On the whole, urbanization appears to promote a decline in native species and increased abundance of alien species, since the latter are more often human symbionts (Jokimäki and Suhonen 1993, Zalewski 1994, Blair 1996, Rolando et al. 1997, Clergeau et al. 1998, Adams 2005, van Heezik et al. 2008). Many authors have thus argued that the net effect of urbanization is homogenization, i.e. a decrease in the avian biodiversity of a region despite possible increases at localized sites augmented by introduced species or species that have been able to use anthropogenic habitat change as a vehicle for range expansion (Jokimäki et al. 1996, Olden et al. 2004, Crooks et al. 2004, Adams 2005, Marzluff 2005, McKinney and Lockwood 2005, McKinney 2006). One possible mechanism behind this pattern of homogenization may be competition, with urban-adapted species with excellent colonizing abilities competitively excluding less disturbance-adapted species (Bennett 1990, Shochat et al. 2004, Shochat et al. 2006); however, it is important to note that competitive exclusion is likely a secondary mechanism under these circumstances with primary mechanisms such as higher productivity and resource abundance (Imhoff et al. 2000, Bolger 2001, Shochat et al. 2004, Kaye et al. 2005, Shochat et al. 2006), reduced predation (Marzluff 2001, Shochat et al. 2004, Shochat et al. 2006), the urban heat island (Shochat et al. 2006) and habitat change (Shochat et al. 2004) first increasing the carrying capacity of urban areas (Emlen 1974, Shochat et al. 2006) and thereby altering the dynamics of interactions and time-energy budgets. This creates a competitive advantage for those disturbance-adapted

species that are best suited to the characteristics of urban settings either through more efficient resource exploitation or interspecific aggression (Copley et al. 1999; Tryjanowski and Kuczynski 1999, Shochat et al. 2004, Shochat et al. 2006).

Although attempts to provide generalizations about urbanization often fail, many authors have sought to provide some clarity and predictability by examining the impact on higher taxonomic groupings (genus or family) or avian guilds — groups of species with similar habitat preferences, foraging strategies, migratory strategies or some other uniting feature. Dispersal capability is one of the features that may distinguish birds from many other taxa and yet there is considerable variability in the dispersal capability of different avian species and groups (Donnelly and Marzluff 2006). In the fragmented urban matrix, an ability not only to utilize small fragments but also for effective dispersal between fragments is essential. Dispersal is biologically stressful, and barriers to dispersal in urban areas such as roads can limit survivorship and gene flow (Pearce et al. 2007). For this reason good dispersers are favored over poor dispersers in urban environments (Garden et al. 2006) and the dispersal of some urban-exploiting species is facilitated by human activities and landscape changes (McKinney 2008). Nonetheless, long-distance dispersers (migrants) are disadvantaged in urban areas that they might exploit for only a limited portion of the year (Friesen et al. 1995, Lindsay et al. 2002, Green and Baker 2003, Kark et al. 2006). Resident species may have advantages over migrants in urban environments by acquiring local knowledge that enables them to adapt to fluctuating (human influenced) food supplies, altering disturbances regimes and localized predation threats (Stratford and Robinson 2005, Chace and Walsh 2006, Marzluff et al. 2007). One

study of a Nearctic to Neotropical migrant, the Acadian Flycatcher (*Empidonax virescens*) found that urbanization delayed nesting, lowered productivity (possibly via increased brood parasitism with fewer nesting attempts), and increased turnover in site occupancy, implicating both individual responses and population-level responses in this migrant's urban disadvantage (Rodewald and Shustack 2008).

Large body size can be a disadvantage in the patchy urban matrix where an ability to utilize small fragments is key (Chace and Walsh 2006). This may explain why top predators may be excluded from urban areas, providing mesopredators with reduced competition and access to ample resources (Crooks and Soulé 1999). Perhaps even more important than body size is home range size, since species with small territories and home ranges are more likely to be able to utilize urban fragments (Jokimäki 1999, Chace and Walsh 2006). A possible exception to this generalization may be species that do not necessarily reside in the urban matrix but which are able to move into urban areas for specific activities or to exploit temporary resources such as gulls that visit dump sites far from nesting colonies (Chace and Walsh 2006).

Habitat selection is another key factor in urban environments. Urban environments with their manicured lawns and shrubbery and profusion of roads and other impervious surfaces more closely resemble open habitats (e.g. early successional habitats) than mature forests. For this reason forest interior species tend to be excluded from urbanizing areas whereas open-country or early successional (disturbance-adapted) species may not be (Diamond 1986, Kluza et al. 2000). Habitat specialists are unlikely to find the

resources to match their foraging and breeding requirements in the urban mosaic, whereas habitat generalists, by virtue of their ability to exploit different habitats and resources, are more likely to be able to meet their needs (Aldrich and Coffin 1980). Ground-nesting species are frequently excluded from suburban areas with mowed lawns and easy access by predators and pedestrians; however, shrub-nesting species such as the Northern Cardinal (*Cardinalis cardinalis*) may have an advantage in such habitats where shrubs grow in rows and may be very dense as a result of pruning (Jokimäki 1999). Often related to habitat preferences, certain aspects of behavior are also important for a species ability to exploit urban landscapes. Neophobic species that for evolutionary reasons are geared towards stability of environment and resources are less likely to adapt to the rapid changes imposed on them in the urban matrix than species whose evolution has forced some degree of behavioral plasticity (e.g. in response to disturbances or environmental flux) (Sol and Lefebvre 2000, Kristan 2001, Sol et al. 2002).

Like habitat specialists, diet specialists are more likely to be excluded from developing areas whereas diet generalists, in particular omnivores, species that can capitalize on anthropogenic food sources such as bird seed or refuse, and some opportunistic nest predators are more likely to be suburban-adapted (DeGraaf and Wentworth 1986, DeGraaf 1991, Andren 1992, Zalewski 1994, Nilon et al. 1995, Jokimäki and Suhonen 1998, Haskell et al. 2001, Garden et al. 2006, Chace and Walsh 2006, Kark et al. 2006, Smith and Wachob 2006). Increased water availability around human settlements in dry habitats provides an advantage to many species, especially granivores, since this facilitates the digestion of dry seed permitting greater resource exploitation (Kotler et al.

1998). Some species have been shown to switch the composition of their diets in urban areas to favor seeds whereas they rely on food with higher moisture content such as fruit and flowers in undisturbed xeric habitats (Wolf and del Rio 2000).

None of the above generalizations offer the ability to predict which species will benefit and which will suffer from urbanization. A species' particular preadaptations, which can form the basis for microevolution, must also be considered (Fuller et al. 2006). The most obvious examples of microevolution include altering habitat selection from natural microhabitats to human structures, e.g. Metallic Starlings (*Aplonis metallica*) nesting in vents not tree cavities (Diamond 1986) or Chimney Swift switching from hollow trees to chimneys as nest and roost sites (Graves 2004). However, despite the general trend of increased likelihood of colonization success with increased behavioral plasticity (Sol et al. 2002), other secondary cavity nesting species have either not undergone a similar microevolution or not altered habitat selection to the same extent, necessitating a case-by-case examination of preadaptations and the plasticity of individual species.

An excellent example of species with different preadaptations at different points along the continuum of urban avoidance to suburban preadaptation is provided by three owl species, viz. Northern Spotted Owl (*Strix occidentalis caurina*), Great Horned Owl (*Bubo virginianus*) and Eastern Screech-Owl (*Megascops asio*).

The Northern Spotted Owl is the least suburban-adapted of these species. Despite being a relatively small-bodied (45cm) resident predator, the average home range of the Northern

Spotted Owl is extremely large, averaging over 10km² (Carey et al. 1990) and sometimes larger than 40km² (Hamer 1988). The Spotted Owl is a forest-dweller that avoids non-forested areas (Carey et al. 1990) and a specialist of old-growth forest (Gutiérrez et al. 1995) with old growth constituting as much as 75% of individual home ranges (Carey et al. 1990). Dispersing juveniles must be able to travel long-distances from their parent's territory to find suitable habitat and can therefore be compromised by deforested landscapes (Gutiérrez et al. 1995). As such, this species is unlikely to be able to meet its habitat requirements in human-altered landscapes.

The breeding biology of the Northern Spotted Owl is geared toward environmental stability in a relatively unchanging habitat (old-growth forest). The Northern Spotted Owl is long-lived, has somewhat delayed sexual maturity for a medium-sized owl (at least 2 years old), a low reproductive rate with few young per brood, and deferred breeding when food supplies are inadequate (Gutiérrez et al. 1995). This diet niche of the Northern Spotted Owl is relatively narrow as it preys mainly on squirrels, rodents and lagomorphs and to a lesser extent birds and invertebrates (Gutiérrez et al. 1995). As a consequence, the Northern Spotted Owl has not adapted well to human activity, and is considered an endangered species (U.S. Fish and Wildlife Service 1990). The Northern Spotted Owl is currently outcompeted in most habitats except large tracts of old growth forest by its closely related sister species, the Barred Owl (*Strix varia*), which is a generalist with smaller spatial requirements, a broader diet niche, and less specialized habitat requirements (Mazur and James 2000). The Barred Owl has benefited from

anthropogenic habitat change and spread into the range of the Northern Spotted Owl (Hamer 1988, Mazur and James 2000).

The Great Horned Owl (56cm) is larger than the Northern Spotted Owl and yet it is more disturbance-adapted and has not suffered the declines that the Northern Spotted Owl has. Of course these owls share some similarities such as cryptic plumage and a sit-and-wait hunting style that makes them relatively inconspicuous to human eyes — a considerable advantage to a predator around human settlements. They are both year-round residents in their respective habitats and reach sexual maturity at a similar age. However other biological differences translate in very different relationships with human beings. The Great Horned Owl is found throughout the Americas in almost every habitat type available from deserts to forests. This species even hunts over large untreed areas and can breed in small copses of trees in fragmented habitat matrices (Houston et al. 1998). As such the Great Horned Owl is able to utilize human-altered habitats and breeds in suburban areas with sufficient green space (Smith et al. 1999, Artuso 2007b).

The Great Horned Owl has other preadaptations to human-altered habitats. In addition to being a habitat generalist, this species is also a diet generalist and an opportunistic hunter able to exploit a wide variety of prey items. Unlike the Northern Spotted Owl, the Great Horned Owl also exhibits broader nest-site selection, utilizing stick nests made by other birds, cliff ledges, caves, hollow logs, goose nests on the ground, and even buildings or other human structures such as pipes or bridges (Houston et al. 1998). Such behavioral plasticity compensates for this owl's large size, giving access to a wide variety of

resources not available to a specialist. Therefore, despite its larger size, the home range size of the generalist Great Horned Owl (1 – 9km²) averages much smaller than the specialist Northern Spotted Owl (Houston et al. 1998). Living in more open habitats, the Great Horned Owl is not only able to disperse better across human-altered landscapes but is also more geared towards environmental flux than the Northern Spotted Owl, although northern populations do show periodic population trends following lagomorph cycles (Houston et al. 1998). The Great Horned Owl also commences breeding very early in the spring, perhaps another disturbance-adapted feature that permits re-nesting if required (Marti 1969).

The Eastern Screech-Owl (22cm) is by far the smallest of the three owl species discussed here and the most suburban-adapted of these species. The small body size and small spatial requirements (home-range size) of this species permit the utilization of relatively small urban habitat patches that could not provide sufficient resources for larger species. In the breeding season, the home ranges of Eastern Screech-Owls in southern Manitoba, at least as far as can be determined from repeat observations of territorial pairs, appear to be <1km², although this greatly increases during the non-breeding season (C. Artuso, unpublished data). In addition to its small body size, the Eastern Screech-Owl's cryptic plumage and nocturnal sit-and-wait hunting style make it extremely inconspicuous and thus less likely to experience human disturbance than larger predators. Like the Great Horned Owl, the Eastern Screech-Owl is a remarkable diet generalist and is capable of exploiting a variety of seasonal resources (Chapter 4), making it highly suited to suburban areas where it may benefit from concentrations of prey around bird feeders with

fallen seed or invertebrate abundance created by watering and fertilizing suburban gardens (Chapter 4).

Although the nest-site selection of the Eastern Screech-Owl (cavity nesting) is much more restrictive than the Great Horned Owl, its small size affords it a wider selection of suitable cavity nest-sites and the ability to use some human-made nest-boxes (Chapter 3). The Eastern Screech-Owl is also more restricted in habitat-selection than the Great Horned Owl, generally preferring mature but relatively open woodlands (Gehlbach 1995); however, in the open habitats of suburbia with tree-lined boulevards, city parks and open spaces such as lawns it finds a human-altered habitat that closely mimics its preferred open woodland habitat. Lawns and parks with open undergrowth are particularly well suited to the hunting style of the Eastern Screech-Owl, which does most of its hunting by pouncing on prey on the ground (Gehlbach 1994).

The Eastern Screech-Owl also has some preadaptations to life in suburban areas, associated at least in part with small body size. Unlike the Northern Spotted Owl, Eastern Screech-Owls breed annually, although clutch size appears to vary with food availability (Chapter 2). They have relatively large broods (2 – 6) in Manitoba (Chapter 2) and possibly as many as seven (Gehlbach 1995) with a relatively short incubation period that permits renesting if required (smaller species are likely to require renesting after predation events) (Gehlbach 1994). This species is also polyterritorial. In this thesis I use the term polyterritorial to mean defending multiple cavities within a single territory, not to indicate a polygynous species. The presence of several potential nest-sites means that

re-nesting following a disturbance does not require abandoning a resource-rich territory. Reaching sexual maturity at one year old, this species is capable of breeding rapidly and can exhibit a faster gene turnover than larger-bodied species (Gehlbach 1988, 1995), allowing for recovery following disturbance and exploitation of newly-available habitats, e.g. following the erection of nest-boxes. In this thesis, I will explore how the Eastern Screech-Owl exploits these preadaptations in suburban areas.

The Effect of Urbanization on Birds

Preadaptations and avian guild characteristics alone do not adequately describe the way urbanization affects birds. Avian ecologists have been searching for patterns specific to the types of fragmentation and disturbance that urbanization produces and the resulting influences on biodiversity (Fahrig 2003) and habitat connectivity (Sasvári and Moskát 1988, Jokimäki 1999, Platt and Lill 2006) in order to understand the various mechanisms behind such patterns and ultimately to inform the process of development such that impacts on avian communities are minimized (Rodewald 2006). Birds in urban environments have also been changing their behaviors and adapting in order to contend with human-altered conditions that affect their ability to reproduce and survive. Birds in urban or urbanizing areas face various forms of direct and indirect human disturbance, altered food sources and resource availability, altered competition and predation regimes due to changes in species composition, rapid habitat change, altered temperature (urban heat island) and mitigation of various natural cycles such as floods and droughts and other processes or of climatic variability (Shochat et al. 2004, Yeh and Price 2004, Parris and Hazel 2005, Shochat et al. 2006).

One possible consequence for birds living in urban settings is exposure to pollution and disease. Various effects of toxicity on birds have been documented in urban areas including the accumulation of lead (Getz et al. 1977), altered blood indices as a consequence of pollution (Kostelecka-Myrcha et al. 1997), and bioaccumulation of group elements such as platinum (Jensen et al. 2002). Noise pollution has also been shown to affect birds in urban areas causing them to expend energy by vocalizing louder and more frequently (Estes and Mannan 2003, Brumm 2004), to adjust calling frequencies (Slabbekoorn and Peet 2003) or to alter song phenology to favor times with less anthropogenic noise (Fuller et al. 2007). Since song is a fundamental mechanism of reproductive isolation in many birds, adapting to noise pollution may have evolutionary consequences for some species, leading to development of urban “subspecies” (Slabberkorn and Ripmeester 2008). As discussed above, urban conditions can promote higher avian densities but this has the potential to augment disease transmission (Johnson and Glahn 1994). One well-documented example of this pertains to Cooper’s Hawks (*Accipter cooperii*) in suburban Tucson, Arizona, which suffers 50% juvenile mortality as compared to 5% in rural populations due to a disease carried by their main prey, pigeons and doves (Estes and Mannan 2003), although this does not necessarily mean that urban areas are acting as population sinks for this species (Mannan et al. 2008). Red-winged Blackbirds (*Agelaius phoeniceus*) nesting in stormwater wetlands in residential and commercial areas with high human disturbance and moderate water quality were compromised in their nesting success resulting in a population sink one year but a source in another (Sparling et al. 2007).

The urban heat island is another factor that birds in cities and towns must contend with. For some species, the urban heat island provides benefits including permitting earlier nesting (Gehlbach 1994, Korpimäki 1978, Rollinson and Jones 2002), higher overwinter survival (Gehlbach 1994) and a potential increase in invertebrate prey (Gehlbach 1994, Rollinson and Jones 2002 but see Burke and Nol 1998). In association with these three factors, the urban heat island is also implicated in reduced migratory propensity and increased sedentariness (Adriaensen and Dhondt 1990, Luniak et al. 1990, Partecke and Gwinner 2007), which in turn provides individuals that overwinter in urban areas a reproductive head start over migratory conspecifics (Partecke and Gwinner 2007). On the other hand, the urban heat island may also create stresses such as heat stress, which can be highly detrimental to nestlings and adults in the nesting period (Korpimäki 1985, McCollin 1998, Kristan 2001). A further complication is altered song phenology from artificial lights (Adams 2005).

Direct anthropogenic disturbance is typically pronounced in urban areas (Forman and Alexander 1998). Activities such as development and land clearing, mowing, pruning, tree removal or removal of dead branches and other forms of manicuring can create ecological traps for birds that establish territories or begin nesting only to have their territories or nests disturbed during critical periods (Dwernychuk and Boag 1972, Gates and Gysel 1978, Best 1986, Remes 2000, Battin 2004). Vehicles also cause considerable mortality as do collisions with buildings, especially glass structures (Klem 1989, Millsap 2002, Rollinson and Jones 2002). Other disturbance types with significant consequences include collision with power lines and electrocution (Bevanger 1998). Eurasian Eagle

Owls (*Bubo bubo*) abandon territories and show higher risk of nest failure within 200m of power lines, as well suffering a 17% loss of fledged young from electrocution (Sergio et al. 2004). Seemingly innocuous activities such as pedestrians or cyclists using trails may also have negative impacts on breeding (Fernández-Juricic and Tellería 2000).

Nonetheless, trail use by pedestrians was not found to negatively influence reproductivity in the Northern Cardinal in Ohio, but rather influenced their nest-site selection (Smith-Castro 2008). Likewise, Eurasian Magpies (*Pica pica*) alter their nest-site selection in urban areas, selecting higher nest sites in proximity to pedestrian activity (Wang et al. 2008).

Aside from direct ecological traps and mortality there are many more subtle effects of anthropogenic disturbance. One notable problem is the way animals are forced to alter their time/energy budgets in urban settings. Roads can constrain foraging or limit territory size or access to other resources, e.g. the Spanish Imperial Eagle (*Aquila adalberti*) avoids certain key foraging areas on weekends and at times when vehicular traffic is high (Bautista et al. 2005). Some birds will adjust their dispersal patterns to avoid areas of high human use (Chace and Walsh 2006). Some mammals have been shown to become increasingly nocturnal in order to minimize disturbance from human beings (McClennen et al. 2001, Tigas et al. 2002, Riley et al. 2003). This has not yet been demonstrated in birds; however, European Robins (*Erithacus rubecula*) in noisy urban environments sing at night rather than during the day (Fuller et al. 2007). Birds adjust their time/energy budgets in more subtle ways, e.g. suburban Ferruginous Hawks (*Buteo regalis*) in Colorado perched less frequently on poles or on the ground (conspicuous

perches) in winter than in less disturbed sites and spent more time at roost sites (Plumpton and Andersen 1998). Red-tailed Hawks (*Buteo jamaicensis*) reduced their alarm call and dive-bombing rates as they became accustomed to increased human presence (Knight et al. 1989).

In most cases however, anthropogenic presence and habitat change have complicated effects that are likely to benefit some species while disadvantaging others. The number of buildings in urban parks has been shown to be detrimental to the breeding of Willow Warbler (*Phylloscopus trochilus*), Hooded Crow (*Corvus cornix*), and Spotted Flycatcher (*Muscicapa striata*) (Jokimäki 1999). On the other hand, some birds derive advantages under such conditions, e.g. Eurasian Blackbirds (*Turdus merula*) nesting in proximity to buildings benefit from reduced nest predation from the Eurasian Magpie (Møller 1988). Anthropogenic features can affect birds in surprising ways, e.g. the Spotted Towhee (*Pipilo maculatus*) in Washington parks has better breeding success close to trails, perhaps because of increased feeding opportunities or by using pedestrians as a form of predator shield (Bartos Smith et al. 2006). Mourning Doves (*Zenaida macroura*) in Texas selected nest sites in proximity to roads but away from buildings and had better nesting success close to roads and far from buildings. To this species, roads represent an excellent foraging opportunity to obtain both grit and water, whereas buildings present a disturbance (Muñoz et al. 2008).

As demonstrated by the example of Red-tailed Hawks reducing their alarm call and dive-bombing rates, birds are sometimes capable of relatively rapid adjustments that alleviate

potential stresses or disturbances. Acquired tameness is beneficial in urban settings in reducing stress and energy expenditure (Chace and Walsh 2006), although there are risks associated with tameness such as the exploitation of tame birds by some human beings or the abandonment of breeding efforts following a level of disturbance that has been tolerated during less critical times of the year (Adams 2005). Anthropogenic disturbance can have profound effects on population dynamics (Pierotti and Annett 2001, Shochat et al. 2006), e.g. juvenile Burrowing Owls (*Athene cunicularia*) in urban settings have greater survival rates than adults because the highly mobile adults are more likely to be killed by collisions with vehicles or other similar accidents. The result is that juveniles are recruited into the breeding population faster than normal and gain more access to the best quality breeding sites. This in turn reduces breeding success because most of the breeders are relatively inexperienced (Millsap 2002). Suburban Eastern Screech-Owls in Texas produce more offspring than rural birds but high mortality rates in the first year of life due to vehicle collisions and predation by domestic cats produces faster gene turnover, higher genetic diversity and a more r-selected breeding biology (Gehlbach 1988). On the other hand, the Western Screech-Owl (*Megascops kennicottii*) has been shown to avoid suburban habitats in Baja California unlike its closely related sister species the Eastern Screech-Owl and possibly unlike some other conspecific populations (Rodríguez-Estrella and Peláez Careaga 2003).

The diet of birds in urban and suburban areas can be very different from typical diets (Robbins 1993). Urban areas sometimes offer concentrated food supplies although these pose risks of toxins and disease as discussed above. One of the best-known examples of a

concentrated food supply is rubbish dumps, which encourage gulls, crows and other birds to forage preferentially in proximity to human settlements. Bird feeders have a similar effect for a different guild of birds. Sewage and organic waste provides a rich food source for some gull species and their numbers have been shown to decline when sewage is properly treated (Raven and Coulson 2001). Anthropogenic food often results in increased concentrations and densities of certain species (Botelho and Arrowood 1996). The indirect consequences of such foraging behavior are more complex, e.g. this can lead to increased intraspecific and interspecific interactions altering social dominance hierarchies and feeding schedules (Ditchkoff et al. 2006). Some concentrated urban food sources offer poor nutritional value with potentially significant consequences, e.g. suburban American Crow (*Corvus brachyrhynchus*) nestlings are smaller than rural nestlings and have reduced protein and calcium levels (Heiss et al. 2006), suburban Blue Tits (*Parus caeruleus*) and Great Tits (*P. major*) suffer from poor nutrition and fledge 50% fewer young than woodland conspecifics (Cowie and Hinsley 1987), and House Sparrows that rely on human food sources exhibit altered physiology with greater nitrogen & cholesterol levels (Gavett and Wakely 1986).

As with artificial food sources, artificial water sources can also have profound effects, e.g. Common Ravens (*Corvus corax*) in the Mojave Desert cluster nest around anthropogenic water and food and produce more fledged young, potentially impacting other species breeding in the area (Kristan 2001). Proximity to irrigation systems is implicated in the colonization by Dark-eyed Juncos (*Junco hyemalis*) of some urban areas of southern California (Yeh and Price 2004). The watering of suburban lawns (along with

reduced predation) has extended the breeding season of the Rufous-banded Honeyeater (*Conopophila albogularis*) (Noske 1998). Open water in winter as a result of dams, sewage works or effluent from factories has enabled many waterfowl to winter either further north than they previously did or in greater numbers than previously possible (Sugden et al. 1974, Wobeser 1997), although this behavior is associated with additional diseases and pollution effects (Wobeser 1997). Open water combined with the nutritionally rich food supply from crops has meant that some goose species for which suitable overwintering sites may formerly have been limiting (Alisauskas 1998, Gauthier et al. 2005, Sherry et al. 2005) have now greatly expanded their populations (Ankney 1996, Alisauskas 1998, Abraham et al. 2005, Gauthier et al. 2005). In some cases this results in potentially detrimental effects to the floral substrate of arctic breeding grounds (Ankney 1996, Abraham et al. 2005).

Along with dietary changes comes an array of potentially profound biological changes. Altered winter and pre-nesting diets, in particular, can alter both the time and output of breeding activity, e.g. urban Australian Magpies (*Gymnorhina tibicen*) have advanced breeding due to food and water availability (Rollinson and Jones 2002). Suburban Florida Scrub-Jays (*Aphelocoma coerulescens*) breed three weeks earlier than rural jays due primarily to increased foraging efficiency (Fleischer et al. 2003). This advanced breeding may in fact result in lower fecundity due to different food resource availabilities at different times of year (Schoech and Bowman 2001). Food concentrations alter other behaviors such as roosting patterns (Robbins 1993, Kristan et al. 2003), e.g. urban

European Starlings behave differently from rural starlings, exhibiting high fidelity to roost sites near food (Johnson and Glahn 1994).

The starling example provided above highlights an apparent trend of increasingly sedentary behavior in urban settings due to supplementary resources and climate mitigation through the urban heat island and a reduction of the impact of wet/dry cycles due to water provisioning (Adams 2005). With increasing sedentariness comes other population changes such as higher densities (Tomialojc and Gehlbach 1988, Rosenfield et al. 1996) and altered territoriality and habitat selection (Newton 1986). Interesting examples of this phenomenon include Eurasian Sparrowhawks (*Accipiter nisus*) in villages in The Netherlands, which enjoy a different diet than rural birds, utilizing a greater variety of nest types and producing larger clutches (Diermen 1996); Ospreys (*Pandion haliaetus*) sponsored by urban fish stocks altering their nest-site selection (Spitzer et al. 1985); and urban Cooper's Hawks with access to concentrated prey sources reducing their territory size and altering nest-site selection with a preference for non-native trees as nesting substrate (Chiang et al. 2006).

Diet is also implicated in some more subtle changes, e. g. suburban American Crows subjected to a low quality food regime occupy smaller territories but with more helpers at each nest, producing higher nesting densities in these areas. This leads to higher nesting success and post-fledging survival despite the fact that these crows produce smaller young with fewer offspring per nest (McGown 2001). American Crows also exhibit a high degree of suburban to urban dispersal producing what Marzluff et al. (2001) termed

a “habitat sponge”. The sponge is created by continual development in the suburbs constantly producing new early successional habitats favored by the crows and the subsequent dispersal of the large numbers of juveniles born in these suburban habitats into urban feeding areas (Marzluff et al. 2001). Urbanization affects much more than species-specific dietary regimes and foraging strategies. It influences the whole trophic web such that the relative importance of top-down controls such as predation versus bottom-up limitations such as the limited availability of resources can be altered significantly in urban areas (Faeth et al. 2005).

Changes to the process of predation in urbanizing areas are more disputed than other aspects discussed above. Several studies have reported increased predation in urban areas (see Haskell et al. 2001) due to “sponsored” populations or supplemental food resources (Chace and Walsh 2006), abundance of mesopredators due to exclusion of larger predators, including non-native predators sponsored by humans as in the case of domestic cats (Crooks and Soulé 1999, Rollinson and Jones 2002, Sorace 2002, Woods et al. 2003). Other studies have reported decreased predation in urban areas, e.g. Northern Mockingbirds (*Mimus polyglottos*) (Stracey et al. 2006), Common Woodpigeon (*Columbia palumbus*) (Tomialojc 1980) and Lesser Kestrel (*Falco naumanni*) (Tella et al. 1996) all experience lower predation in suburban areas. The Eastern Screech-Owl apparently benefits from reduced Great Horned Owl densities (Gehlbach 1994, see also Chapter 2). The Rufous-banded Honeyeater enjoys higher reproductive success in the city of Darwin, Australia than in the surrounding countryside due at least in part to a reduction in predators and a lengthened breeding season (Noske 1998). Yet other studies

have reported no significant difference in (sub)urban versus rural predation rates (Coleman and Temple 1993) or suggested that domestic cats and dogs have negligible impacts on the presence of small birds (Parsons et al. 2006). At least some examples of mesopredator release may be only temporary as large predators that desert developing areas may return to those same areas as habitats mature (Munyenyembe et al. 1998).

Even more controversial than predation rates are the effects on the process of brood parasitism in developing areas. The debate around parasitism extends beyond the context of urbanization and pertains mostly to the controversial hypothesis that fragmentation (increased edge) increases both parasitism and predation rates. This hypothesis has received some support (e.g. Wilcove 1985, Robinson et al. 1995, Hobson and Bayne 2000, Rodewald and Shustack 2007) while other authors have found no supporting evidence (Paton 1994, Yahner 1996, Tewksbury et al. 1998, Keyser et al. 1998, Harrison and Bruna 1999, Lahti 2001). One recent study found strong support for increased parasitism from the Brown-headed Cowbird (*Molothrus ater*) with increased human presence (density of farms and houses) but suggested that the relationship between fragmentation and predation was complex and varied at different spatial scales (Tewksbury et al. 2006). Several recent review papers have suggested that studying fragmentation rates per se cannot produce meaningful generalizations but that rather species and context specific interactions must be explored (Haskell et al. 2001, Lahti 2001, Chalfoun et al. 2002). Furthermore, the effects of fragmentation on a given species may not be straightforward, e.g. the Northern Saw-whet Owl (*Aegolius acadicus*) may

benefit from small amounts of fragmentation but suffer reduced reproductive success as the level of fragmentation increases (Hinam and Cassady St. Clair 2008).

Alongside the discussion on the impacts of fragmentation, a similar debate regarding the influence of urbanization on brood parasitism and predation has begun. The hypothesis that urbanization increases brood parasitism and predation rates has received some support (e.g. Nilon et al. 1995, Remes 2000, Haskell et al. 2001) but has also been criticized (Lahti 2001, Marzluff et al. 2001, Smith & Wachob 2006). Some artificial nest experiments found increased predation with increasing human density and/or agricultural land use (Wilcove 1985, Andren 1992, Major et al. 1996, Bayne and Hobson 1997, Wong et al. 1998, Hogrefe et al. 1998, Saracco and Collazo 1999, Jokimäki and Huhta 2000, Haskell et al. 2001, Thorington and Bowman 2003); however, other experimental studies found no significant trend (Russo and Young 1997, Danielson et al. 1997, DeGraaf et al. 1999, Gering and Blair 1999, Melampy et al. 1999, Zegers et al. 2000). Other studies have suggested that avian nest predators may benefit from urbanization (Kluza et al. 2000, Smith and Wachob 2006) although this is countered by Marzluff et al. (2001). Some recent evidence suggests that any effect of human density is unlikely to be uniform but rather strongly influenced by regional processes (Pidgeon et al. 2007). As with the fragmentation debate therefore, it is extremely difficult to make generalizations on the effect of urbanization on the processes of predation and parasitism and wiser to consider context specific examples.

Changes in predation and parasitism interactions demonstrate the influence of other aspects of avian ecology such as habitat selection and productivity in urban areas. Eurasian Blackbirds that breed in small fragments in urban settings have been shown to alter their nest-site selection to nest preferentially in conifers and hedgerows (dense cover) and in proximity to buildings (Møller 1988). A particularly interesting aspect of predation in urban settings is the possibility of ecological traps and population sinks, for example, House Sparrow, Dunnock (*Prunella modularis*), and European Robin all experience ecological traps as a result of high predation by domestic cats on juveniles (Baker et al. 2005).

Urbanization in fact creates a distinctive pattern of fragmentation (Bierwagen 2007). Altered plant species composition (including the presence of many exotics) and structural complexity (Rottenborn 1999, Savard and Falls 2001) as well as different age and maturation profiles (Munyenyembe et al. 1998) make urban environments structurally different from any surrounding landscape with different avian community composition (Batten 1972, Walcott 1974, Aldrich and Coffin 1980, Horn 1985). In Florida this produces increased shrub density in some urban areas to the benefit of Northern Mockingbirds and Northern Cardinals but to the detriment of Acadian Flycatchers (Tracey and Robinson 2006). Some species have been able to exploit these differences and used urban areas as stepping stones for range expansion, e.g. by exploiting non-native fruiting trees with different fruiting phenology from native species (Reichard et al. 2001, Corlett 2005). I will argue in Chapter 6 that the Eastern Screech-Owl has benefited from anthropogenic activities to expand its range into Manitoba, Canada. Differences in

urban environments can produce more subtle effects such as competitive exclusion, e. g. a checkerboard distribution pattern among several species of *Ptilinopus* fruit doves has emerged in Papua New Guinea as a result of the availability of different fruiting trees in different towns (Diamond 1986). On the Canary Islands, the House Sparrow dominates in urban areas, the Spanish Sparrow (*Passer hispaniolensis*) dominates in towns and villages, and the Rock Sparrow (*Petronia petronia*) is thereby confined to the surrounding countryside unless its competitors are absent (Cullen et al. 1952, Summers-Smith 1988, Newton 2003). Urbanization also influences breeding success, for example, despite the fact that raptor diversity is correlated to wilderness area (Bosakowski and Smith 1997), several raptor species have higher breeding success in urban areas (Bloom and McCrary 1996, Botelho and Arrowood 1996, Parker 1996, Tella et al. 1996, Rosenfield et al. 1996).

A particularly complex and fascinating aspect of this phenomenon is the way urbanization influences the process of habitat selection often in indirect ways such as by altering foraging opportunities or nesting substrates (Haskell et al. 2001, Chace and Walsh 2006). Interestingly, such effects are not confined to urban areas but may also spill over into surrounding forests (Rottenborn 1999). Well known examples include Peregrine Falcon (*Falco peregrinus*) nesting on urban high-rises as opposed to cliffs and the accompanying change in diet that this entails (Horak 1986, Septon et al. 1996, Temple 1988). The link between altered habitat selection and dietary changes is a common theme and has been noted in other species such as the American Kestrel (*Falco sparverius*) which accepts artificial nest boxes as a nesting resource when these occur alongside

concentrated food sources (Berry et al. 1998). Great Horned Owls in suburban areas exhibit higher nest-site selectivity than rural birds due to the increased structural complexity of suburban environments (Smith et al. 1999). Monk Parakeets (*Myiopsitta monachus*), which are habitat generalists in their native South America, exhibit very specific nest-site selection for tall palms in the city of Barcelona where they have been introduced (Sol et al. 1997). Tawny Owls (*Strix aluco*) in northern Italy settled in adjacent territories forming an aggregation in large wooded patches in rural areas but settled at a distance from earlier arrivals in fragmented urban areas (Galeotti 1994).

Another much discussed attribute of urbanization is landscape connectivity and how birds move between habitats in the urban matrix. Urban obstacles such as roads can have strong negative impacts on many species by blocking or slowing their movement (Knight 1990, Soulé 1991, Shafer 1997, Soulé et al. 2005); however, other disturbance-adapted species such as crows and some non-native species are capable of using roads and other features of the urban matrix as corridors that aid dispersal (Crooks and Soulé 1999, D'Antonio and Meyerson 2002, McKinney 2006). The issue of connectivity is arguably emerging as less of a concern to avian ecologists than to mammalogists and herpetologists as many authors have concluded that patch size is more significant than connectivity to birds in urban landscapes (Bunnell 1999, Harrison and Bruna 1999, Clergeau et al. 2001, Thomas et al. 2001, Lichstein et al. 2002, Alberti and Marzluff 2004, Bierwagen 2005, Donnelly and Marzluff 2006). Some authors have argued that the reason that connectivity in the urban matrix poses less of a problem to birds may be because the mobility afforded to them by flight permits detecting environmental features

readily, allowing birds to move through non-habitat into suitable habitat (Zollner and Lima 1997, Donnelly and Marzluff 2006).

When the degree of connectivity in a landscape as perceived by a given species is altered, this has multiple complex effects on numerous aspects of that species' life cycle. These effects are not confined to dispersal. Increased connectivity can alter immigration / emigration rates, leading to greater genetic homogeneity (Bierwagen 2007); increase disease transmission rates (Simberloff and Cox 1987); hasten parasite infection rates (Simberloff and Cox 1987); facilitate the spread of invasive species (Simberloff and Cox 1987); and increase the impact of disturbances such as fire (Bierwagen 2007). The strongest effects on connectivity are argued to be in areas where large cities have arisen in formerly contiguous habitat and the smallest effects where urbanization has occurred in formerly disaggregated habitats (Bierwagen 2007).

Urbanization is proving to have evolutionary consequences for many birds by means of a variety of mechanisms. Urban Herring Gulls (*Larus argentatus*) have faster heritable mutation rates (Yauk and Quinn 1996) and suburban Eastern Screech-Owls have altered rates of genetic input and outflow (Gehlbach 1988). In other cases, sexual selection is altered due to changes in contextual biological demands, e.g. following colonization of an urban area in California, a population of Dark-eyed Junco enjoying mollified climate (in terms of both temperature and water provisioning) extended their breeding season and experienced reduced competition for mates but increased selection pressure for parental investment. The result was a 22% decrease in the amount of white in their tail feathers

(used for sexual/territorial signaling) in less than 25 years (Yeh 2004, Yeh and Price 2004). Urban House Sparrows in Hungary are smaller in size and perpetually in worse physiological condition than rural conspecifics. This is not due to short-term resource availability but rather to adaptive divergence in urban environments (Liker et al. 2008). Urbanization is also producing genetically determined sedentariness in Eurasian Blackbirds (Partecke et al. 2005, Partecke and Gwinner 2007).

The picture emerging from the above discussion is the great complexity of interrelated factors and the potentially profound consequences of even very small habitat changes or avian responses to small changes. This means that when assessing the patterns of urbanization and the consequences for birdlife, cause and effect is often difficult to ascribe, e.g. the absence of certain passerine species in suburban areas of Sydney, Australia might be related to characteristics of suburban gardens in those areas, competition and aggression from dominant and introduced species, or increased predator densities (Parsons et al. 2006). In other cases, different populations of the same species appear to have very different responses to urbanization in different geographic areas, e.g. the Red-shouldered Hawk (*Buteo lineatus*) avoids suburban habitat in New Jersey (Bosakowski and Smith 1997), uses non-native trees as a nesting substrate in California (Bloom and McCrary 1996) and shows no significant difference in habitat selection in urban versus rural Ohio other than using residential areas less than expected (Dykstra et al. 2000, Dykstra et al. 2001).

The Red-shouldered Hawk example illustrates both the difficulty in finding meaningful generalizations and the importance of understanding context-specific conditions. In other words, urbanization is a complex process (or processes) further complicated by the fact that it functions in concert with other factors such as climatic and geographical clines, metapopulation structure, and other biological and ecological characteristics under regionally variable selection pressures. In this thesis, therefore, I chose to research the Eastern Screech-Owl, a reasonably well-studied species (VanCamp and Henny 1975, Gehlbach 1994) which is known to be suburban-adapted at least in the southerly portion of its range (Gehlbach 1994). Suburban Eastern Screech-Owls possess advantages in terms of fecundity and population recruitment over rural populations (Gehlbach 1994). I conducted my research at the very northern periphery of the Eastern Screech-Owl's range in order to test whether the patterns and mechanisms of suburban adaptation observed in the south might hold true in the north. The study area for this thesis (Winnipeg, Manitoba) is above 49°N and experiences a radically different climate from southern Texas where the pattern of suburban-exploitation by the Eastern Screech-Owl was first documented (Gehlbach 1994). Since Gehlbach (1994) demonstrated the benefit of the urban heat island to Texan owls in terms of advanced breeding phenology, my initial prediction was that population density and reproductive success of Eastern Screech-Owls in Winnipeg, where winter temperatures approach the cold tolerance threshold of these birds (Mosher and Henny 1976), would also be influenced by the urban heat island. I also predicted that anthropogenic habitat features including the use nest-boxes and buildings as roost sites would benefit this species as has been suggested for the Barn Owl (*Tyto alba*) at the northern edge of its range in North America (Andrusiak and Cheng 1997).

LOCAL CONTEXT: A CENTURY OF CHANGE IN WINNIPEG'S AVIFAUNA

Considering the difficulty in providing generalization on the effect of urbanization on birds and noting the variation in the way birds have reacted to urbanization in different contexts, it is worth outlining the changes that urbanization has brought to the avifauna of the study area of this thesis — Winnipeg, Manitoba. Centered on the junction of the Red and Assiniboine Rivers, Winnipeg is situated in an ecological transition zone, the aspen parkland belt that lies between the boreal shield to its north and east and the grassland ecosystems to its south and west. Despite the establishment of a small Hudson Bay Company settlement in 1811, Winnipeg did not experience significant urbanization until well after its incorporation in 1872 (Boyens 2007). Nonetheless, considerable changes to the area's fauna and flora have occurred within that time span.

European settlement of North America brought several introduced birds of Palearctic origin to the Winnipeg area, mostly indirectly, i.e. following range expansion subsequent to introduction in eastern parts of the continent. These include Rock Pigeon (*Columba livia*), House Sparrow, European Starling and Gray Partridge (*Perdix perdix*) (Manitoba Avian Research Committee 2003). The first three of these species have become the dominant residents of Winnipeg's urban area. This is not surprising since urbanization creates suitable conditions for alien species, of which many are human symbionts (Jokimäki and Suhonen 1993, Blair 1996, Adams 2005). These introduced species have likely increased competition for food and nesting and roosting sites, with a profound impact on many native species. Nonetheless, they are important prey items from several urban raptor species including Peregrine Falcon (R. W. Nero, unpublished data), Merlin

(*Falco columbarius*) (Oliphant and McTaggart 1977, Manitoba Avian Research Committee 2003), and Eastern Screech-Owl (Chapter 4). House Finch (*Carpodacus mexicanus*) has also become a common resident in the Winnipeg area and a regular visitor to feeders, after being brought from southwestern North America to New York and then spreading westward across the continent (Aldrich and Weske 1978), reaching Manitoba in the early 1980s (Koes 1985). Ground-dwelling birds are relatively poor dispersers and, along with ground-nesting species, are thought to be particularly vulnerable to disturbance from human activity and domestic pets, leading to their exclusion from most urban areas (Rottenborn 1999, Cicero 1989, Winters and Wallace 2006). It is therefore noteworthy that the introduced Gray Partridge is one of only two ground bird species (Phasianidae, Odontophoridae) that breed within the city limits. The other is the Wild Turkey (*Meleagris gallopavo*), also introduced into Manitoba (Manitoba Avian Research Committee 2003). The Wild Turkey breeds in the Saint Norbert area just south of the city and apparently moved into Winnipeg during the 1997 Red River flood, when birds were pushed northward by the advancing floodwater and subsequently established themselves in certain suburbs such as Wildwood Park (G. Ball, pers. comm.). Native ground birds have fared more poorly with urbanization, both the Ruffed Grouse (*Bonasa umbellus*) and the Sharp-tailed Grouse (*Tympanuchus phasianellus*) having disappeared from Winnipeg. The former was last recorded on a Winnipeg Christmas Bird Count (CBC) in 1978 and the latter in 1998 (National Audubon Society, n.d.).

In addition to introduced species, several suburban-adapted native species are common in Winnipeg. The Chimney Swift is highly urbanized in Manitoba and elsewhere in North

America (Johnston 2001). Common Grackles (*Quiscalus quiscula*) utilize feeders and sometimes form large flocks on suburban lawns where they probe for food. They also use many human structures as a nesting substrate (C. Artuso, pers. obs.). This species reaches its highest numbers in Manitoba in residential areas but despite increases in the 1980s appear to have declined since 1995 (Manitoba Avian Research Committee 2003). Other interesting adaptations to suburban life include rubbing their feathers with granular lawn chemicals as a substitute for anting (Nero 1996). Black-capped Chickadee (*Poecile atricapillus*) and White-breasted Nuthatch (*Sitta carolinensis*) are other examples of native species that are common in the suburban areas.

Winnipeg's geographical position places it on the northern periphery of the range of a suite of species of southeastern woodlands, some of which have apparently expanded their range over the course of the late 19th and 20th Centuries, e.g. Wood Duck (*Aix sponsa*), American Woodcock (*Scolopax minor*), Barred Owl (*Strix varia*), Eastern Screech-Owl, Red-headed Woodpecker (*Melanerpes erythrocephalus*), Yellow-throated Vireo (*Vireo flavifrons*), Purple Martin (*Progne subis*), Golden-winged Warbler (*Vermivora chrysoptera*), Eastern Bluebird (*Sialia sialis*), and Indigo Bunting (*Passerina cyanea*) (Manitoba Avian Research Committee 2003, Chapter 6). In addition to birds, some mammals such as the raccoon (*Procyon lotor*) have undergone a similar expansion (Larivière 2004). Some of these species now comprise a regular component of Winnipeg's avifauna, e.g. Wood Duck, Yellow-throated Vireo and Indigo Bunting, whereas others such as American Woodcock and Eastern Bluebird utilize suburban habitats as migration stopover sites (C. Artuso, pers. obs.). Other open-country or edge

species whose population shifts, range expansions or movements have brought them to the Winnipeg area in the late 19th and 20th Century include Mourning Dove (*Zenaidura macroura*), Western Kingbird (*Tyrannus verticalis*), and Barn Swallow (*Hirundo rustica*) (Thompson [Seton] 1890, Speechly 1922, Houston 1979, Houston 1986, McNicholl 1988, Houston and Schmutz 1999). Other species that have not undergone range expansion per se have shown increasing adaptation to urbanized environments and become a regular part of Winnipeg's avifauna including American Crow (*Corvus brachyrhynchos*) (Houston 1977a) and the so-called "prairie" subspecies of Merlin (*F. c. richardsonii*), which first colonized Winnipeg in the 1980s (McCowan 1978, Bancroft 1989, Houston and Schmutz 1999). After a pattern of range collapse and subsequent expansion Black-billed Magpie (*Pica hudsonica*) breeds in certain areas of the periphery of the city (Houston 1977a, Manitoba Avian Research Committee 2003) such as the University of Manitoba campus (C. Artuso, pers. obs.).

Neotropical migrants are generally thought to be disadvantaged by urbanization (Friesen et al. 1995, Lindsay et al. 2002, Green and Baker 2003, Kark et al. 2006); however several species breed in Winnipeg. Among Neotropical migrant passerines that breed in Winnipeg suburbs and parks are Great Crested Flycatcher (*Myiarchus crinitus*), Eastern Kingbird (*Tyrannus tyrannus*), Eastern Phoebe (*Sayornis phoebe*), Red-eyed Vireo (*Vireo olivaceus*), Yellow-throated Vireo, House Wren (*Troglodytes aedon*), Gray Catbird (*Dumetella carolinensis*), Cedar Waxwing (*Bombycilla cedrorum*), Indigo Bunting, Yellow Warbler (*Dendroica petechia*), Chipping Sparrow (*Spizella passerina*), Clay-colored Sparrow (*Spizella pallida*), and to a lesser extent Rose-breasted Grosbeak

(*Pheucticus ludovicianus*) (C. Artuso, unpublished data). Some of these use human structures to varying degrees, e.g. Eastern Phoebes readily nest on bridges, docks, abandoned and even occupied buildings (Manitoba Avian Research Committee 2003). The Yellow-throated Vireo reaches its northwestern range limit in Manitoba and appears to reach its highest densities in suburban parks in Winnipeg, e.g. Assiniboine Park, Kildonan Park, Saint Vital Park and King's Park or just outside the city, e.g. La Barrière Park (Manitoba Avian Research Committee 2003). These parks all possess very large deciduous riparian trees and are also attractive to a suite of open woodland residents including Eastern Screech-Owl, Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), Black-capped Chickadee, and White-breasted Nuthatch. The eastern subspecies of the Loggerhead Shrike (*Lanius ludovicianus migrans*) is unusual in that it is a threatened subspecies (Government of Canada, n.d.) that, at least in Manitoba, is associated with low-density human development, currently being restricted to areas on the northern boundary of Winnipeg (Blouin et al. 2001, Manitoba Avian Research Committee 2003).

Numerous other species have undergone relatively recent and sometimes remarkable colonization of the urban and suburban areas. Some of these cases may be linked to the provisioning of nest boxes, e.g. the Wood Duck was once rare in Manitoba and elsewhere (Manitoba Avian Research Committee 2003); however, the suburban breeding population, many of which use nest-boxes, reach seemingly large concentrations in parts of the city such as Saint Vital and Kildonan Park, where they are also fed by park visitors and nearby home owners (C. Artuso, unpublished data, Artuso 2006). Eastern Screech-Owls

also readily use nest-boxes and 34% of the nest sites found between 2004 and 2007 in Winnipeg were in boxes designed for Wood Ducks (Chapter 2). Eastern and Mountain Bluebirds (*Sialia currucoides*) regularly use nest-boxes in Manitoba and the former once nested in Winnipeg after range expansion in the late 19th century (Houston 1977b) although they no longer appear to do so (C. Artuso, pers. obs.). House Wrens have frequently used nest boxes and other human structures in Winnipeg since 1921 and are typically encountered near human habitation (Manitoba Avian Research Committee 2003). Like Chimney Swifts, Cliff Swallows (*Petrochelidon pyrrhonota*) now use anthropogenic structures almost exclusively as a nesting substrate, especially bridges and dams, and are readily found in suburban areas (Manitoba Avian Research Committee 2003).

Urbanization entails habitat change that typically favors open-country or light woodland species (Aitken et al. 2002, Diamond 1986, Kluza et al. 2000). Not surprisingly, some open-woodland species such as Downy Woodpecker are most likely to be encountered in Manitoba in suburban or rural areas with large trees (Manitoba Avian Research Committee 2003). Many suburban areas differ from the surrounding aspen parkland in that they contain a more open understory and exotic species including fruit-bearing and coniferous trees. Conifers have become an important nesting substrate for several species including American Crow, Black-billed Magpie, Merlin (which reuse crow and occasionally magpie nests in conifers) and Chipping Sparrow (Manitoba Avian Research Committee 2003). Conifers are implicated in the colonization of some prairie cities by the Merlin, which only nest in conifers in these cities (McCowan 1978, Bancroft 1989).

Conifers have apparently facilitated the boreal forest-dwelling Red-breasted Nuthatch (*Sitta canadensis*) to move into certain parts of the city in very recent years to attempt breeding (R. W. Nero, pers. comm.). This pattern also appears to be increasing in North Dakota (C. D. Ellingson, pers. comm.) and Minnesota (Wann et al. 1981). Pine Siskins (*Carduelis pinus*) occasionally breed in Winnipeg and other cities and towns. According to the Prairie Nest Record File, their nests in these areas are almost invariably in planted spruces, matching their general preference for conifers (Middleton 1998). Urban conifers also appear to be a key element in the nest-site selection of Chipping Sparrows in Winnipeg. Thompson [Seton] (1890) considered the Chipping Sparrow rare in Manitoba but “tolerably common” in Winnipeg in the late 19th century. This suggests that this species has enjoyed a relatively long association with urbanization, fitting with its preference for edges, clearings and open habitats (Middleton 1998). Eastern Screech-Owls select nest-sites close to conifers that provide a concealed and protected roost site for the male in the early nesting period before deciduous trees have foliated (Chapter 3). The planting of conifers therefore can have a considerable effect on the avifauna of northern temperate cities.

Some species that may have been excluded from the Winnipeg area as it was developed due to persecution, disturbance or habitat alteration, may move back to the city as habitats mature. Due to their large spatial requirements, many large predators cannot easily establish home ranges in fragmented urban areas (Crooks and Soulé 1999, Jokimäki 1999, Chace and Walsh 2006). Some raptors are therefore sensitive to disturbance and have also been the victims of direct persecution. The Great Horned Owl

is not common in Winnipeg; however, the Prairie Nest Record File shows that some pairs have nested in the city since 1958. I have found 4 – 10 nests annually in the city and surrounding area since 2005. Some pairs have used human structures as nest sites, e.g. a steel tower in a Winnipeg oil refinery (Manitoba Avian Research Committee 2003) and a sewer pipe no longer in use (C. Artuso, pers. obs.). Great Horned Owls exhibit a greater degree of nest-site selection in suburban areas than in rural areas essentially because they have a greater variety of options available (Smith et al. 1999). CBC data show that the highest detection rates, at least in winter, occur in urban and agricultural areas (Manitoba Avian Research Committee 2003) although the rate of detection in Winnipeg has remained fairly constant since the 1960s (0.04 individuals per party hour in the 1960s, 0.02 in the 1970s, 1980s, and 1990s, and 0.03 from 2000 – 2007 (National Audubon Society, n.d.). Cooper's Hawk have an increasing breeding presence in suburban areas, and since the 1990s have nested annually in Assiniboine Park (Manitoba Avian Research Committee 2003). I now find or am informed of at least a dozen nests every year in Winnipeg greenspaces. Occasionally two pairs have nested simultaneously within Assiniboine Park and Saint Vital Park as close as 725m apart (C. Artuso, unpublished data). After a significant recovery from near population collapse (Gerrard and Bortolotti 1988, Koonz 1988), the Bald Eagle (*Haliaeetus leucocephalus*) now breeds along the Red River just north of Winnipeg (G. Machnee, pers. comm.). Bald Eagles attempted nesting in several consecutive years along the Red River in Kildonan; however, they abandoned this site after a new housing development was erected (R. Koes, pers. comm.).

In addition to raptors other birds have been frequently disturbed by human activity. Common Raven (*Corvus corax*) was also once persecuted and disappeared as a breeding species from the Canadian prairies in the 19th century (Houston 1977a). Nonetheless, ravens have recently begun breeding in the Canadian prairies including several locations in Winnipeg (Reaume 2006, C. Artuso, pers. obs.). American Crow has also dramatically increased its breeding presence in Winnipeg and other cities and towns on the Canadian prairies (Houston 1977a). The Pileated Woodpecker (*Dryocopus pileatus*) was once frequently shot by hunters and trappers and is relatively intolerant of disturbance (Bull and Jackson 1995). A bird of mature woodlands with large trees, requiring relatively large forest tracts (Bull and Jackson 1995), few would expect to find this species in urban areas. Nonetheless, the number of sightings in the city appears to be increasing in recent years as Winnipeg's urban forest matures. This species was first detected on the Winnipeg CBC in 1947 but then not again until 1999. From 1999 – 2002 and in 2004, one or two were recorded on each Winnipeg CBC. In 2003, 2005, 2006, and 2007 three or four were recorded on each count (National Audubon Society, n.d.). Pileated Woodpeckers are also occasionally encountered in large suburban parks in the summer and reproduced at the St. Charles Golf and Country Club in 2000 (R. Koes, pers. comm.).

Urban areas provide concentrated food resources for numerous birds, e.g. rubbish dumps and sewage outlets are frequented by corvids and gulls (Robbins 1993, Botelho and Arrowood 1996, Berry et al. 1998, Raven and Coulson 2001). There are several large dumps on the outskirts of Winnipeg, including the Brady Road Landfill just south of the city's Perimeter Highway, where thousands of Ring-billed (*Larus delawarensis*), Herring

species has disappeared from some sites after pesticides were sprayed, whereas populations remained intact in nearby unsprayed areas (Walcott 1974, Rising and Flood 1998) and, therefore, spraying for mosquitoes in Winnipeg warrants investigation for its effect on this and other insectivores. American Kestrel was formerly a relatively common breeder in city but is now almost absent (R. Koes, pers. comm.). This species has used nesting boxes and even nested on buildings in downtown Winnipeg (Manitoba Avian Research Committee 2003). Although nesting sites would not therefore seem to be limiting in the city, the removal of dead trees and suitable nesting snags in open areas, competition for cavities from European Starlings and other cavity nesters, and decreasing supplies of certain grass-dwelling insects such as grasshoppers are all potential factors in this decline that warrant investigation. Similarly to the kestrel, the Red-headed Woodpecker, another cavity-nester of open woodlands with a sparse understory (Smith et al. 2000), has disappeared from many Winnipeg golf courses and parks where it formerly bred (Manitoba Avian Research Committee 2003). It is possible that a similar suite of mechanisms are influencing both this species and the American Kestrel. Common Nighthawk (*Chordeiles minor*) formerly bred on gravel rooftops in cities such as Winnipeg but this has become increasingly rare as construction materials have changed and this species is now only recorded in the city on passage (Manitoba Avian Research Committee 2003). Lark Sparrow (*Calamospiza melanocorys*) was reportedly once common around Winnipeg (Thompson [Seton] 1890) and were reported breeding in North Kildonan (Cartwright 1931). They no longer breed in the city but are found in nearby Bird's Hill Park (G. Budyck, pers. comm.).

components are exploited; and fourth-order selection, i.e. which specific resources utilized, in this case which available cavities are used for breeding.

This chapter furthers the theme of differences between suburban and rural birds by comparing nest-site selection in relation to human density. Finally, this chapter also attempts to address some of the mechanisms that may play a role in any of observed patterns of habitat selection. Habitat selection in human altered landscapes is still poorly understood (Sodhi and Oliphant 1993, Jokimäki and Suhonen 1998, Smith et al. 1999). The ways in which habitat selection in range peripheral populations may differ from population closer to the center of the range is also poorly studied, except in theoretical terms of expected differences of population dynamics (Pulliam 2000, Swihart et al. 2003). Likewise, how the influences of urbanization on avian populations might be enhanced or mitigated in range-peripheral areas is poorly understood. Chapters 2 and 3 therefore offer a significant contribution to our understanding of range-peripheral populations.

Chapter 4, The diet of the Eastern Screech-Owl at the northern periphery of its range, addresses the question of the diet of Eastern Screech-Owl in the study area in terms of biologically significant period and in terms of differences in the diets of suburban and rural pairs. As with Chapters 3 and 4, this paper discusses the differences in diet in a range-peripheral context and makes comparisons with other studies in more southerly locations. The selectivity of avian prey is also discussed based on point counts in the study area. This chapter is based on the identification of prey by direct field

observations, video footage, dissection of pellets and the inspection of nest boxes in the post-fledging period. This chapter pertains to Johnston's (1980) fourth-order selection in that it examines the selection of prey resources. The comparison of diet and degree of specialization in a northern context with diet proportions found in other studies furthers the theme of the biological importance of range-peripheral contexts and contributes to our understanding of how this species is able to survive in Manitoba and the importance of anthropogenic influences on diet and hence survival.

Chapter 5, Eastern Screech-Owl hatches Wood Duck eggs, is an account of an observation of an interaction between the Wood Duck and the Eastern Screech-Owl in competition for a nesting site. This chapter discusses one aspect of resource competition for suitable cavities for nesting sites. It therefore furthers the theme of habitat selection discussed in Chapter 3, in particular, providing evidence of the potentially limiting effect of cavity availability discussed in that chapter. This paper was published in 2007 in *The Wilson Journal of Ornithology* 119:110-112 (Artuso 2007a).

Chapter 6, Eastern Screech-Owl in Manitoba: Evidence of historical range expansion, addresses the question of whether or not the Eastern Screech-Owl was present in Manitoba before European settlement. This paper is based on a database from multiple sources of Eastern Screech-Owls recorded in Manitoba from 1920 to 2007. A similar database of records from northern Minnesota and North Dakota is used for comparative purposes. This chapter draws heavily on the discussion of the previous chapters in evaluating the degree to which Eastern Screech-Owl is dependent on human-altered

of the urban heat island and anthropogenic sources of food and shelter. The following chapters test those predictions.

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Based on the random stratified survey and assuming a maximum detection distance of 125m around each listening station, the density of territorial males detected ranged from 0.2 – 0.8 males/km² per year. When data were pooled over the four years of the survey and repeat detections of the same male (i.e. detected at the same location in consecutive years) were removed, this gave a density of 0.7 males/km². I used the pooled data to calculate a density for each of the 18 survey categories and multiplied this by the amount of land in each category in the study area as a whole. This produced a population estimate of 59.77 ± 3.95 males (standard error of the mean of area x density per category) or 0.01 territories/km² over the entire study area (5026.4km²). This estimate needs to be interpreted with caution as not all males were paired and this can therefore not be extrapolated to the density of breeding pairs. Furthermore, it is possible that some owls approached the observer from greater than 125m, although, with the high level of background noise at most listening points, this is unlikely. Another problem with this extrapolation is that riparian and non-riparian areas were given equal survey effort whereas the total area of riparian habitat is many times less than non-riparian habitat. Every year, 25 – 35 territories were located, although some males on territory did not have a partner and no more than 14 pairs attempted breeding in any one year (Table 2.5). Taking just the territories found within the perimeter of the city of Winnipeg (534km²), produced a density estimate of 0.05 – 0.07 territories/km². Survey data (Table 2.1, Figure 2.2) showed that screech-owl densities are much higher in suburban areas within the city than outside the city. The survey density estimate of 0.11 territories/km² should therefore be revised up if just suburban areas are considered. Therefore, if the wildlands category

(areas <1 p/ha) is removed from the survey calculation (no screech-owls detected) then screech-owl density is 0.15 males/km² across the rural – urban gradient.

DISCUSSION

Survey Data

In the study area, screech-owls show a strong preference for riparian areas both in terms of survey detections and in number of nest sites located. This was also suggested by Kelso (1944) in New York. In the study area, the tallest trees and those most likely to produce suitable cavities (American elm, Manitoba maple, green ash, eastern cottonwood and basswood —see Table 3.1) are typically found in the riparian zone (Bird 1930, Scoggan 1957, Moffat et al. 2004). Taller trees of urban habitats are selected by some raptors, e.g. Great Horned Owl (Smith et al. 1999) and may have positive effects on population density, e.g. Cooper's Hawk (*Accipiter cooperii*) (Boal and Mannan 1998). In the study area, riparian woodlands also contain a more open understory than aspen or bur oak copses found further from the river (Staniforth 2003), especially where flooding regularly deposits silt. This is particularly suited to the hunting style of the Eastern Screech-Owl, which most frequently hunts the ground layer from a perch (Gehlbach 1994). Riparian areas are also noted for their diversity and abundance of potential prey (Doyle 1990, Naiman and Décamps 1997, Lock and Naiman 1998, Sanders 1998). The Eastern Screech-Owl appears less dependent on riparian habitat further south towards the core of the range, where they utilize a wide variety of forest and woodland types (Gehlbach 1995).

Fig. 2.1 suggests that Eastern Screech-Owl density may peak at 20 p/ha; however, the 120 transects of this survey proved insufficient to adequately assess this pattern. The 20 p/ha figure represents an intermediate human density and most suburbs with this density in the study area were well-treed. Other studies have also found cavity-nesting birds to have higher diversity and reproductive success in suburbs with relatively contiguous tree cover (Blewett and Marzluff 2005). The number of nesting attempts was highest in the S2 category (44%) as compared to only 15% in the S3 category, providing further evidence of high reproductivity in medium-density suburban areas. The paucity of sightings in the downtown core with clusters of territories in suburban areas along the major rivers (Fig. 2.2) also indicate reduced usage of true urban areas with the highest amounts of impervious surfaces. Nonetheless, one successful nest was situated alongside several high-rise condominiums near the downtown core with a human density of 99 p/ha and comparatively few trees except in a narrow strip along the river.

This study found minimal differences in Eastern Screech-Owl's use of urban greenspace as opposed to residential areas, suggesting a high tolerance for human activity. Eastern Screech-Owl's small size and highly nocturnal habits mean that even when breeding in densely-populated areas, interactions with humans may be minimal. Conversely, all 10 Great Horned Owl nests located in the study area in the same period were situated in rural or suburban greenspace, in particular in or on the edge of golf courses that were seldom visited by humans at night. The small open lawns of residential neighborhoods with large trees may be more suitable to screech-owls, while larger open spaces are more readily exploited by Great Horned Owls. The Great Horned Owl is a moderately disturbance-

adapted species (Bosakowski and Smith 1997) and the fact that peak densities were recorded in the rural category is indicative of this. When transects were separated by year, Great Horned Owls were found on only five transects (12%) where screech-owls were detected, suggesting that their presence may deter screech-owls; however the average detection rate of Great Horned Owl was not statistically significant in predicting screech-owl density (Table 3). This may be because Great Horned Owl calls were not broadcast and detection rates thus not accurately reflective of population densities.

Breeding

Although I found differences between high-density suburban, low-density suburban, and rural breeding pairs in terms of brood size and fledging dates, these were not significant due to small sample sizes in the rural category. High-density suburban areas show the highest average brood size per nesting attempt and rural pairs the lowest; however, lifetime production, as opposed to brood size, would be a better indicator of biologically significant differences. The combination of breeding data with the least squares means test and orthogonal contrasts from the survey data suggest that the high and moderate density suburban areas pattern similarly in terms of Eastern Screech-Owl population density, brood size and fledging, and differ from lower suburban, rural and wildland areas in these aspects. Smaller differences exist between lower suburban and rural areas.

There is considerable evidence for a link between warm temperatures and early breeding in owls, especially in northern temperate climates (Watson 1933, Elder 1935, Marti 1994, Andrusiak and Cheng 1997, Holt and Drasen 2001, Artuso 2007b). The urban heat island in combination with unusually warm winters can advance breeding phenology in owls by

up to six weeks (Artuso 2007b). Earlier fledging closer to the city center and with warmer March temperature and earlier melting of snow cover point to the influence of the urban heat island in advancing breeding phenology. The five-day difference between the average fledging dates of suburban versus rural fledging dates in this study was closely matched by the six-day difference noted in Texas (Gehlbach 1994b). Early breeding is presumably advantageous to owls to reduce predation and competition from other raptors (Sunde 2005) and increase fledgling survival (Gehlbach 1994). The urban heat island may also increase the carrying capacity of urban areas (Emlen 1974, Shochat et al. 2006), providing greater food resources (Gehlbach 1994, Rollinson and Jones 2002) or earlier access to some food resources (Chapter 4), as well as a head start to breeding (Korpimäki 1978, Gehlbach 1994b).

The correlation between brood sizes and precipitation suggests that increased moisture provides either increased prey abundance and/or improved access to prey, e.g. earthworm capture was highest in the wettest year (Chapter 4). The watering of suburban lawns and gardens is therefore an artificial form of climate mitigation that can benefit certain species (Shochat et al. 2004, Adams 2005, Parris and Hazel 2005, Shochat et al. 2006). Increased access to water and increased moisture in soils have been factors in the colonization of urban areas (Yeh and Price 2004) and have had a positive influence on the breeding of other birds (Noske 1998, Kristan 2001, Rollinson and Jones 2002).

Screech-owl density in the study area appears to be much lower than other parts of the geographical range. The density calculated for the city of Winnipeg (0.15 males/km^2) is

only a fraction of densities in suburban Connecticut (1.2 pairs/km²) and in a suburban area of central Texas (4.4 – 7.4 pairs/km²) (Gehlbach 1995). The nearest neighbor distances of nesting pairs in Winnipeg was 612m versus 30m (suburbia) and 190m (rural area) in Texas (Gehlbach 1995). Of the 61 cavities, no more than 42% of those available (not within the territory of another owl, clogged by squirrel activity or otherwise damaged) were used in any given year. These data suggest that the population in the study area is unsaturated. Cavity use rates suggest that the number of potential nest-sites is not limiting (Chapter 3). The larger brood sizes than elsewhere in the range recorded here, combined with large distances between territories suggest that this population is limited by mechanisms that impact survival rates (Greene and Stamps 2001, Sunde et al. 2001, Brown et al. 2002). Given the low cold tolerance of this species (Mosher and Henny 1976) and the lack of invertebrate food sources in winter (Chapter 4), winter survival rates, especially of young birds, may be very low.

Screech-owl territory occupancy was not consistent over the four years of this study, with several pairs occupying formerly unoccupied territories or abandoning them. This was also the case for the Tawny Owl (*Strix aluco*) in a range-peripheral context (Sunde et al. 2001). The reasons why screech-owls abandoned cavities and/or territories are not clear; however, in four cases (of 39) abandonment coincided with the appearance of a larger owl species moving into the area. Great Horned Owl breeding appeared to cause screech-owls to vacate three territories and in one case the presence of a Barred Owl in the early spring coincided with the abandonment of a territory after 2 years of successful breeding. Some unpaired males may have abandoned territories after failing to attract females or

replacement partners (9 cases) and increased human disturbance such as construction activity or tree-felling close to a former nest site may have resulted in four cases of abandonment. Although these cases represent anecdotal evidence, they suggest that predator avoidance is at least one cause of the density pattern observed in the study area (positive correlation between screech-owl density and human density versus negative correlation between Great Horned Owl density and human density). This is not surprising since large owls have been shown to significantly impact the breeding and site occupancy of other smaller sympatric raptors (Sergio et al. 2003, Brambilla et al. 2006, Elliott 2006). Boreal Owls (*Aegolius funereus*), which are similar in size and weight to Eastern Screech-Owls, appear to avoid nesting in proximity to the larger Ural Owl (*Strix uralensis*) but not the very large Eurasian Eagle-Owl (*Bubo bubo*) (Hakkarainen and Korpimäki 1996). Despite being closely related to the Eurasian Eagle-Owl (cited as 2.8kg in Hakkarainen and Korpimäki 1996), the Great Horned Owl (average of Manitoba specimens in Manitoba Museum = 1.2kg, n = 16 of which 9 male, 2 female and 5 undetermined) is much more similar to the Ural Owl (cited as 0.9kg in Hakkarainen and Korpimäki 1996) in size and weight.

Both density and breeding success may peak above 20 p/ha but it is possible that increasing human occupancy and development above a threshold higher than 30 p/ha could negatively influence screech-owls. Owls that benefit from suburban conditions may still be disturbed if the human presence becomes too high, e.g. Burrowing Owls in Florida benefited from high prey densities around human homes but increasing development lead to a reduction in nesting success (Millsap and Bear 2000). Powerful

Owls (*Ninox strenua*) that breed in suburban areas have abandoned nests, even eating their own young, when human activity increased (Cooke et al. 2002).

The differences between suburban and rural broods in Manitoba was less pronounced than in Texas (Gehlbach 1994b); however this may be an artifact of the gradient approach of this study versus the comparison of different study sites in Texas and different definitions of “rural” versus “suburban” areas, e.g. Gehlbach’s (1994b) suburban study sites had only 4 p/ha and 5 p/ha, versus <1 p/ha in the rural site. In Manitoba, rural and wildlands nests fledged on average 5 days later than suburban nests, very similar to the 6-day difference between first egg laying/hatching in suburban and rural sites in Texas (Gehlbach 1994b). Nonetheless, the urban heat island appears to be a significant factor in the higher densities of Eastern Screech-Owls in suburban Winnipeg, as evidenced by the correlation of fledging date to distance from city center and the larger brood sizes in suburban areas.

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3. Habitat selection by the Eastern Screech-Owl along a rural – urban gradient

ABSTRACT.— Secondary-cavity nesting birds rely on a potentially limiting resource that governs their nest-site selection. Cavity-nesting birds may be sensitive to urbanization due to changes in the availability of this resource. Altered selection pressures in urban environments may also produce changes in the process of habitat selection. I examined the nest-site selection of the Eastern Screech-Owl (*Megascops asio*) in Winnipeg, Manitoba and surrounding area and compared habitat features in suburban and rural nest sites. Conditional regression analysis indicated that canopy cover, the number of potential nest cavities, percent conifer and the DBH of trees taller than 10m were selected for at the level of habitat around the nest. Nest-site variables selected for were the height of the nest tree, distance to river, and shrub density below the nest. Screech-owls also selected sites with fewer buildings within a 50m radius and less domestic cat (*Felis catus*) activity. Rural nests differed from low-density suburban and high-density suburban nests in having denser canopy and vegetation but with more smaller and slender trees (more convoluted middle story), fewer coniferous trees, more cavities but fewer nest boxes, and more raccoons (*Procyon lotor*) and Great Horned Owls (*Bubo virginianus*) but less domestic cat activity. In the study area, Eastern Screech-Owls prefer riparian habitat. Some selected features such as the presence of coniferous trees close to the nest and minimal shrub density below the nest were more likely to be found in suburban areas than rural areas. Eastern Screech-Owls nest in higher densities in suburban areas; which may offer more preferred habitat characteristics than rural areas.

Keywords: Eastern Screech-Owl, *Megascops asio*, Winnipeg, Manitoba, habitat preference.

INTRODUCTION

Secondary cavity-nesting birds are dependent on the availability of suitable cavities, a potentially limiting resource (Lundberg 1979, Korpimäki 1987, Brawn and Balda 1988, Newton 1994b, Holt and Martin 1997, but see Southern 1970, Mossop 1997, Severinghaus 2007, Wesolowski 2007). Most cavity-nesting owls show strong territoriality and site fidelity, believed to be a response to securing access to limited

nesting resources (Taylor 2002). As a polyterritorial species, the Eastern Screech-Owl (*Megascops asio*) is further limited by this resource because each territorial pair defends several cavities (Gehlbach 1994b). Secondary cavity nesters may not select for certain features that are important to primary cavity nesters, e.g. many woodpeckers exhibit selection for cavity orientation with associated benefits in terms of microclimate (Conner 1975, Crocket and Hadow 1975, Inouye et al. 1981, Hooge et al. 1999, Wiebe et al. 2001) whereas cavity-nesting small owls often do not (McCallum and Gehlbach 1988, Belthoff and Ritchison 1990a, Gehlbach 1994b). However secondary cavity nesters still experience context-specific selection pressures for such features, e.g. Northern Spotted Owls (*Strix occidentalis caurina*) on the Olympic Peninsula of Washington state avoid cavities facing the prevailing direction of inclement weather (Forsman and Giese 1997) and Elf Owls (*Micrathene whitneyi*) in the Sonoran desert select for cavity orientation, either reflecting the preferences of the woodpeckers that excavated their cavities or the heightened importance of microclimate in an arid climate (Hardy and Morrison 2001). The latter hypothesis is strengthened by the fact that Elf Owls nesting in cooler upland areas of the Sonoran desert do not select for cavity orientation (Goad and Mannan 1987).

The principal selection pressures that influence nest-site selection by cavity-dependant species include, but are not limited to, predation risk (Nilsson 1984, Sonerud 1985b, Martin 1988, Rendell and Robertson 1989, Severinghaus 2007), interspecific and intraspecific competition (van Balen et al. 1982, Nilsson 1984, Artuso 2007, Aitken and Martin 2008); parasite load (Mappes et al. 1994, Aitken et al. 2002), and weather-related factors (Forsman and Giese 1997, Severinghaus 2007). Furthermore, social behavior

such as the degree of intraspecific interactions, territoriality, dominance, and the likelihood of facultative polygamy are also important (Rendell and Robertson 1994, Aitken and Martin 2008). Such pressures are manifest in selection preferences related to cavity entrance size (Sonerud 1985b, Korpimäki 1987, Belthoff and Ritchison 1990a, Yetter et al. 1999), cavity depth (Belthoff and Ritchison 1990a), cavity volume (Korpimäki 1987, Carlson et al. 1998, Aitken and Martin 2004), cavity height (Stauffer and Best 1982, McCallum and Gehlbach 1988), cavity floor dryness (Severinghaus 2007), cavity wall thickness (Carlson et al. 1998), diameter of branch or stem at cavity height (Carlson et al. 1998), degree of concealment (Semel et al. 1988), the proximity of alternate cavities (van Balen et al. 1982, Martin 1988), and the species-specific likelihood of cavity reuse (Aitken et al. 2002).

Many recent studies point to differences in the habitat selection process at different spatial scales (Johnson 1980, Jones 2001) and, in addition to cavity-specific features, vegetation characteristics surrounding the nest and at the landscape-level are also important. In the case of secondary cavity nesters, nest-site vegetation features have been found by some studies to be less significant than cavity-specific features (Gutzwiller and Anderson 1987, Belthoff and Ritchison 1990a, Sedgwick and Knopf 1990, Severinghaus 2007). Nonetheless, cavity-nesting owls have been shown to select for features such as the amount of shrubbery in front of the nest tree (McCallum and Gehlbach 1988, Flammulated Owl *Otus flammeolus*), relative canopy height (McCallum and Gehlbach 1988, Flammulated Owl), moist deciduous forest (Mikkola 1983, Tawny Owl *Strix aluco*), open mature forest (McCallum and Gehlbach 1988, Flammulated Owl), large

trees with considerable understory vegetation (Devereux and Mosher 1984, Barred Owl *Strix varia*), and the density of mature saguaro cacti (Hardy and Morrison 2001, Elf Owl). These authors linked these selection features to predator avoidance, prey availability, and hunting style.

The range of the Eastern Screech-Owl covers most of eastern U.S.A, extending from approximately 22°N in northeast Mexico to 50°N degrees in Manitoba and southeastern Saskatchewan, Canada (Gehlbach 1995), and occasionally as far as 52°N (Walley and Clyde 1996). Different populations of this species experience very different climates and habitats, which could influence habitat selection. This species is resident in parts of Manitoba that lie between the -10°C and -20°C average January temperature isotherms (Bartholomew 1985), which approaches the cold tolerance threshold of these birds (Mosher and Henny 1976). There are numerous ways that such a range-peripheral context could influence habitat selection (Fuller et al. 2007). If cold temperatures and limited resources resulted in lower survival rates and lower population densities (Brown et al. 1995), then density-dependent competition and territoriality could conceivably be somewhat relaxed, resulting in either larger territories or greater distances to nearest neighbor (Greene and Stamps 2001, Sunde et al. 2001, Brown et al. 2002) or more pronounced seasonal shifts in areas occupied (Sunde et al. 2001). On the other hand, climate, food supply, or the limited availability of trees large enough to contain suitable nesting cavities could limit these birds to very specific habitats, e.g. riparian zones or areas influenced by the urban heat island, resulting in a more clustered population (Sasaki 1997). Such context-specific density constraints influence habitat selection (Bult et al.

1999, Fernandez-Juricic 2001), e.g. selection for vegetation around the nest-site was indicated in a population of Flammulated Owls believed to occur in low density (McCallum and Gehlbach 1988), whereas such selection was not found in a population of Eastern Screech-Owls believed to occur at higher density (Belthoff and Ritchison 1990a). Eastern Screech-Owls in Manitoba might also be influenced by a different predation regime than conspecifics in more southerly locations, contending with raccoons (*Procyon lotor*) but not the suite of smaller nest predators found further south including the black ratsnake (*Elaphe obsoleta*), Virginia opossum (*Didelphis virginiana*) and ringtail (*Bassariscus astutus*) (Gehlbach 1994b).

In addition to broad geographical variables, urbanization and other forms of human alteration of landscapes can influence avian habitat selection. Some species have expanded their choice of nest site to include human structures, the best-known example being the Peregrine Falcon (*Falco peregrinus*) nesting on urban high-rises as opposed to cliffs and the accompanying change in diet that this entails (Horak 1986, Septon et al. 1996, Temple 1988). Great Horned Owls (*Bubo virginianus*) have also come to use buildings, pipes and bridges for nest-sites (Houston et al. 1998). Habitat changes associated with urbanization areas have other consequences for Great Horned Owls, since in suburban areas they exhibit higher nest-site selectivity than rural birds due to the increased structural complexity of suburban environments (Smith et al. 1999). Eurasian Sparrowhawks (*Accipiter nisus*) in villages in The Netherlands, which enjoy a different diet than rural birds, utilize a greater variety of nest types and produce larger clutches (Diermen 1996). Urban Cooper's Hawks (*Accipiter cooperii*) with access to concentrated

prey sources have smaller territories and alter their nest-site selection to favor non-native trees (Chiang et al. 2006). For cavity-nesting birds, the availability of natural cavities may be much more limiting in habitats that are altered by human activity to varying degrees (Newton 1994a) than in pristine habitats (Wesolowski 2007), and the provisioning of nest-boxes may alter broad habitat-selection or reproductive success (Mänd et al. 2005).

Human activity can influence avian habitat selection in subtle ways; for example, Eurasian Magpies (*Pica pica*) select higher nest-sites in proximity to pedestrian activity to minimize disturbance (Wang et al. 2008). Eurasian Blackbirds that breed in small fragments in urban settings have also altered their nest-site selection and prefer conifers and hedgerows (dense cover) in proximity to buildings for predator avoidance (Møller 1988). Northern Cardinals (*Cardinalis cardinalis*) selected nest-sites that were higher from the ground and more peripheral in the nest plant when near trails than when in forest interior possibly as a result of different predation risks (Smith-Castro 2008). The effects of urbanization and broad geographical variables can also interact, e.g. the Red-shouldered Hawk (*Buteo lineatus*) avoids suburban areas in New Jersey (Bosakowski and Smith 1997), nests in groves of non-native trees in California (Bloom and McCrary 1996) and shows no difference in habitat selection in urban versus rural areas of Ohio (Dykstra et al. 2000, Dykstra et al. 2001).

Cavity-nesting birds are thought to be particularly sensitive to urbanization (DeGraff and Wentworth 1986, Natuhara and Imai 1996, Bull et al. 1997, Rottenborn 1999, Fraterrigo

and Wiens 2005, Blewett and Marzluff 2005) because human intervention and increased exposure to weather events may remove potential nesting, roosting and foraging sites (Blewett and Marzluff 2005) and in some cases they may be susceptible to increased competition from a non-native cavity nester, the European Starling (*Sturnus vulgaris*) (Ingold 1989, 1994, 1996). Nonetheless, the Eastern Screech-Owl has higher population density and fecundity in suburban areas in the southern portion of its range (Gehlbach 1994b). The influences of urbanization on this species' habitat selection is not well understood (see Belthoff and Ritchison 1990a). I examined the nest-site selection of Eastern Screech-Owls across an urban – rural gradient (defined by human density) in Winnipeg, Manitoba, at the northern edge of this species' geographical range. I tested for selection by comparing cavities used by the owls with those that were available but unoccupied by owls at two spatial scales, firstly at the cavity and cavity tree-specific level and secondly at the level of habitat surrounding the nest (50m radius). I also investigated potential influences to habitat selection including predation pressure, the amount of urban greenspace, human density, building density and distance to nearest building, distance to roads and pedestrian activity.

METHODS

The study area was defined as a circle with a radius of 40km from the center of Winnipeg, which encompasses the city limits and also areas outside the city with lower human densities. In the study area, riparian areas are dominated by American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), and Manitoba maple (*Acer negundo*), as well as bur oak (*Quercus macrocarpa*), eastern cottonwood (*Populus*

deltoides), basswood (*Tilia americana*) and peachleaf willow (*Salix amygdaloides*) to a lesser extent. Further away from the rivers, trembling aspen (*Populus tremuloides*) and bur oak become dominant. Many planted native and exotic species also occur throughout the study area, in particular conifers such as white spruce (*Picea glauca*), eastern white cedar (*Thuja occidentalis*) and the non-native Colorado blue spruce (*Picea pungens*) and Scots pine (*Pinus sylvestris*). Although some relatively “natural” areas with mixed tree and shrub composition occur, in many parts of the city only one or two tree species were planted, e.g. American elm may line streets in rows and conifers are often planted as shelterbelts or tall “fences” (pers. obs.). Riverbanks may be wooded, converted to open lawn or banked with rock. The shrub layer is particularly variable with many non-native ornamentals and/or cultivars, depending greatly on the preference of individual homeowners. For this reason I measured shrub and tree density but did not use plant species diversity counts as a variable. Tree composition by species was therefore chosen rather than a large-scale habitat classification scheme.

Nests were located using a three-step process. I first narrowed the search area by triangulation from spontaneous calling sites and then undertook a ground search for the roost sites of males. Once a roosting male was located, I searched for all potential nest-sites within 100m of his roost and then waited at these cavities at dusk or dawn to observe the female. Females typically left the nest for 15-minute periods at dusk and dawn to defecate, drink, bathe or accept a food item from their partner on a transfer perch close to the nest (Gehlbach 1994b), enabling detection in this manner. Nests were then monitored and the number of chicks and fledging dates determined (Chapter 2).

Two random directions in degrees and distances 350 – 700m were then selected using a random number generator and a cavity search found suitable cavities closest to these points. This distance range was chosen based on observation of local breeding pairs, the closest nests I had located being 704m apart. Later in the study I found two nests that were 612m apart across the Red River (150m wide in the relevant area). Observations of males trilling were within 300m of the nest site or defended cavity. The cavities chosen for comparisons were therefore far enough away from a nesting cavity to be considered “off” the defended territory even though they would fall well within the owl’s home range, hence increasing the likelihood that they were selected against (McCallum and Gehlbach 1988, Hardy and Morrison 2001), i.e. these cavities were available to the owls but not used. This method risks a bias of spatial autocorrelation since adjacent cavities may produce similar values for certain variables due to specific characteristics of the local area rather than describing differences between used and unused cavities (Lennon 2000); however, in site-attribute design studies, the comparison of used versus unused habitats can only speak to selection if unused habitat is demonstrably available (Jones 2001). The key advantage of this technique is therefore that it focuses on sites that the owls can be reasonably expected to have access to. This technique also permitted selection of cavities within areas of similar human density and similar distance to a river, which are both important to the owls (Chapter 2). Where possible, natural cavity nests and nest-boxes were matched with off-territory cavities and boxes respectively. Off-territory cavities were also chosen to match nests in terms of being situated in a green space or in a residential neighborhood, although this distinction was less significant to density or breeding (Chapter 2). These measures were designed to facilitate assessment of

selection of microhabitat. Off-territory cavities were inspected with a Sandpiper treetop peeper video inspection system (TT4W) to ensure that they were not occupied and of suitable dimensions for nesting. Only cavities with an entrance 8 – 16cm in diameter and 25 - 60cm deep (pers. obs., see also Belthoff and Ritchison 1990a, Gehlbach 1995) and not clogged with vegetative matter were considered available to the owls for nesting. Dusk observations and tape playback around the off-territory cavity were also conducted on three nights 8 – 14 days apart to ensure that it was not within the territory of another screech-owl or larger owl. Habitat measurements were then made in the post-fledging period in order to minimize potential disturbance to nesting owls and to ensure consistency in vegetation measurements, since all tree and shrub species were fully foliated by this time.

Two habitat models were planned - 1) broad habitat variables collected in plots of a radius of 50m around the nest tree or off-territory cavity tree, and 2) nest-site context variables, most of which were measurements made on the cavity tree itself or else collected in a smaller plot of 12m radius around the tree (e.g. shrub density). The variables measured for each model were 1) habitat variables: % canopy cover, number of natural cavities and nest boxes, number of trees >10m tall, number of trees 5 – 10m tall, average diameter at breast height (DBH) of trees >10m tall, average DBH of trees 5 – 10m tall, % native riparian canopy trees (percentages of American elm, Manitoba maple, bur oak, eastern cottonwood, and basswood independently counted and then combined), % other deciduous trees, % coniferous trees, % open understory, and % impervious surface and 2) nest-site variables: nest tree species, DBH nest tree, cavity height, height

of nest tree, tree diameter at cavity height, diameter of cavity entrance, orientation of cavity, distance to nearest permanently flowing watercourse, % canopy cover of nest tree, relative canopy height (defined as the average height of the three tallest canopy trees nearest to the nest tree), % shrub density, and minimum flight path (defined as the minimum distance unobstructed by vegetation in a 45° angle forward from nest entrance, at or below nest height and >30cm off the ground). A maximum of eight variables were used per model and some variables were omitted due to colinearity (see Tables 3.2.1, 3.2.3 and 3.2.4).

For statistical calculations, only independent cavities were considered (several cavities with repeat usage were only entered once). Measurements were made with a tape measure where possible, otherwise with a Suunto clinometer. Large horizontal distances were measured by tape measurements where possible or by reading from a map in GIS Arcview 3.2. Percent density measurements are all estimations made by subdividing the appropriate area into quadrants and then calculating total density.

In addition to the habitat models, a predator and disturbance model was planned based on information gathered around used and unused cavities. A series of predator-board trials were conducted at all sites in the post-fledging period. Fine-grained sand was spread over 45 x 39cm trays, wet with a mist spray and then smoothed to produce an even surface. The center of the tray was baited with a small amount of fish-flavored cat food. At each site, trays were laid at dusk at the most secluded site within 50m of the cavity and collected one hour after dawn. Sampling was repeated on three separate occasions at least

one week apart. This was to ensure minimal risk of disturbance by humans. If a nest was used over two consecutive years, the trays were laid in the same positions in the second year. Raccoon and domestic cat indices were generated as the number of animals detected divided by the number of nights where trays were laid. In addition, a Great Horned Owl index was generated by calculating the proportion of Great Horned Owls detected on survey transects within the same census subdivision (Chapter 2) as the cavity. Other variables, including distance to road, number of buildings wholly or partly within 50m of nest, distance to nearest building, and human density (see Chapter 2) were also used in the disturbance model. For the purposes of classification, riparian areas were defined as within 500m of a permanent river or watercourse. Greenspace was defined as parks, cemeteries, golf courses, and green corridors such as riparian buffer strips as well as naturally occurring uninhabited copses (see Chapter 2).

I used a conditional logistic regression analysis for each of the three models because this technique permitted the comparison of two available sites per used site, increasing sample size and statistical power. Furthermore, the regression approach would allow for the possibility of including both categorical and continuous variables (Hull Sieg and Becker 1990). However, since homogeneity of variances is assumed, I first examined box plots (Quinn and Keough 2002) and used an *F*-test for variances between used and available sites for each variable and then log-transformed any variable with heterogeneous variances, except for percentage data where the arcsine transformation was used (Zar 1974), and then reexamined box plots. Correlation matrices were examined to ensure that collinear variables were not included in the same model. The method of

selecting two unused cavities per used site and using tightly controlled selection parameters meant that unused sites often exhibited less variation (larger sample size with similar range) than used sites for many variables as indicated by the standard error of the means and the coefficients of variation (Tables 2.1, 2.2, and 2.3). The method of comparing variances between used and unused cavities across a range of variables as pioneered by McCallum and Gehlbach (1988) is therefore unsuited to this data set.

In order to analyze the effects of human activity on habitat selection, I grouped independent cavity uses into three types: high-density suburban, low-density suburban, and rural nests for three multiple discriminant function analyses (MDA) following the three regression models. High-density suburban areas were defined as having a human density of >30 people per hectare (p/ha) (the S3 category, Chapter 2) and averaged 4.37 ± 0.57 km from the city center. Two on-territory plots and three off-territory plots with slightly less than 30 p/ha (>27 p/ha) but which were less than 3 km from city center and in areas with high building density (12 private dwellings per hectare, plus non-residential buildings, Statistics Canada 2004) were reclassified as high-density suburban areas. Low-density suburban areas were defined as having 10 – 30 p/ha (the S1 and S2 categories, Chapter 2); however, two on-territory plots and five off-territory plots with slightly greater than 30 p/ha (<34 p/ha) that were >4 km from the city center and few houses in proximity to the cavity in question were reclassified as low-density suburban areas. These sites all had approximately 12 private dwellings per hectare but without non-residential buildings. Rural sites were defined as having <10 p/ha (the wildlands and rural categories, Chapter 2); however, it is important to note that the definition of the rural

category here is based on human density and hence these areas are not necessarily associated with agriculture. The greatest number of nest-sites was in low-density suburban areas (n = 38, compared to 15 high-density sites and 8 rural sites).

MDA is not robust to heteroscedacity so I examined box plots and either log transformed variables or, where transformations were insufficient to solve the problem of heteroscedacity, removed the variable from the MDA analysis. One variable, the pedestrian index was added to the disturbance MDA. The pedestrian index was only calculated on active territories because I only made three nighttime visits to off-territory sites, which was insufficient to produce a meaningful index. The pedestrian index was calculated by dividing the night into two-hour periods, P1: 8 – 10pm, P2: 10 – 12pm, P3: 12 – 2am, P4: 2- 4am, and P5: 4- 6am. On each visit to a territory the number of pedestrians within 50m of the nest or fledged young was recorded. The number of pedestrians was divided by a correction factor for each period: P1 correction = 4, P2 correction = 3, P3 correction = 2, P4 = 1, and P5 = 1.5. This purpose of the correction factor was to avoid biasing pedestrian counts by time of night (the number of people averaged approximately four times higher near dusk than at 3am at any given site). The corrected number of pedestrians were then summed and divided by the total number of minutes from all visits and multiplied by 100.

RESULTS

From 2004 – 2007, 46 successful Eastern Screech-Owl nests, 6 failed nests, and 37 stable territories (where a pair was active but did not breed or where one or more cavities was

advertised by an unpaired male over a period greater than 6 weeks) were located (Chapter 2). Excluding repeat cavity uses, a total of 61 nest sites and territory centers were located, of which 38 (62%) were in natural cavities, 21 (34%) in nesting boxes for Wood Ducks (*Aix sponsa*), and two (3%) at sites where cavity choice was undetermined. The majority of natural cavities were found in American elm and Manitoba maple (Table 3.1). None of the nest-sites used in this study were excavated by woodpeckers, presumably because the only two woodpeckers species in southern Manitoba that excavate cavities of sufficient size to be used by screech-owls, Northern Flicker (*Colaptes auratus*) and Pileated Woodpecker (*Dryocopus pileatus*) (Gehlbach 1995) do not regularly breed in the suburban and urban parts of the study area.

Table 3.1. Distribution of natural cavities by tree species. Used cavities include only sites where at least one young fledged

	used	unused
<i>Ulmus americana</i> - American elm	5 (25%)	23 (30%)
<i>Acer negundo</i> - Manitoba maple	5 (25%)	29 (38%)
<i>Quercus macrocarpa</i> - bur oak	3 (15%)	7 (9%)
<i>Fraxinus pennsylvanica</i> - green ash	2 (10%)	5 (6%)
<i>Populus deltoides</i> - eastern cottonwood	2 (10%)	10 (13%)
<i>Tilia Americana</i> - basswood	2 (10%)	3 (4%)
<i>Populus balsamifera</i> - balsam poplar	1 (5%)	0 (0%)

Selection of Used Versus Unused Cavities

HABITAT FEATURES

Four variables differed significantly between used and unused cavity habitat plots (Table 3.2.1). Screech-owls selected territories with more potential nest sites, averaging 3.4 potential nest sites on-territory but only 1.8 off-territory ($z = 3.52$, $df = 8$, $p < 0.001$). Nest sites selected by screech-owls also had significantly greater canopy cover within a 50m radius around the nest tree (40% versus 30% respectively, $z = 2.7$, $p = 0.007$) although a

few nests were in snags with no canopy foliage directly above the nest. Screech-owls selected sites with a higher percentage of coniferous trees (15% versus 12% respectively, $z = 2.13$, $p = 0.03$) and where the DBH of tall trees (>10m) averaged slightly lower than unused sites (38.7cm versus 39.5cm, $z = -2.03$, $p = 0.04$).

Table 3.2.1. Averages \pm standard error of the mean of habitat variables with coefficient of variation (CV) and output of the conditional regression model

	Used cavities		Unused cavities		z	p
	$\bar{X} \pm SE$	CV	$\bar{X} \pm SE$	CV		
% Canopy cover	40.41 \pm 2.22	39.05	29.5 \pm 1.91	61.36	2.7	0.007*
# cavities and boxes§	3.35 \pm 0.31	68.76	1.83 \pm 0.15	71.84	3.52	<0.001*
% conifer	15.11 \pm 1.72	89.57	12.4 \pm 1.17	88.8	2.13	0.03*
DBH trees >10m (cm)	38.7 \pm 0.99	20.45	39.5 \pm 0.92	21.73	-2.03	0.04*
# trees >10m	50.22 \pm 3.47	53.22	53.95 \pm 3.31	58.24	-1.51	0.13
% native riparian cavity sp†	74.53 \pm 2.6	26.78	74.76 \pm 2.02	26.31	0.65	0.52
% open understory	78.8 \pm 2.1	20.85	79.06 \pm 1.77	20.89	1.12	0.26
% impervious surface†	14.58 \pm 1.95	105.16	23.37 \pm 2.03	82.03	-1.49	0.14

Conditional regression: (n=151): § indicated that the variable was log transformed. † indicates the arcsine transformation. * indicates significance, $p < 0.05$. $R^2 = 0.33$ of maximum possible 0.51. Likelihood ratio test = 59.9 on 8 df, $p < 0.001$.

I further investigated the importance of conifers by compiling a database of roost sites and then reducing the sample to reflect independent uses by deleting repeat entries of sites used more than once per month (Table 3.2.2). In winter and in the early part of breeding before trees are foliated (November – April), conifers constitute 30% of roost sites (versus 14% deciduous), but this drops to 14% from May – October (versus 76% deciduous). This difference is significant, ($\chi^2 = 74.5$ with Yates' continuity correction, df = 1, $p < 0.001$). Conifers and cavities combined constitute 70% of roost sites from November – April suggesting their importance for efficient thermoregulation and concealment in northern regions. Roosting in or on buildings likely provides a similar thermoregulatory advantage. Buildings were rarely used as roost sites in the summer (only 5% of roost sites from May to October).

Table 3.2.2. Roost site by period

	Conifer	Cavity	Building	Deciduous	Total
Nov - Feb	9 (13%)	35 (49%)	17 (24%)	10 (14%)	71
Mar - Apr	35 (45%)	25 (32%)	7 (9%)	10 (13%)	77
May - June	37 (14%)	10 (4%)	12 (4%)	210 (78%)	269
July - Oct	5 (15%)	4 (12%)	4 (12%)	20 (61%)	33
Total	86 (19%)	74 (16%)	40 (9%)	250 (56%)	450

Birds roosting in cavities were sometimes perched at the mouth (sunning). Cavities and tree hollows (open to the floor of the hollow area) are not distinguished here.

The ground layer around nesting cavities was 79% open (Table 3.2.1), with few shrubs and tall forbs or grasses. Lawns comprised between zero and 78% of the area in a 50m radius around nest-sites, averaging 35% of that area ($34.7 \pm 2.4\%$).

NEST-SITE FEATURES

Nest-site specific variables showed less significance than habitat variables. Screech-owls selected taller nest trees (average 13.3m on-territory versus 11.4m off-territory, $z = 3.35$, $df = 8$, $p < 0.01$), lower shrub density at the base of the nest tree (10% versus 16%, $z = -1.98$, $p = 0.05$), and chose trees closer to rivers or creeks even though the category averages were extremely similar ($z = -1.2$, $p = 0.05$) (Table 3.2.3).

Table 3.2.3. Averages \pm standard error of the mean of nest-site variables with coefficient of variation (CV) and output of the conditional regression model.

	Used cavities		Unused cavities		z	p
	$\bar{X} \pm SE$	CV	$\bar{X} \pm SE$	CV		
Height of nest tree (m) §	13.26 \pm 0.5	27.42	11.38 \pm 0.32	25.8	3.35	<0.001*
Cavity height (m)	5.66 \pm 0.4	53.26	5.5 \pm 0.27	46.08	-0.405	0.69
DBH nest tree (cm) §	50.96 \pm 2.57	37.19	54.87 \pm 2.69	45.25	-1.77	0.08
Diameter entrance (cm) §	10.7 \pm 0.42	29.27	10.54 \pm 0.21	18.0	-0.5	0.61
Distance to river (m)	255.3 \pm 69.1	211.42	254.8 \pm 35.9	166.57	-1.99	0.047*
% canopy cover	41.77 \pm 2.96	52.5	42.25 \pm 2.31	50.63	0.17	0.87
% shrub density†	10.2 \pm 2.39	175.43	15.69 \pm 2.7	160.44	-1.98	0.048*
Minimum flight path (m)	6.69 \pm 0.74	81.1	5.71 \pm 0.49	80.32	1.11	0.27

Conditional regression: (n=143): § indicated that the variable was log transformed. † indicates the arcsine transformation. * indicates significance, $p < 0.05$. $R^2 = 0.17$ of maximum possible 0.5. Likelihood ratio test = 27 on 8 df, $p < 0.001$.

DISTURBANCE AND PREDATION RISK

This model evaluates variables related to the threat of predation and anthropogenic and natural disturbance (Table 3.2.4). Distance to building was not included in the disturbance model because of colinearity with the number of buildings. The number of buildings is also correlated with percentage impervious surface; hence they were not used in the same model. Two significant variables emerged from this analysis. Firstly the domestic cat index averaged significantly lower at on-territory nest sites versus off-territory sites (0.2 versus 0.3 respectively, $z = -2.5$, $df = 6$, $p = 0.01$) suggesting that high domestic cat activity might be a deterrent in the nest-site selection process. Secondly, the number of buildings wholly or partly within a radius of 50m around the nest-site averaged significantly lower at on-territory sites (4.5 versus 6.9, $z = -2.2$, $p = 0.03$).

Table 3.2.4. Averages \pm standard error of the mean of disturbance variables with coefficient of variation (CV) and output of the conditional regression model.

	Used cavities		Unused cavities		z	p
	$\bar{x} \pm SE$	CV	$\bar{x} \pm SE$	CV		
Great Horned Owl index	0.09 \pm 0.02	156.77	0.1 \pm 0.02	154.01	-0.34	0.74
Cat index	0.2 \pm 0.04	131.95	0.34 \pm 0.03	85.21	-2.89	0.004*
Raccoon index	0.13 \pm 0.03	193.27	0.14 \pm 0.03	179.6	-1.21	0.22
# buildings	4.53 \pm 0.79	135.27	6.9 \pm 0.73	99.82	-2.55	0.01*
Percent greenspace †	16.87 \pm 2.38	110.1	17.55 \pm 1.98	107.12	-1.11	0.27
Distance to road (m)	58 \pm 8.16	107.2	47.31 \pm 7.55	146.25	-0.44	0.66

Conditional regression: (n=151): † indicates the arcsine transformation. * indicates significance, $p < 0.05$. $R^2 = 0.15$ of maximum possible 0.51. Likelihood ratio test = 25 on 6 df, $p < 0.001$.

I further investigated the potential effect of variables that might be related to predator avoidance using a simple classifying scheme of the success rate of all pairs (n = 44). Pairs that had produced young for every year of occupancy were scored 100%, pairs that produced young in two of three years of occupancy 67%, one of two years occupancy 50%, one of three years occupancy 33%, and never produced young 0%. A regression

analysis (residual standard error = 29.33, $df = 22$, $R^2 = 0.42$) of success as a function of distance to building, shrub density, pedestrian index, raccoon index, cat index, Great Horned Owl index, cavity depth, height of cavity, diameter of cavity, number of buildings within 50m, distance to water, minimum flight path, and the number of cavities + boxes found that shrub density was significantly lower below more successful nests ($t = -2.39$, $p = 0.03$) and distance to building was significantly greater from successful nests ($t = 2.17$, $p = 0.04$). Nests with 100% success rate averaged 55.62m from the nearest building whereas unsuccessful nests averaged 38.24m from the nearest building.

Differences between Suburban and Rural Nests

Habitat features around nest sites differed considerably between high-density suburban, low-density suburban and rural nests (Table 3.3.1).

Table 3.3.1. Averages \pm standard error of the mean of habitat features around used and unused nest sites (plots of 50m radius) in three categories.

	High-density suburban		Low-density suburban		Rural	
	Used (n = 15)	Unused (n = 20)	Used (n = 38)	Unused (n = 58)	Used (n = 8)	Unused (n = 12)
% canopy cover	37.33 \pm 3.47	27.73 \pm 3.77	39.34 \pm 2.54	28.78 \pm 2.38	51.25 \pm 6.28	36.67 \pm 5.84
# cavities	2.6 \pm 0.49	1.80 \pm 0.3	2.0 \pm 0.31	1.64 \pm 0.2	3.5 \pm 0.76	1.75 \pm 0.37
# boxes	0.67 \pm 0.3	0.2 \pm 0.16	1.32 \pm 0.39	0.12 \pm 0.04	0.25 \pm 0.25	0.08 \pm 0.08
Cavities + boxes	3.27 \pm 0.51	2.0 \pm 0.33	3.32 \pm 0.43	1.76 \pm 0.19	3.75 \pm 0.62	1.83 \pm 0.34
# Trees>10m	45.67 \pm 5.91	43.3 \pm 3.17	49.55 \pm 4.29	57.16 \pm 4.35	60.88 \pm 12.07	51.58 \pm 11.21
Tr>10m DBH	39.82 \pm 1.7	40.72 \pm 1.41	37.42 \pm 1.35	39.2 \pm 1.15	39.63 \pm 2.74	38.39 \pm 3.16
#Trees >5m	23.6 \pm 6.52	33.1 \pm 4.28	33.37 \pm 3.58	44.33 \pm 5.8	41.5 \pm 8.29	39.83 \pm 6.07
Tr>5m DBH	14.76 \pm 0.90	13.91 \pm 0.78	14.58 \pm 0.65	15.12 \pm 0.46	15.4 \pm 1.40	16.2 \pm 1.08
% Conifer	18.77 \pm 3.83	17.16 \pm 2.52	14.96 \pm 2.15	12.16 \pm 1.41	7.27 \pm 2.62	6.21 \pm 2.72
% NRCT	73.78 \pm 3.93	72.83 \pm 3.45	75.99 \pm 3.03	76.83 \pm 2.36	68.51 \pm 11.48	64.95 \pm 8.53
% elm	32.59 \pm 4.93	31.16 \pm 3.1	20.78 \pm 2.36	23.5 \pm 2.38	23.49 \pm 6.17	18.04 \pm 4.76
% maple	16.86 \pm 3.47	19.81 \pm 2.56	15.8 \pm 2.4	16.01 \pm 1.59	9.08 \pm 4.72	17.71 \pm 4.27
% ash	7.96 \pm 1.63	9.04 \pm 1.34	15.38 \pm 2.33	11.46 \pm 1.16	20.06 \pm 4.3	13.44 \pm 4.24
% oak	12.03 \pm 4.89	5.74 \pm 2.47	18.74 \pm 3.48	19.0 \pm 2.99	8.68 \pm 3.4	6.6 \pm 2.74
% cottonwood	3.34 \pm 1.26	4.53 \pm 1.51	1.92 \pm 0.8	1.62 \pm 0.81	4.66 \pm 2.32	8.41 \pm 2.94
% basswood	1.01 \pm 0.58	2.55 \pm 0.87	3.36 \pm 2.01	5.24 \pm 1.81	2.53 \pm 1.36	0.75 \pm 0.54
% Other dec	7.45 \pm 2.38	10.0 \pm 1.83	9.05 \pm 1.9	11.02 \pm 1.56	24.21 \pm 12.05	28.84 \pm 8.85
% open ugr	79.13 \pm 4.79	80.71 \pm 3.7	78.26 \pm 2.49	78.78 \pm 2.2	78.0 \pm 6.66	77.75 \pm 4.75
% impervious	15.72 \pm 4.32	33.95 \pm 4.25	15.32 \pm 2.47	23.45 \pm 2.42	7.09 \pm 3.37	5.5 \pm 1.97

Abbreviations: tr = trees, DBH = diameter at breast height, NRCT = native riparian cavity tree (American elm, green ash, Manitoba maple, bur oak, basswood, and eastern cottonwood), other dec = other deciduous trees other than those in NRCT, open ugr = open understory (ground layer).

The MDA comparing the habitat variables from used cavities in three groups (high-density suburban, low-density suburban, and rural) identified one significant axis and one non-significant axis, viz. canonical 1: canonical correlation = 0.7, likelihood ratio = 0.38, $F = 1.65$, $df = 32, 86$, $p = 0.04$ and canonical 2: canonical correlation = 0.5, likelihood ratio = 0.75, $F = 0.97$, $df = 15, 44$, $p = 0.5$. The % other deciduous trees variable (Table 3.3.1) and the % native riparian cavity tree, as well as the total number of cavities + boxes were removed to avoid producing an ill-conditioned matrix (number of boxes and cavities were included separately). The MDA correctly classified 88% of rural sites, 74%

of low-density suburban and 80% of high-density suburban sites, suggesting strong habitat differences between these categories.

Table 3.3.2. Pooled within-class standardized canonical coefficients and total canonical structure from MDA for habitat variables

	Pooled Within-Class Standardized Canonical Coefficients		Total Canonical Structure	
	Can1	Can2	Can1	Can2
% canopy cover	0.23	-0.01	0.35	-0.22
# cavities	0.42	-0.01	0.10	-0.51
# boxes	0.37	0.70	-0.11	0.43
# Trees>10m §	-0.47	-0.17	0.25	-0.06
Tr>10m DBH	-0.27	-0.20	-0.04	-0.34
#Trees >5m	0.95	0.27	0.45	0.21
Tr>5m DBH	-0.21	-0.08	0.07	-0.12
% Conifer †	-0.76	0.01	-0.35	0.02
% elm †	-1.00	-0.31	-0.33	-0.40
% maple †	-1.02	0.45	-0.29	0.20
% ash †	0.29	0.31	0.38	0.10
% oak †	-0.69	0.41	-0.02	0.45
% cottonwood †	0.25	-0.22	0.08	-0.48
% basswood †	0.03	0.27	0.15	0.14
% open ugr †	0.86	-0.03	-0.03	-0.09
% impervious †	0.29	0.45	-0.24	0.20

§ indicated that the variable was log transformed. † indicates the arcsine transformation.

The MDA for habitat variables found canonical axis 1 to be most strongly correlated (total canonical structure) with the number of trees 5 - 10m (0.45), the % green ash (0.38) the % canopy cover (0.35), and the number of trees >10m (0.25). It was negatively correlated with % conifer (-0.35), % American elm (-0.33), % Manitoba maple (-0.29), % impervious surface (-0.24). Canonical axis 1 was also less strongly correlated with the number of cavities (0.11) and negatively with number of nest boxes (-0.12). Canonical 1 is therefore a gradient of denser canopy with more medium-sized trees 5-10m (and to a lesser extent tall trees >10m) with more green ash but less conifer, Manitoba maple and

American elm (the latter are often planted in suburban areas as boulevard trees). American elm and Manitoba maple interestingly were the tree species with the most cavities (Table 3.1). In addition, canonical axis 1 is correlated with lower impervious surface area, more cavities and less nest boxes. Rural sites score highest on canonical variable 1 and high-density suburban sites lowest (Fig 3.1).

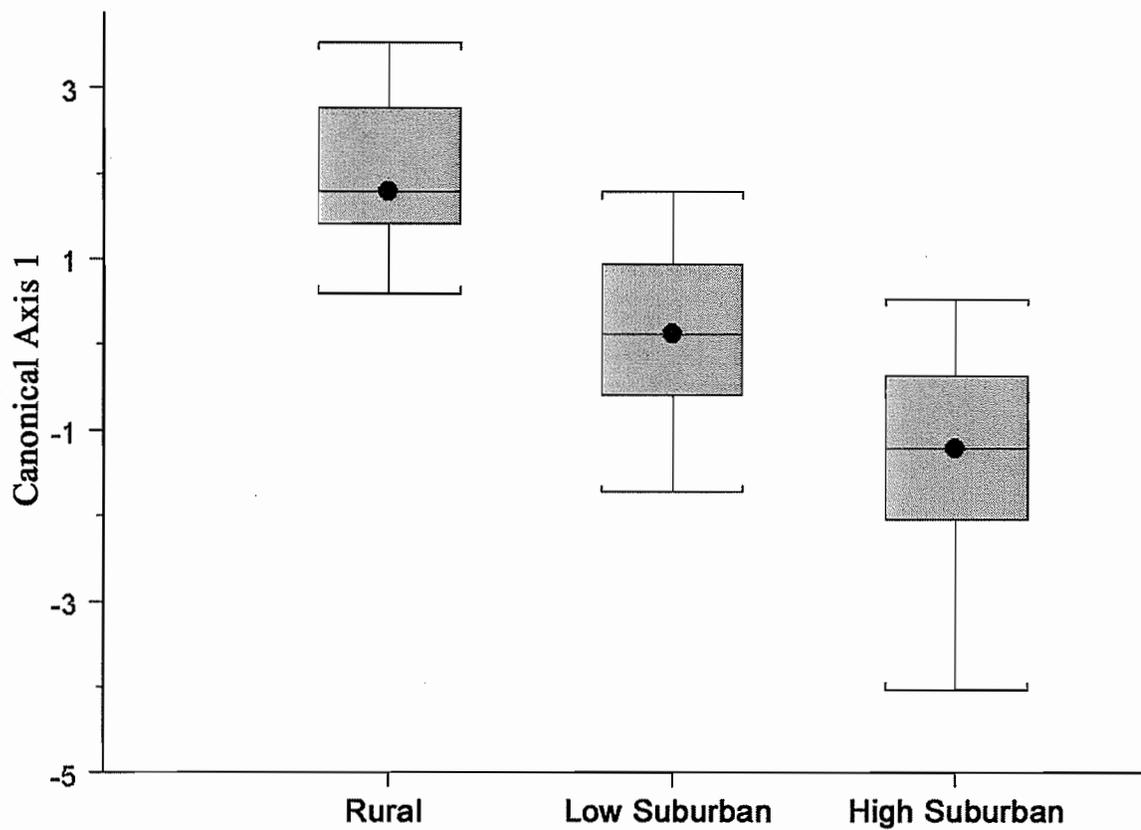


Fig. 3.1. Box plots of canonical 1 scores for habitat variables.

Nest-site features around nest sites also differed between high-density suburban, low-density suburban and rural nests (Table 3.4.1).

Table 3.4.1. Averages \pm standard error of the mean of nest-site features around used and unused nest sites (plots of 12m radius) in three categories

	High-density Suburban		Low-density Suburban		Rural	
	Used (n = 15)	Unused (n = 20)	Used (n = 38)	Unused (n = 58)	Used (n = 8)	Unused (n = 12)
DBH nest tree (cm)	55.67 \pm 4.55	59.26 \pm 3.06	50.97 \pm 3.39	52.39 \pm 3.07	44.75 \pm 7.25	58.25 \pm 12.2
Cavity height (m)	5.87 \pm 0.65	5.81 \pm 0.79	5.37 \pm 0.52	5.13 \pm 0.28	5.87 \pm 1.36	6.38 \pm 0.76
H. nest tree (m)	12.67 \pm 0.75	13.21 \pm 0.66	13.6 \pm 0.62	10.79 \pm 0.32	13.06 \pm 1.88	11.05 \pm 1.2
DmCavH (cm)	32.07 \pm 1.73	37.21 \pm 2.0	37.27 \pm 2.4	36.05 \pm 1.1	33.5 \pm 2.26	37.08 \pm 4.15
Diameter (cm)	11.55 \pm 1.06	10.83 \pm 0.43	10.59 \pm 0.5	10.37 \pm 0.25	9.44 \pm 0.46	10.67 \pm 0.63
Dist. water (m)	180.8 \pm 53.95	184.94 \pm 39.69	182.29 \pm 46.99	227.52 \pm 31.8	741.44 \pm 454.75	755.83 \pm 320.51
Relcanheight (m)	13.77 \pm 0.71	15.6 \pm 1.68	13.77 \pm 0.55	13.06 \pm 1.39	14.03 \pm 1.64	11.26 \pm 0.61
% Candense	47.05 \pm 5.64	45.86 \pm 4.75	37.77 \pm 3.57	38.03 \pm 2.0	52.53 \pm 9.62	55.52 \pm 4.04
% shrub density	8.12 \pm 2.84	9.94 \pm 2.9	8.62 \pm 2.81	14.39 \pm 3.24	19.54 \pm 10.54	28.64 \pm 10.44
Minflpath (m)	7.9 \pm 0.96	5.76 \pm 0.54	5.95 \pm 1.01	6.19 \pm 0.75	7.9 \pm 2.4	4.62 \pm 0.74

Abbreviations: H. = height, DmCavH = diameter of trunk or branch at the height of the cavity, Dist. water = distance to nearest river or creek, Relcanheight = relative canopy height, % candense = % canopy density above nest tree, and Minflpath = minimum flight path.

The MDA of the nest-site variables identified one significant axis and one non-significant axis, viz. canonical 1: canonical correlation = 0.58, likelihood ratio = 0.51, $F = 1.74$, $df = 20, 88$, $p = 0.04$ and canonical 2: canonical correlation = 0.47, likelihood ratio = 0.78, $F = 1.43$, $df = 9, 45$, $p = 0.21$. Nests-sites differed comparatively little between areas and the MDA thus only correctly classified 75% of rural sites, 70% low-density suburban sites and 67% of high-density suburban sites.

Table 3.4.2. Pooled within-class standardized canonical coefficients and total canonical structure from MDA for nest-site variables

	Pooled Within-Class		Total Canonical Structure	
	Standardized Canonical Coefficients		Can1	Can2
	Can1	Can2		
DBH nest tree (cm)	-0.65	-1.11	-0.17	-0.31
Cavity height (m)	0.37	0.05	0.11	-0.12
H. nest tree (m)	-0.12	0.94	-0.10	0.20
DmCavH (cm)	0.10	0.63	-0.22	0.35
Diameter (cm)	-0.31	-0.46	-0.19	-0.38
Dist. water (m) §	0.86	0.18	0.61	0.01
Relcanheight (m)	0.43	-0.08	0.05	0.02
% Candense	0.77	-0.36	0.41	-0.23
% shrub density §	0.00	0.19	0.31	0.08
Minflpath (m)	0.52	-0.35	0.23	-0.25

§ indicated that the variable was log transformed. † indicates the arcsine transformation.

In the analysis of nest-site features, canonical one was very strongly correlated to distance to water (0.61), canopy density directly above the nest tree (0.41), and shrub density directly below the nest tree (0.31). It is also less strongly correlated with minimum flight path (0.22) and negatively correlated with diameter at cavity height (-0.22), DBH of nest tree (-0.17), and diameter of the cavity's entrance (-0.19). In addition to distance to water, canonical one represents a gradient of denser vegetation at the nest (canopy, middle story, and shrub layer) and decreasing width of the nest tree (DBH and diameter at cavity height) with a smaller entrance. Rural sites score highest on this axis (Fig. 2), as they tend to show denser vegetation and slightly smaller trees.

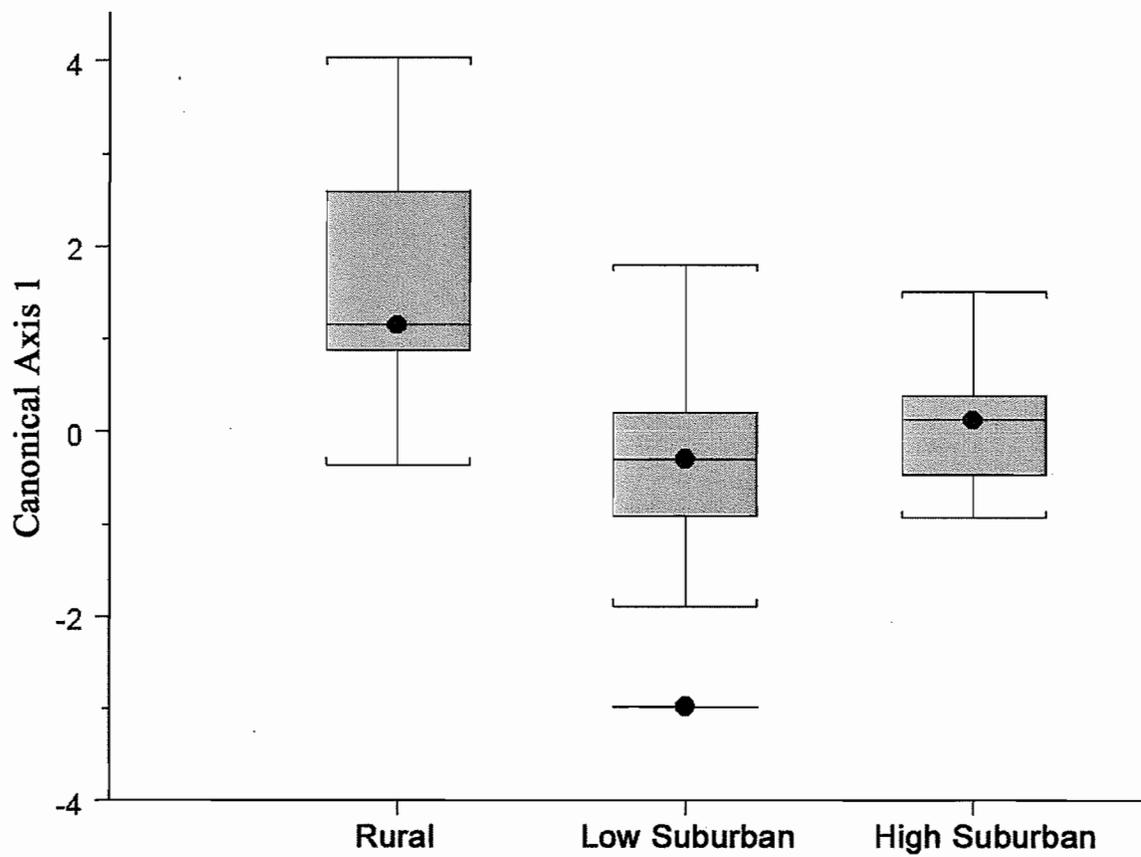


Fig. 3.2. Box plot of canonical 1 scores for nest-site variables.

Predation risk, disturbance and anthropogenic features around nest sites showed strong differences between high-density suburban, low-density suburban and rural nests (Table 3.5.1).

Table 3.5.1. Averages \pm standard error of the mean of disturbance and anthropogenic features around used and unused nest sites (plots of 12m radius) in three categories.

	High-density Suburban		Low-density Suburban		Rural	
	On (n = 15)	Off (n = 20)	On (n = 38)	Off (n = 58)	On (n = 8)	Off (n = 12)
Raccoon index	0.11 \pm 0.05	0.14 \pm 0.04	0.09 \pm 0.03	0.13 \pm 0.04	0.38 \pm 0.13	0.21 \pm 0.09
Cat index	0.32 \pm 0.09	0.43 \pm 0.07	0.18 \pm 0.04	0.31 \pm 0.04	0.08 \pm 0.05	0.37 \pm 0.09
GHOW index	0.03 \pm 0.02	0.04 \pm 0.02	0.09 \pm 0.03	0.11 \pm 0.02	0.21 \pm 0.05	0.19 \pm 0.04
Dist. road (m)	51.45 \pm 12.72	37.35 \pm 15.32	51.85 \pm 7.86	34.29 \pm 4.71	98.48 \pm 40.84	126.61 \pm 36.77
# buildings	6.67 \pm 2.45	10.40 \pm 1.71	4.39 \pm 0.75	6.88 \pm 0.83	1.0 \pm 0.46	0.50 \pm 0.23
Dist. bldg (m)	69.89 \pm 31.41	29.71 \pm 9.21	43.34 \pm 7.73	31.99 \pm 3.64	87.92 \pm 47.29	130.76 \pm 42.41
% green space	11.63 \pm 3.87	16.92 \pm 4.83	14.14 \pm 1.91	13.79 \pm 1.38	39.65 \pm 11.63	36.8 \pm 9.14
Pedestrian index	2.8 \pm 0.41	N/A	1.82 \pm 0.19	N/A	1.03 \pm 0.48	N/A
Human density	44.63 \pm 4.69	49.02 \pm 4.6	22.94 \pm 0.89	23.52 \pm 0.83	5.69 \pm 1.58	5.75 \pm 1.23

Human density was not included in the discriminant function analysis as it predefines the three categories. Abbreviations: Dist. road = distance to nearest road, dist. bldg = distance to nearest building.

The MDA of the disturbance variables identified one significant axis and one non-significant axis, viz. canonical 1: canonical correlation = 0.57, likelihood ratio = 0.57, $F = 2.4$, $df = 14, 104$, $p = 0.006$ and canonical 2: canonical correlation = 0.38, likelihood ratio = 0.86, $F = 1.47$, $df = 6, 53$, $p = 0.21$. The MDA correctly classified 88% of rural sites, 61% of low-density suburban sites and 80% of high-density suburban sites (Table 3.5.2).

Table 3.5.2. Pooled within-class standardized canonical coefficients and total canonical structure from MDA for disturbance variables

	Pooled Within-Class Standardized Canonical Coefficients		Total Canonical Structure	
	Can1	Can2	Can1	Can2
# buildings	0.52	0.32	0.47	-0.08
Dist. Bldg (m) §	0.29	0.64	-0.11	0.54
Dist. Road (m) §	0.23	0.28	-0.41	0.00
Raccoon index	-0.31	0.83	-0.44	0.74
Cat index	0.27	0.38	0.48	0.12
GHOW index	-0.39	-0.06	-0.59	0.20
Pedestrian index	0.68	0.23	0.76	0.23

§ indicated that the variable was log transformed.

Canonical one was very strongly correlated to the pedestrian index (0.76), the domestic cat index (0.48) and the number of buildings (0.47), and negatively correlated to the Great Horned Owl index (-0.59), the raccoon index (-0.44), and distance to road (-0.41). This gradient typifies the urban - rural distinction with more people, buildings, and domestic cats but fewer natural predators (Great Horned Owl and raccoon). Unsurprisingly, high-density suburban sites score highest on this axis and rural sites lowest (Fig. 3.3).

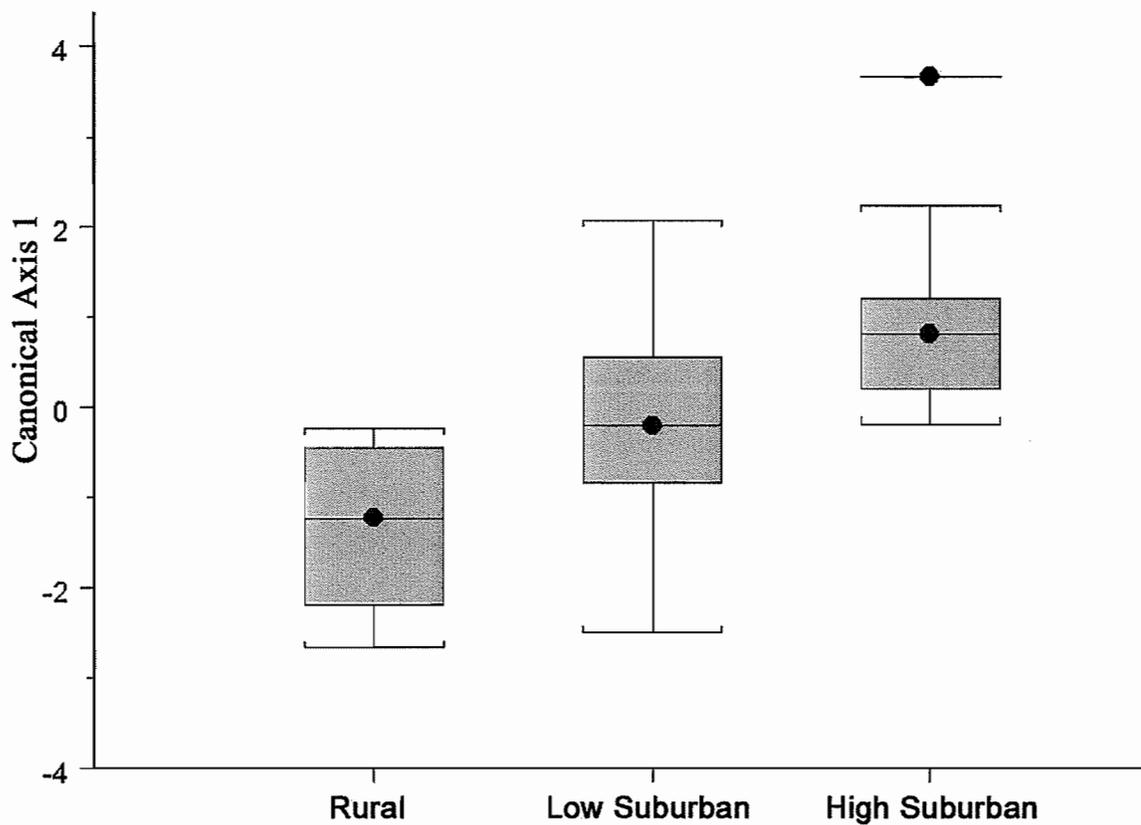


Fig. 3.3. Box plot of canonical 1 scores for disturbance variables.

DISCUSSION

Selection of Used versus Unused Cavities

The preferred nesting habitat of screech-owls in the study area contains a moderately closed canopy (average 40% canopy cover), consistent with the range-wide preference for open areas in the subcanopy (Gehlbach 1995). Taller trees were selected for nests; however, screech-owls did not select for cavities that were higher above the ground, which has been suggested as a predator avoidance strategy (Nilsson 1984, Rendell and Robertson 1989, Belthoff and Ritchison 1990a), nor were their nests lower than unused cavities, which has been suggested as an energy saving measure (Collias and Collias 1984). An open subcanopy thus appears important and may permit maneuverability around the nest and the opportunity to detect predators easily and attack them from above when necessary (Gehlbach 1995). These owls are mostly breeding in areas that can be described as “disturbed” and often close to buildings, roads and other anthropogenic features but still require a minimal level of canopy cover. The lowest canopy closure of any successful nest was 16% and there were several cases where nesting territories were in areas with only a few tall trees and large open lawns.

Eastern Screech-Owls chose territories with an average of three potential nest-sites and avoid sites with fewer potential nest sites (Table 3.1). Alternate cavities are thus a significant habitat selection feature for this polyterritorial species (Gehlbach 1995). Alternate cavities may serve as the site for renesting attempts (Gehlbach 1995) or occasionally for food-caching (pers. obs). Males also occasionally roosted at the entrance of alternate cavities when these were in line of sight with the nest cavity (pers. obs). In

some cases, screech-owls were observed alternating between two similar nest-sites over a three-year period. Although some predators may increase their search intensity when many cavities are present (Martin 1988), the switching of cavities may reduce the likelihood of nest predation from predators that rely on memory (Sonerud 1985a, 1989, Gehlbach 1994b) or reduce the effect of ectoparasites (Aitken et al. 2002).

The presence of coniferous trees around a nest-site may not be a significant factor over most of the range of the Eastern Screech-Owl; however, in Manitoba where there are no native non-coniferous evergreen shrubs, conifers provide excellent roosting sites close to the nests for both shelter and concealment especially early in the nesting season. Male screech-owls have been shown to roost close to their nests early in the breeding season, perhaps as an anti-predator behavior (Sproat 1997). Many paired males in this study used conifers close to the nest as roost sites, especially in the early stages of nesting before deciduous trees had fully foliated. It is not surprising therefore that the owls select nest sites with an average of 15% coniferous trees within a 50m radius of the nest (Table 3.2.1). Nonetheless there were five successful nests where no conifer was present within 50m of the nest, although in these cases conifer was present within 100m of the nest. The presence of roost sites with suitable thermoregulatory properties (coniferous trees, cavities, and buildings) in the early period of the breeding season therefore appears to be an important habitat selection feature at very northern latitudes. Further south, cavities were found to be important winter roost sites in Virginia (Merson et al. 1983) and in Texas for thermoregulatory reasons (Gehlbach 1994b). Conifers may also offer concealment at other times of year, e.g. in Kentucky, 17.4% of adult and juvenile Eastern

Screech-Owl roost sites in the post-fledging period were in conifers, when these family units were roosting on average 252m from their nest site (Belthoff and Ritchison 1990b).

The most unusual finding of this habitat model was that the DBH of trees >10m tall averaged significantly lower on-territory than off. A possible explanation is an effect created by the placement of nest boxes in areas with smaller trees that would increase the attractiveness of those areas to secondary-cavity nesters (Perrins 1979, Tiainen et al. 1984), although nest boxes only constituted 34% of nest-sites (21% of total sample size). Despite an effort to match used boxes with unused boxes and used cavities with unused cavities, boxes constituted 38% of used nest sites versus only 11% of unused sites. The DBH of trees on which boxes were placed was 40.9cm, 16cm less than the DBH of trees with natural cavities (56.8cm). The overall average of the DBH of all trees within a 50m radius of natural cavities was 39.3cm versus 37.6cm around nest-boxes. The latter small difference suggests that boxes had minimal influence on broad-scale habitat selection. Furthermore, in both Manitoba (Chapter 2) and Texas (Gehlbach 1994b), no significant differences in productivity were found between boxes and natural cavities, despite the fact that larger broods may occur in boxes than in natural cavities in other owl species (Korpimäki 1981).

The nest-site model suggests that screech-owls select cavities in taller nest trees which are closer to water and with low shrub density around the base of the nest tree. This may imply less selection regarding the characteristics of the cavity than the surrounding vegetation; however, this stems at least in part from the fact that variability of the off-

territory cavities was reduced by only selecting cavities that conformed to the characteristics of a potential nest-site in order to avoid biologically trivial findings (McCallum and Gehlbach 1988). Cavity availability could influence cavity selection, e.g. low use of suboptimal cavities would imply high nest-site availability in proportion to owl density (Severinghaus 2007) and the relatively low variance in certain features such as cavity entrance size in this data set suggests that this may be the case in Winnipeg. In 2007, only 11 of the 55 (20%) nest sites where breeding was confirmed between 2004 and 2007 that were available (not clogged by squirrels or within the territory of another pair) were used. This percentage would be much lower if other cavities that appeared suitable but which were never found to be used by screech-owls in these four years were included. The cavities in question were found vacant on at least three repeat visits and not used by squirrels or Wood Ducks or other secondary-cavity nesters. These low occupancy rates suggest an unsaturated population, with low density in proportion to the number of cavities available, even if polyterritoriality is considered. This suggests that cavities are not limiting in the study area, at least when supplemented with nest-boxes at the present rate. In addition, high nesting success (Chapter 2) and apparent lack of competition with non-native species such as European Starling are further suggestive of high cavity availability in proportion to owl density (Blewett and Marzluff 2005), although some competition for nest-boxes with Wood Duck (*Aix sponsa*) was recorded (Artuso 2007). Given the local climate and the cold tolerance of this species (Mosher and Henny 1976), winter food supply or energetic demands are likely to be limiting factors in this region. Several authors have argued that an abundance of a resource with preferred characteristics and unsaturated conditions will result in greater selection for those

characteristics (Stephens and Krebs 1986, McCallum and Gehlbach 1988, Greene and Stamps 2001, Hardy and Morrison 2001, Brown et al. 2002) which might explain why in this study I found more selection, at least at the habitat level, around nests in Manitoba than was found in Kentucky (Belthoff and Ritchison 1990a).

Screech-owls in the study area selected nest-sites with less shrubbery at the base of the nest tree and had higher nesting success where shrub density was low, as was the case in Texas (Gehlbach 1994b). Although some shrubbery or thick vegetation on a territory might be important for certain behaviors such as hunting, roosting and territorial “singing” (Gehlbach 1995), a convoluted lower or middle story produces certain risks. Shrubs below a nest can provide opportunities for ambush predators such as domestic cats, and high shrub density decreases the owls’ ability to detect predators (Gehlbach 1994b). The selection of nest-sites with lower shrub density at the base of the nest tree may also be related to the owl’s habit of approaching the nest by flying low to the ground and swooping upward (Gehlbach 1994b). An open area at the base of the nest tree permits such behavior and reduces the likelihood of detection (Gehlbach 1994b). More generally, sparse shrubbery permits greater maneuverability and more open areas to hunt prey at ground level (Robbins et al. 1989, Gehlbach 1995). Likewise, a more open middle story might not only improve the ability to detect potential predators (Nilsson 1984, Belles-Isles and Picman 1986, Martin 1988, Martin and Roper 1988, Finch 1989, but see Martin 1991 for the opposing view that dense vegetation improves nest concealment) but also provide flying room to swoop at predators should they approach too closely.

In Texas, proximity to buildings was correlated with higher nesting success (Gehlbach 1994b). In Winnipeg, screech-owls selected nest-sites with fewer buildings within a radius of 50m and had higher nesting success further from buildings. Human density was much higher in the Winnipeg study site, where 83% of nests occurred in suburban areas with >10 p/ha, than in Gehlbach's (1994b) study site in Texas with <5 p/ha. A possible explanation therefore is a non-linear response to human activity: a certain proximity to buildings may offer advantages where human density is low, but there is a greater risk of disturbance in areas of higher human density. An alternative explanation is that screech-owls may avoid nest-sites that contain too high a proportion of non-habitat. Screech-owls will use houses as perches or roost sites but large areas of impervious surfaces offer poor-quality habitat. If moderate proximity to buildings does provide an advantage, two possible mechanisms for this are increased prey accessibility and reduced predation (Gehlbach 1994b). Some important prey species such as House Sparrow (*Passer domesticus*) and house mouse (*Mus musculus*) were routinely captured close to buildings and screech-owls were also observed using window ledges as hunting perches and hunting near bird feeders (pers. obs). Screech-owls are known to use artificial lights and the light from windows when hunting (Gehlbach 1994). Cooper's Hawks also benefit from increased density of avian prey items correlated to housing density (Germaine et al. 1998, Mannan and Boal 2000). Higher prey densities around homes appear to benefit Burrowing Owls in Florida; however, increasing development lead to a reduction in nesting success (Millsap and Bear 2000). Eastern Screech-Owls, on the other hand, enjoyed both higher densities and higher reproductive success in high-density suburban areas (Chapter 2). Nesting in proximity to buildings may alter the predation risk or type

since as building density increased (also correlated with pedestrian index and human density), raccoon and Great Horned Owl indices decreased, whereas cat index increased (Table 3.5.1). However, the relative importance of natural versus domestic predators is not currently known. There is general support for a decrease in the density of large predators with increasing human density (Crooks and Soulé 1999, Chace and Walsh 2006, Chipman et al. 2008), and nesting near buildings to reduce predation has been documented at least one species, the Eurasian Blackbird (Møller 1988).

In the study area, screech-owls exhibit a very strong preference for riparian habitat. Only eight nest sites or territory centers (13%) were located >500m from a river or creek. Studies using radio transmitters have also found strong habitat associations with running water and wet woodlands and avoidance of dry upland woods (Ellison 1980, Smith and Gilbert 1984). The majority of screech-owl territories in the study area are in riparian strips strongly characterized by American elm, Manitoba maple, green ash, and basswood (Moffat et al. 2004). These species are all relatively close to the northern limit of their range in the study area (Hosie 1979), where they are associated with water courses, especially the floodplains of larger rivers (Bird 1930, Scoggan 1957). Another cavity tree, eastern cottonwood, is most strongly associated with the shelf immediately adjacent to rivers (Bird 1930). Especially within the city of Winnipeg, where the extent of seasonal flooding is partially contained, riparian strips in the flood plain of the Red and Assiniboine Rivers are most likely to meet the habitat requirements of tall mature trees with an open understory (sparse shrub cover) due at least in part to silt deposition from seasonal flooding (pers. obs.). Outside of Winnipeg in undisturbed areas, screech-owl are

also likely to hunt close to water because shrubs become denser and more diverse towards the dry outer margins of riparian forests (Staniforth 2003). Riparian areas also have very high diversity and abundance of various taxa that are potential prey items for screech-owls (Doyle 1990, Naiman and Décamps 1997, Lock and Naiman 1998, Sanders 1998) and screech-owls in the study area frequently hunt along river edges for aquatic prey as well as some voles and shrews (Lynch and Smith 1984, Belthoff and Ritchison 1990a). Eastern Screech-Owls are not absolutely dependent on riparian areas in the study site perhaps because planted shade trees and lawns also create open-forest conditions and bird feeders with fallen seed may sometimes produce prey concentrations.

The predator and disturbance model shows that screech-owls also select areas with low domestic cat activity. In the suburban/urban parts of the study area domestic cats have been observed attacking screech-owls when they came to the ground to hunt (pers. obs.) and even killing an entire brood of fledglings (G. Walz, pers. comm.). Nonetheless, the relative impact of cats on screech-owls as compared to natural predators such as Great Horned Owls is unknown. Raccoons may be the only nest predator in the study area although American mink (*Mustela vison*) may be able to access some nests during spring floods. Other known nest predators such as Virginia opossum (*Didelphis virginiana*), ringtail (*Bassariscus astutus*), and black ratsnake (*Elaphe obsoleta*) (Gehlbach 1995) do not occur this far north. The relative abundance of raccoons does not appear to influence screech-owl habitat selection directly. The Great Horned owl index was also non-significant; however, this finding may stem from the difficulty of assessing proportional use of any given area by Great Horned Owls. Great Horned Owls exhibit the opposite

distribution pattern to Eastern Screech-Owls in the study area, being detected most often on survey transects in rural areas are much less often in suburban and urban areas (Chapter 2). The habitat selection of Eastern Screech-Owls could therefore be influenced by Great Horned Owls, as has been shown for Tawny Owls, which avoid the larger Eurasian Eagle Owl (*Bubo bubo*) (Sergio et al. 2007). More detailed data, e.g. radio telemetry data on proportional habitat use, would be needed to address the impact of predatory owls on nest-site selection by small owls.

Differences between Suburban and Rural Nests

Suburban sites in the study area have higher densities of Eastern Screech-Owls than rural sites and this higher density is linked to more nesting attempts with higher breeding success (Chapter 2). Discriminant function analysis (Fig. 3.1, Fig. 3.2, and Fig. 3.3) suggests a distinction between high-density suburban and rural sites but with low-density suburban sites being intermediate in many variables. There are several key differences between rural and suburban sites including the number of trees around the nest and canopy cover, the number of coniferous trees, the amount of impervious surface, shrub density below the nest tree, distance to water, the number of pedestrians, the number of buildings, and the number of natural and domestic predators. Suburban sites also had more American elm and Manitoba maple but less green ash than rural sites. This suggests that anthropogenic features and different levels of exposure to human activities are influencing the owls' habitat selection and the predation regime they experience.

Although screech-owls select for canopy cover (Table 3.2.1), the low average canopy closure on territories (40%) means that the reduction in canopy cover along the rural – urban gradient is unlikely to deter screech-owls from occupying high-density suburban areas. Screech-owl territories on rural sites had more tall trees >10m than suburban sites, and, perhaps correspondingly, more natural cavities. Other studies have also noted a reduction in the number of cavities in suburban areas (Gehlbach 1994b, Isaac et al. 2008) due perhaps to the removal of dead or dying trees or branches of mature trees or the plugging of cavities with cement (Gehlbach 1994b). Anthropogenic habitat alteration can negatively influence the breeding of owls in managed forests (Löhmus 2003) presumably because human-altered habitats contain many fewer cavities than pristine ones (Wesolowski 2007). In the study area however, suburban areas contained more nest boxes and there were thus minimal differences in the overall number of potential nest sites.

Rural sites differed in having a slightly different tree composition and a denser middle story due to more trees in the 5 – 10m height range than suburban sites. These trees tend to produce a denser middle story than trees above 10m. The other deciduous trees variable had to be removed from the analysis because of heteroscedacity; however, rural sites also had the highest percentages of tree species that typically form denser stands, such as trembling aspen, which creates a denser middle story because it grows in clones of same-aged trees. Trembling aspen contained very few cavities in the study area, perhaps because several of the woodpecker species that regularly make holes in this

species, for example the Pileated Woodpecker, are rare (pers. obs). Rural sites also have less planted conifer, which the owls select (Table 3.2.1) and use as roost sites.

In the study area, trees in older suburbs are often larger than in the surrounding rural area (pers. obs.) and more suitable to screech-owls both as nest sites and in terms of general habitat preference. Two significant trends emerged: the DBH of cavity trees is negatively correlated with the distance to the city center (linear regression: $t = -2.47$, $df = 141$, $p = 0.01$, $R^2 = 0.04$) or alternatively the DBH of trees above 10m is also negatively correlated to distance to city center (linear regression: $t = -2.09$, $df = 149$, $p = 0.03$, $R^2 = 0.03$). This finding is unexpected since urban trees often have slower growth rates in proximity to impervious surfaces and with increased soil compaction (Quigley 2004). It is possible that the suburban nest trees in this data set are older and hence have wider girth or that other factors such as the reduced competition for light in the canopy (Quigley 2004) or even the urban heat island in a northern latitude may balance other factors that hinder growth. The urban heat island has also been documented to advance flowering and leafing phenologies (White et al. 2002, Neil and Wu 2006) and earlier foliated trees would be beneficial to nesting owls.

Rural sites are characterized by more Great Horned Owls and raccoons suggesting greater predation pressure. Other studies have also found that small owls face more predators in rural areas as opposed to suburban areas (Gehlbach 1994, Chipman et al. 2008). Although the domestic cat index is lower in rural areas, the conditional regression analysis suggests that screech-owls avoid sites with a large number of cats (Table 3.2.3), which could

minimize the negative influence of cats in suburban and urban areas. In rural areas screech-owls nests were closer to buildings (average 88m) than unused cavities (average 131m from a building). Both high and low-density suburban nests averaged closer to buildings than rural nests; however, the opposite pattern occurred with nest-sites much further from buildings than unused cavities (Table 3.5.1). Furthermore, nest-sites were closer to buildings in low-density suburban areas than in high-density suburban areas. One possible explanation is that cavities were more likely to be close to buildings in low density suburbs that usually had larger yards, whereas the houses in higher denser suburbs were often closer together with space for trees being more limited. Proximity to buildings might therefore offer a greater advantage to screech-owls in rural areas for prey concentrations or predator avoidance, since Great Horned Owls and raccoons are more common in rural areas (Chapter 2, Table 3.5.1). A greater need for predation avoidance in rural areas is also suggested by the diameter of nest entrances since rural pairs chose cavities with the smallest entrance (Table 3.4.1), a defense against nest predators (Sonerud 1985b, Belthoff and Ritchison 1990a).

Even at the northern limit of its geographical range, the Eastern Screech-Owl exhibits patterns of habitat selection that are similar to more southerly populations. When nest sites are compared with unused sites, Eastern Screech-Owls selected greater canopy closure; more potential nest cavities, also found in Texas (Gehlbach 1994a); more coniferous trees within 50m of the nest; lower DBH of tall trees around the nest-site; taller nest trees; nest sites closer to running water, similar to Texas (Gehlbach 1994) and habitat use in Massachusetts (Ellison 1980); lower shrub density below the nest, also

important in Texas (Gehlbach 1994) and selected for by Flammulated Owls in New Mexico (McCallum and Gehlbach 1988); less domestic cat activity; and fewer buildings within 50m of the nest. The degree of selection for vegetation features was greater than in Kentucky (Belthoff and Ritchison 1990a), perhaps related to sample size. The greatest difference found for this northerly population was the selection for coniferous trees close to nest-sites for concealment and thermoregulation, which does not appear necessary in most parts of the range, confers often being avoided in habitat selection (Ellison 1980, Smith and Gilbert 1984) with the possible exception of southern pine forests (Gehlbach 1995). The preference for riparian habitats and nest-sites within 500m of a river or permanently flowing creek is highly pronounced in Manitoba. Though described as a habitat generalist, the preference for riparian woods appears more general throughout the range of the Eastern Screech-Owl (Gehlbach 1995) and was also noted in New York (Kelso 1944), and Massachusetts (Ellison 1980) but may be less pronounced in more moderate climates, e.g. upland woods were used in greater proportion than their availability in Connecticut (Smith and Gilbert 1984).

Linked with greater breeding success in suburban areas, suburban nest sites differed from rural nests in having fewer trees, especially fewer trees less than 10m tall and correspondingly lower canopy closure (more open middle story and subcanopy), less green ash, fewer raccoons and less Great Horned Owl activity but more coniferous trees, more American elm and Manitoba maple (the species with the most cavities), more buildings and a larger area of impervious surfaces, closer to running water and roads, lower shrub density below the nest tree, and more pedestrian and domestic cat activity. In

suburban areas, the mature but more open vegetation facilitates hunting and predator detection, planted conifers create suitable roost sites close to nests before deciduous trees have begun foliating, the lower density of natural predators despite the increased density of domestic cats appears to allow increased nesting success (Chapter 2), the urban heat island enables earlier breeding, which may be linked to higher survivorship (Chapter 2), and prey accessibility and density is increased (Chapter 4). Several anthropogenic features influence the habitat selection process such as the preference for planted conifer in proximity to a nest site and the avoidance of domestic cats and nest-sites surrounded by many buildings.

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4. The diet of the Eastern Screech-Owl at the northern periphery of its range

ABSTRACT.—A total of 2323 prey items of Eastern Screech-Owl (*Megascops asio*) were analyzed over a four-year period in Winnipeg, Manitoba at the northern limit of species' range, using four techniques: pellet analysis, post-fledging nest inspection, video monitoring, and direct observation. Invertebrates comprised 67% of prey captures but only 11% of biomass consumed. Seasonal shifts in diet between biologically significant periods were significant such that multiple discriminant analyses correctly classified 60% of pre-breeding season, 91% of incubation, 67% of brooding, 86% post-fledging and 100% of winter consumption. Rural pairs consumed a higher percentage of invertebrates and fewer vertebrates than suburban pairs. Among avian prey, small passerines (<20g), migrants and winter visitors, foliage feeders and omnivores were selected. Only 37 vertebrate prey species were recorded and the total niche breadth was 6.5, reflective of a much higher degree of diet specialization than more southerly populations.

Keywords: Eastern Screech-Owl, *Megascops asio maxwelliae*, Winnipeg, Manitoba, diet.

INTRODUCTION

The diet of the Eastern Screech-Owl (*Megascops asio*) is comparatively well studied (e.g. Allen 1924, VanCamp and Henny 1975, Turner and Dimmick 1981, Ritchison and Cavanagh 1992, Gehlbach 1994); however most studies have utilized only one or two methods such as pellet analysis, identification of prey remains in nest boxes, and stomach contents. This is problematic because these different methods lead to different conclusions about the relative importance of different prey types, in particular invertebrate versus vertebrate prey (Ritchison and Cavanagh 1992). Of the 11 studies included in Ritchison and Cavanagh's (1992) review, only three examined stomach contents and only one (Allen 1924) contained an observational component. Pellet samples of Eastern Screech-Owl have typically underreported invertebrates (Errington

1932, Craighead and Craighead 1956) and have shown the percentage of mammals consumed to be very high (e.g. Cahn and Kemp 1930, Wilson 1938, Craighead and Craighead 1956, Korschgen and Stuart 1972) whereas some studies of nest box contents also underreported invertebrates (e.g. VanCamp and Henny 1975) and suggested a higher proportion of birds (e.g. Stewart 1969, Duly 1979) in the diet. Studies based on the examination of stomach contents found high predation on invertebrates such as arthropods, especially in the summer months (Fisher 1893, Hanebrink et al 1979, Brown 1989). Duly (1979) found stomach contents contained 93% invertebrates but cached prey only 8% invertebrates. Furthermore, most, if not all of these studies underreported soft-bodied invertebrates such as earthworms which leave no remains in pellets and which are rarely cached (Ritchison and Cavanagh 1992, C. Artuso, pers. obs.). This study therefore aims to give a more comprehensive portrait of the diet of a northern population of Eastern Screech-Owl by using a combination of two observational techniques (direct observation and video recordings) and two non-observational techniques (pellet analysis and nest-box inspection).

In the Winnipeg area, the Eastern Screech-Owl resides at various points along the rural – urban gradient and reaches its highest densities in suburban areas (Chapter 2).

Urbanization can greatly influence the diet of birds, sometimes offering either increased or more varied resources (Botelho and Arrowood 1996, Diermen 1996) and sometimes causing profound changes in dietary regimes (Robbins 1993, Wolf and del Rio 2000, Faeth et al. 2005). Such resources may be accompanied by increased risks such as pollution, toxins or diseases (Getz et al. 1977, Kostelecka-Myrcha et al. 1997, Jensen et

al. 2002) and may even result in ecological traps or population sinks (Remes 2000, Battin 2004, Baker et al. 2005). I therefore examined differences in the diet of nesting pairs of screech-owl in rural, low-density suburban, and high-density suburban areas.

METHODS

The study area was defined as a circle with a radius of 40km from the center of Winnipeg, at the northern periphery of the range of Eastern Screech-Owl, which encompasses the city limits and also areas outside the city with lower human densities. Riparian areas are dominated by American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), and Manitoba maple (*Acer negundo*), with some bur oak (*Quercus macrocarpa*), eastern cottonwood (*Populus deltoides*), basswood (*Tilia americana*) and peachleaf willow (*Salix amygdaloides*) also present. Trembling aspen (*Populus tremuloides*) and bur oak are often the dominant species in non-riparian areas. Many species are also planted in gardens and parks including white spruce (*Picea glauca*), eastern white cedar (*Thuja occidentalis*) and the non-native Colorado blue spruce (*Picea pungens*) and Scots pine (*Pinus sylvestris*).

Each screech-owl territory was classified as belonging to one of three categories pertaining to human density: high-density suburban (>30 people per hectare), low-density suburban (>10 – 30 people per hectare), and rural areas (<10 people per hectare). This follows a random-stratified survey of the study area (Chapter 2) but with the wildlands and rural categories used in that survey merged under the rural category here and with the medium-density suburban category and low-density suburban category merged here and labeled low-density suburban for convenience.

A total of 2323 prey items were identified between March 2004 and February 2008 from four sources: field observations (n = 789) of nesting pairs and territorial birds, occasionally with the aid of flash photography, video footage from inside a single nest box over two nesting seasons (n = 225), analysis of pellets collected under roost sites (n = 837), and the inspection of nest boxes after all young had fledged (n = 472) (Table 1). A total of 637 pellets ranging in size from 8x4mm to 51x12mm (but sometimes as much as 20mm wide in part due to flattening) and averaging 25.4x10.5mm, were analyzed. The sample from the nest with a video camera was supplemented with direct observational data and pellet data and care was taken to cross reference all prey items such that items observed in the field or video were not double counted in pellets or nest box remains. I also compared percentages of avian, mammalian and invertebrate prey from the video recordings with those of nearby nests with direct observational data only to ensure that no biases arose from this single sample. If a prey item was first observed being captured or eaten and item remains were later recovered in a pellet or nest box it was treated as observed once for the purposes of this study. The number of prey items from observations and identified from remains were similar, 1014 (44%) and 1309 (56%) respectively, yielding a reasonably unbiased database. However, the ratio of observations to pellets was not constant at all sites and therefore care is needed when drawing conclusions about comparative capture rates of individuals or pairs.

Mammal and bird remains were identified by consulting the collection at the Manitoba Museum and suitable reference material (Bansfield 1974, Elbroch and Marks 2001, Kays and Wilson 2002, U.S. National Fish and Wildlife Forensics Laboratory, Wageningen

University Experimental Zoology Group). Invertebrates were identified to family or genus level by examining head capsules, elytra and legs with the assistance of Dr. Robert Roughley and Dr. Terry Galloway (University of Manitoba, Entomology). Dr. Richard Westwood (University of Winnipeg, Biology) assisted in the identification of moths to family level from photographs. The number of beetles consumed was calculated from head capsules. Feather remains in nest boxes were always assumed to represent only one individual of each species identified unless the total number of remiges or rectrices exceeded the number found on one bird. Single feathers of Wood Duck (*Aix sponsa*), Northern Flicker (*Colaptes auratus*) and European Starling (*Sturnus vulgaris*) without other remains found in nest boxes were not assumed to be prey items as these may have been shed by these birds visiting the boxes prior to occupancy by the owls. The mass of prey all birds was taken from Sibley (2000), and mammals as the average of the two values (range) given by Kays and Wilson (2002). The average weight of invertebrate species was calculated from weighing similar individuals found in the study area. When a prey item was identified to genus, family, or group only, the average weight of all known members of that group in the sample was calculated and assigned to unidentified items.

The two broad periods of breeding and non-breeding roughly followed Ritchison and Cavanagh (1992) with an adjustment for the northern location of this study such that the breeding season was treated roughly as April through September or, where known, more precisely calculated for individual pairs as the period extending from onset of incubation until 10 weeks after the fledging date of the oldest chick, which corresponds to typical

natal dispersal (Gehlbach 1995). The non-breeding season was thus October through March. Prey consumption was also calculated by significant biological period for individual pairs based on back calculation from fledging dates (Chapter 2). The most typical dates for these periods were: pre-egg laying (Mar 1 - Mar 31), incubating (April 1 - May 8), brooding (May 9 - July 3), post-fledging (July 4 - Sept 30). The “summer” period refers to items collected from nest boxes post-fledging for which the exact time of capture is not known.

I calculated the percentage consumption of mammals, birds, amphibians and fish, and invertebrates per nest/year as well as subdividing bird species consumed into resident and locally breeding species versus winter visitors and passage migrants, mammals into rodents and non-rodents, and invertebrates into hard-bodied (detectable in pellets) versus soft-bodied (only recorded from observations). Niche breadth and overlap were calculated following Gehlbach (1994) for the four prey classes (birds, mammals, amphibians and fish, and invertebrates) to aid comparison with three other significant studies (VanCamp and Henny 1975, Turner and Dimmick 1981, Gehlbach 1994; summarized in Gehlbach 1995, Table 1) as well as for individual prey species. It is nonetheless important to note that the methodologies of those studies, which relied on the inspection of prey remains in nest boxes, are not directly comparable to this study with multiple data sources. I also calculated the total number of prey species identified at each site. For this calculation invertebrates were tallied at the family level only and items identified only to genus or group were only included if no other member of that group had been tallied as a species. Because differences in sample size prevented direct

brevicauda) (1%) were consumed less frequently. House mouse was absent from rural sites and ranged from 3% (low-density suburban) and 2% (high-density suburban) in the breeding season to 6% (low-density suburban) and 10% (high-density suburban) in the non-breeding season.

A total of 26 bird species were recorded as prey; however, this figure is undoubtedly higher since many bird remains could not be identified to species. Birds consumed were largely passerine (82%) and the majority were small species under 40g (55% <20g, 34% 20 – 40g, 11% >40g), contrary to Gehlbach (1994). The most commonly recorded avian prey species were House Sparrow (*Passer domesticus*) (13% of all birds) and Black-capped Chickadee (*Poecile atricapillus*) (9%). House Sparrow was much less common in high-density suburban and rural areas (<1%) than in low-density suburban sites. Yellow-rumped Warbler (*Dendroica coronata*) (3%) was the most commonly captured species that does not breed in the study area, except perhaps for a few isolated boreal pockets (Holland et al. 2003) such as in Bird's Hill Provincial Park. The largest avian prey captured were Rock Pigeons (*Columba livia*) and Blue Jays (*Cyanocitta cristata*), as well as a single Virginia Rail (*Rallus limicola*), a species seldom recorded within the city of Winnipeg (pers. obs.). The only two amphibian prey items confirmed to species were northern leopard frog (*Lithobates pipiens*) and wood frog (*Rana sylvatica*) and only a single unidentified fish was found in this sample.

Fifty-seven percent of invertebrates consumed were detected using observational techniques, compared to 22% for birds and 13% for mammals. Invertebrates consumed

included insects, earthworms, crustaceans, arachnids, gastropods, and many unidentified small invertebrates. The bulk of invertebrates consumed were insects and of these beetles were most commonly recorded (43% of invertebrates), presumably because their remains are more readily found in pellets and nest boxes. The family Scarabidae constituted 83% of the beetles identified, of which many appeared to be in the genus *Phyllophaga*. After beetles, the next most important invertebrate prey were both soft-bodied, the earthworm *Lumbricus terrestris* (5%) and various caterpillars (4%). Earthworms were most commonly captured in low-density suburban areas (1% of all rural prey in the breeding season, 5% low suburban, 3% high suburban). The proportion of invertebrate prey captured by three unpaired males ($\bar{x} \pm SE: 27.3 \pm 14.2\%$) was much lower than for breeding pairs ($\bar{x} \pm SE: 75.7 \pm 5.6\%$). Unpaired males caught mammals (56 \pm 20.9%) more frequently than breeding pairs (12.2 \pm 3.8%) (MANOVA, Wilk's Lambda = 0.6, $F = 6.38$, $df = 2, 19$, $p = 0.008$); however, the data on the diets of unpaired males were collected primarily from pellets found at roost sites and are therefore biased due to a lack of observational information.

Despite being unavailable to the owls in winter in the study area, invertebrates constitute by far the largest proportion of total prey captures (66% overall, 71% in the breeding season, 20% in the non-breeding season) (Table 4.2.1). Mammals are the next highest item consumed (18% overall, 16% during breeding and 40% in the non-breeding season) but only slightly higher than birds (15% overall, 12% during breeding and 40% in the non-breeding season). Amphibians and fish, which are also unavailable to the owls in winter in the study area, were a very small component of prey consumed (<1% overall).

The number of birds, mammals, amphibians and fish, and invertebrates consumed (Table 4.2.1) varied significantly by biological period ($\chi^2 = 854.3$, $df = 15$, $p < 0.0001$).

Mammals were captured more than birds overall; however, birds and mammals were consumed in equal proportions in the non-breeding season (Mammals captured: 16% breeding, 40% non-breeding, 50% winter; birds captured: 12% breeding, 40% non-breeding, 50% winter only).

Table 4.2.1. Prey of Eastern Screech-Owl from 2004 – 2008: prey captures by period

Period	Bird	Mammal	Amphibian and fish	Invertebrate	Total
Winter	22 (50%)	22 (50%)	0	0	44
Pre-egg laying	68 (38%)	66 (37%)	0	44 (25%)	178
Incubating	82 (19%)	209 (49%)	3 (1%)	131 (31%)	425
Brooding	124 (17%)	110 (15%)	5 (1%)	476 (67%)	715
Post-fledging	25 (5%)	18 (3%)	0	491 (92%)	534
Summer	23 (5%)	4 (1%)	0	400 (94%)	427
Total	344 (15%)	429 (18%)	8 (<1%)	1542 (66%)	2323

Percentages indicate the number prey in each period against the total number of prey in that period.

Despite the high percentages of invertebrates captured, invertebrates constituted only 11% of the biomass consumed overall (13% breeding, 2% non-breeding) (Table 4.2.2).

Although the capture rate of mammals was only slightly higher than birds, they contributed more to biomass consumed (58% versus 31% overall, 57% versus 29% breeding, 59% versus 40% non-breeding). Although the ratio of vertebrates to invertebrates did not vary significantly by year ($\chi^2 = 0.36$, $df = 3$, $p = 0.95$), there is annual variation in the type of invertebrates consumed, e.g. earthworms were highest in the wettest year (17% of invertebrate captures in 2004 when precipitation from March – September totaled 531 mm down to zero in 2006 when March – September precipitation was only 231 mm) (Environment Canada, n.d).

The average mass (\pm standard error of the mean) of prey overall was 13.2 ± 0.4 g, lighter than 28.3g reported by Ritchison and Cavanagh (1992). Category averages were birds (27.9 ± 1.6 g), mammals (41.3 ± 0.6 g), amphibians and fish (14.9 ± 1.3 g), and invertebrates (2.1 ± 0.01 g).

Table 4.2.2. Prey of Eastern Screech-Owl from 2004 – 2008: biomass consumed by period

Period	Bird	Mammal	Amphibian and fish	Invertebrate	Total
Winter	588g (40%)	878g (60%)	0g	0g	1466g
Pre-egg laying	1710g (39%)	2599g (59%)	0g	91g (2%)	4399g
Incubating	2689g (23%)	8690g (74%)	34g (<1%)	284g (2%)	11697g
Brooding	3419g (37%)	4645g (51%)	85g (1%)	1033g (11%)	9182g
Post-fledging	627g (26%)	719g (30%)	0g	1067g (44%)	2413g
Summer	568g (37%)	167g (11%)	0g	803g (52%)	1537g
Total	9601g (31%)	17698g (58%)	119g (<1%)	3277g (11%)	30695g

Percentages indicate the total biomass per category in each period against the overall biomass in that period.

The MDA comparison of prey type by period (not including the unspecified summer period) identified two significant axes, viz. canonical 1: canonical correlation = 0.91, likelihood ratio = 0.03, $F = 3.57$, $df = 48$, 113.75, $p < 0.001$ and canonical 2: canonical correlation = 0.84, likelihood ratio = 0.17, $F = 2.21$, $df = 33$, 89.09, $p = 0.001$ (Table 4.2.3). The MDA correctly classified 60% of the pre-breeding period, 91% of the incubation period, 67% of the brooding period, 86% of the post-fledging period, and 100% of the winter period.

Table 4.2.3. Pooled within-class standardized canonical coefficients and total canonical structure from MDA for prey type differences between biologically significant periods

	Pooled Within-Class			
	Standardized Canonical Coefficients		Total Canonical Structure	
	Can1	Can2	Can1	Can2
Birds †	0.34	2.24	0.78	-0.13
Resident birds †	-0.36	-0.32	0.33	-0.19
Migrant birds †	-0.08	-0.04	0.28	0.13
Mammals †	-0.47	4.07	0.85	0.31
Rodents †	0.07	-0.31	0.54	0.23
Non rodents †	0.54	0.18	0.28	0.39
Amphibian/ fish	0.26	0.90	0.03	0.31
Invertebrates †	-1.62	3.85	-0.96	-0.02
Hard bodied †	0.14	0.30	0.19	0.60
Soft bodied †	0.24	0.53	-0.51	-0.05
Diversity §	-0.68	-0.41	0.47	0.26
Niche breadth	-0.06	-0.38	0.54	0.47

§ indicated that the variable was log transformed. † indicates the arcsine transformation.

The first two canonical axes from the MDA (Fig. 4.1.) show strong separation of the diet in biologically significant periods primarily by the distribution of the prey classes and diversity. Canonical axis 1 is highly correlated to percent mammals (0.85, total canonical structure) and birds (0.78) and negatively correlated to percent invertebrates (-0.96). Within the prey classes, this axis was also correlated strongly to rodents (0.54) and negatively to soft-bodied invertebrates (-0.51). Niche breadth (0.54) and prey diversity (0.47) are also important. Canonical axis one therefore represents a gradient of increasing vertebrate consumption and decreasing invertebrate consumption (especially soft-bodied invertebrates) and the winter and pre-breeding periods showed the highest scores (Fig. 4.1). Canonical axis 2 was most strongly correlated with hard-bodied invertebrates (0.6), niche breadth (0.47), non-rodents (0.39), amphibians and fish (0.31), mammals (0.31), and diversity (0.26). It was negatively correlated to birds (-0.13), in particular resident birds (-0.19). Canonical axis 2 is thus a gradient of increasing mammal consumption

including increasing diversity of mammals (addition of non rodents such as bats and shrews to the diet) and higher niche breadth but slightly lower bird consumption in particular fewer migratory species. Accordingly the incubation and brooding periods scored highest on this axis whereas the winter and pre-breeding periods scored lowest (Fig. 4.1)

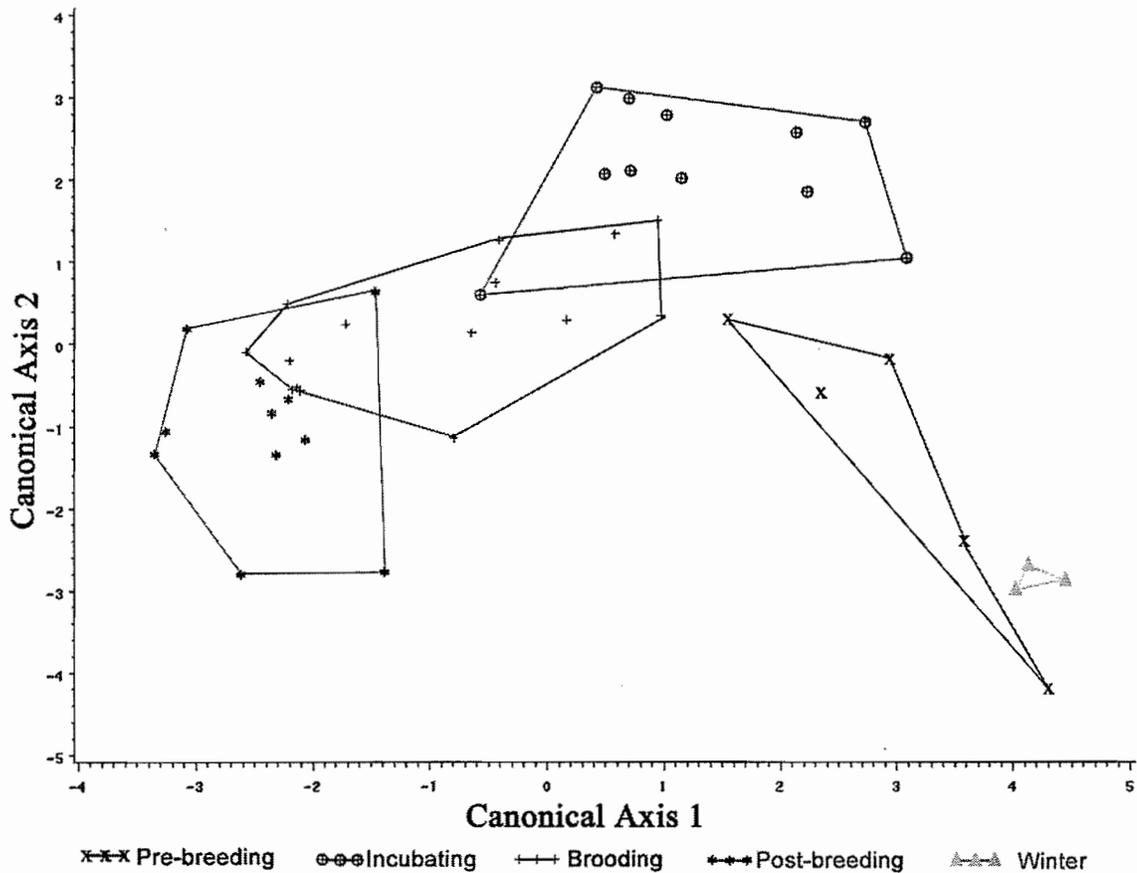


Fig. 4.1. Scatter plot of canonical 1 and 2 scores from MDA for prey types differences between biologically significant periods.

The percentages of birds, mammals, amphibians and fish, and invertebrates consumed overall varied significantly between rural, low-density suburban and high-density suburban sites ($\chi^2 = 17.2$, $df = 6$, $p = 0.008$) (Table 4.3.1). Owls on rural sites consumed

fewer birds than owls in low and high-density suburban sites in both the breeding and non-breeding season (9% fewer than low-density suburban owls in the breeding season and 30% fewer in the non-breeding season). The ratio of resident and locally breeding species to passage migrant and non-breeding visitors was approximately 2:1 on all sites (Table 4.3.1). Owls in low-density suburban sites consumed almost double the amount of birds in the non-breeding season as in high-density sites and triple that of birds in rural sites. Owls in rural areas consumed fewer mammals in the breeding season than either group of suburban owls. However, owls in high-density suburban areas consumed more mammals in the non-breeding season. Mammalian diversity in the diet was greater on low-density suburban sites, there being no shrews or bats found in the diet anywhere else. Owls on rural sites consumed 16% more invertebrates than low-density suburban owls, 20% more than high-density suburban owls in the breeding season, and 21% and 43% more respectively in the non-breeding season ($\chi^2 = 27.6$, $df = 2$, $p < 0.001$). Rural owls also consumed a higher proportion of hard-bodied invertebrates and fewer earthworms and caterpillars. Prey species diversity was highest at low-density suburban sites in both the breeding and non-breeding season. Differences in sample size do not make sites directly comparable; however, the adjusted diversity count (divided by the square root of the sample size) produced the same ratio (rural, low-density suburban, high-density suburban: 1.4, 1.8, 1.0 in the breeding season and 1.6, 2.0, 1.1 in the non-breeding season). Niche breadth was highest at high-density suburban sites in the breeding season; however, it was highest at low-density suburban sites overall. Niche breadth was higher in non-breeding season than in the breeding season for both rural and low-density suburban sites but not at high-density suburban sites (Table 4.3.1).

Table 4.3.1. Percentage prey distribution, diversity and niche breadth in breeding (Br) and non-breeding (Non-br) seasons by human density category

	Rural		Suburban - low		Suburban - high	
	Br	Non-br	Br	Non-br	Br	Non-br
Total sample size	490	7	998	186	613	29
Birds	4.3	14.3	12.9	44.1	17.0	24.1
Resident birds	66.7	100.0	63.2	70.3	65.9	83.3
Migrant birds	33.3	0.0	36.8	29.7	34.1	16.7
Mammals	10.6	42.9	18.0	33.9	17.8	75.9
Rodents	100.0	100.0	92.6	96.7	100.0	100.0
Non rodents	0.0	0.0	5.1	3.3	0.0	0.0
Amphibians and fish	0.4	0.0	0.3	0.0	0.7	0.0
Invertebrates	84.7	42.9	68.7	22.0	64.6	0.0
Hard bodied	94.9	0.0	66.1	85.0	65.5	0.0
Soft bodied	4.8	100.0	33.3	15.0	33.1	0.0
Average prey sp/site	14.0	4.0	15.2	10.5	11.3	7.0
Niche breadth - class	1.4	2.6	1.9	2.8	2.1	1.6
Niche breadth - species	2.2	4.5	6.1	12.4	4.9	3.8

Percentages of birds, mammals, amphibians and fish, and invertebrates are calculated against the total number of prey items for each of the three human density categories. Other percentages are of against the total number of birds, mammals, or invertebrates that could be identified to species or genus level and were thus classifiable into subgroups.

The MDA comparison of prey type among rural, low-density suburban, and high-density suburban sites identified one significant axis and one non-significant axis, viz. canonical 1: canonical correlation = 0.94, likelihood ratio = 0.05, $F = 2.58$, $df = 24, 18$, $p = 0.02$ and canonical 2: canonical correlation = 0.76, likelihood ratio = 0.42, $F = 1.26$, $df = 11, 10$, $p = 0.36$. The MDA correctly classified 100% of rural sites, 100% of low-density suburban sites and 100% of high-density suburban sites.

Table 4.3.2. Pooled within-class standardized canonical coefficients and total canonical structure from MDA for prey type differences among rural, low-density suburban, and high-density suburban sites

	Pooled Within-Class		Total Canonical Structure	
	Standardized Canonical Coefficients		Can1	Can2
	Can1	Can2	Can1	Can2
Birds †	-0.37	1.18	0.25	0.6
Resident birds †	2.08	0.37	0.11	-0.15
Migrant birds †	1.48	-0.08	0.41	0.09
Mammals †	2.36	0.81	0.5	-0.05
Rodents †	1.82	0.11	0.5	0.06
Non rodents †	1.02	0.43	0.14	0.38
Amphibian/ fish	0.20	-0.57	0.23	-0.2
Invertebrates †	0.82	1.57	-0.46	-0.03
Hard bodied †	-1.17	-0.09	0.31	0.34
Soft bodied †	0.98	1.07	-0.12	0.23
Diversity §	3.51	0.11	0.3	0.58
Niche breadth	-3.83	0.50	0.18	0.5

§ indicated that the variable was log transformed. † indicates the arcsine transformation.

The first canonical axis from the MDA (Table 4.3.2, Fig. 4.2.) shows strong separation of the diet between rural, low-density suburban, and high-density suburban sites. Canonical axis 1 is highly correlated to the percentage of mammals consumed (0.5), in particular rodents (0.5); the percentage of birds consumed (0.25), in particular passage migrants and winter visitors (0.41); and amphibians and fish (0.23). It is also correlated with prey diversity (0.3). This axis is strongly negatively correlated with invertebrate consumption (-0.46). Canonical axis 1 is therefore a gradient of decreasing invertebrate consumption and correspondingly increasing vertebrate consumption (as percentages). Since the diversity of invertebrates was only measured to the family level, the higher diversity score on this axis is in mostly explained by diversity of vertebrates consumed. Rural sites scored highest on this axis, i.e. high invertebrate consumption and low vertebrate consumption, and high-density suburban sites the lowest (Fig. 4.2).

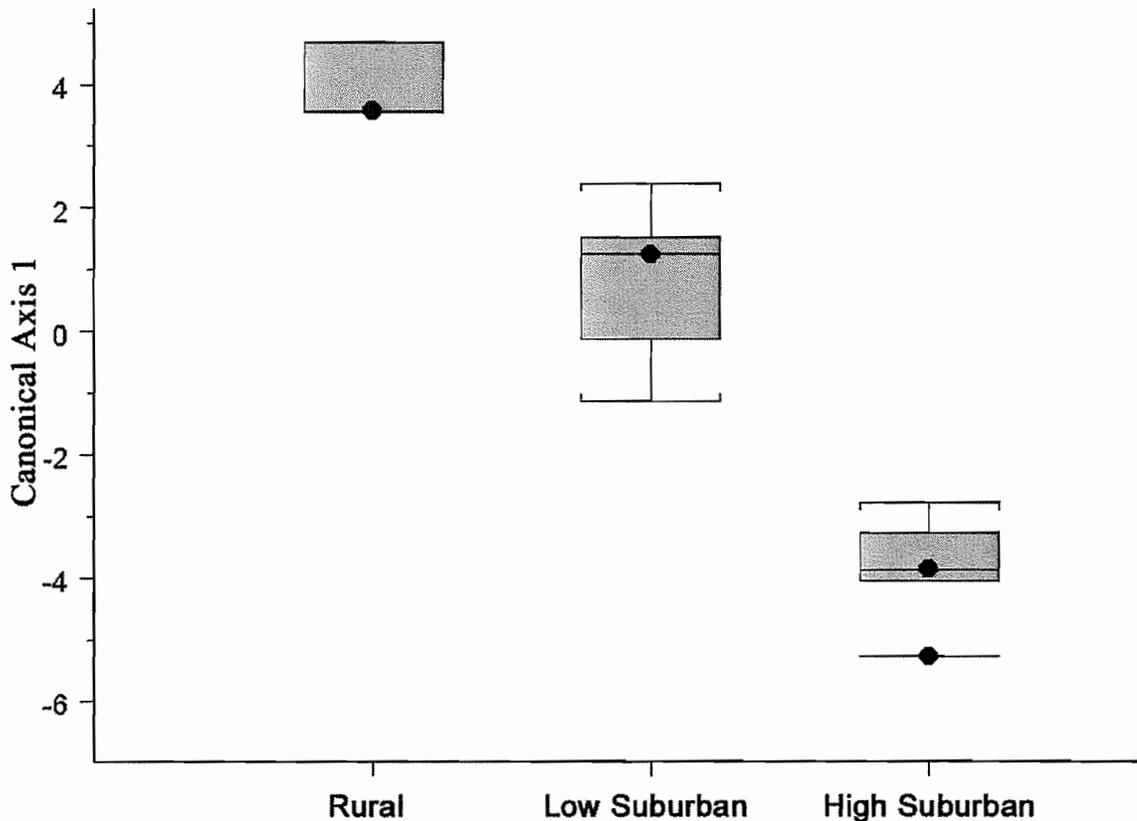


Fig. 4.2. Box plot of canonical 1 scores from MDA for prey types differences between rural, low-density suburban and high-density suburban sites.

Jacob's (1974) selectivity indices were calculated for avian groups only (Table 4.4). In all areas, passerines were captured in greater proportion than their availability, whereas non-passerines had negative selectivity indices. Passage migrants and winter visitors had positive selectivity indices, whereas locally breeding species had negative indices. Small bird less than 20 grams were selected for in all areas whereas medium-sized birds 20 – 40g had negative selectivity indices everywhere except high-density suburban areas and large birds above 40g also had negative selectivity indices everywhere except rural areas. Arboreal feeders were generally selected over ground feeders and insectivores over granivores in most cases. Species with a high tolerance to anthropogenic disturbance (urban-adapted species such as European Starling and House Sparrow) had positive

selectivity indices except in rural areas, whereas suburban-adapted species with moderate tolerance levels, many of which breed in the study area such as American Robin (*Turdus migratorius*) and Cedar Waxwing (*Bombycilla cedrorum*), had negative selectivity indices. Species with lower tolerance to anthropogenic disturbance, a few of which breed in large suburban parks but which are generally uncommon in the urban environment except on passage, e.g. Rose-breasted Grosbeak (*Pheucticus ludovicianus*) and Baltimore Oriole (*Icterus galbula*), had positive selectivity indices in low-density suburban areas.

Table 4.4. Selectivity indices for various guilds of birds at rural (R), low-density suburban (S-l), and high-density suburban (S-h) sites

n	Proportion in diet (r)				Proportion in environment (p)				Selectivity index (s)			
	R	S-l	S-h	All	R	S-l	S-h	All	R	S-l	S-h	All
	21	192	110	323	94	583	231	908				
	(5)	(23)	(8)	(36)	(4)	(37)	(17)	(58)				
Taxonomy												
Pass	0.9	1.0	1.0	1.0	0.9	0.9	0.9	0.9	0.5	0.1	0.7	0.4
Non-p	0.1	0.0	0.0	0.0	0.1	0.1	0.1	0.1	-0.5	-0.1	-0.7	-0.4
Breeding status												
Res	0.7	0.8	0.7	0.8	0.9	0.9	0.9	0.9	-0.6	-0.1	-0.6	-0.3
Mig	0.3	0.2	0.3	0.2	0.1	0.1	0.1	0.1	0.6	0.1	0.6	0.3
Size												
Small	0.4	0.5	0.6	0.6	0.2	0.4	0.4	0.4	0.5	0.3	0.4	0.3
Med	0.3	0.3	0.3	0.3	0.5	0.4	0.3	0.4	-0.5	-0.1	0.2	-0.1
Large	0.3	0.1	0.0	0.1	0.0	0.2	0.3	0.3	0.9	-0.4	-0.9	-0.4
Foraging stratum												
Tree	0.7	0.8	0.8	0.8	0.7	0.6	0.6	0.6	0.0	0.4	0.5	0.4
Ground	0.3	0.2	0.2	0.2	0.3	0.4	0.4	0.4	0.0	-0.4	-0.5	-0.4
Diet												
Grain	0.3	0.5	0.3	0.4	0.4	0.4	0.4	0.4	-0.3	0.0	-0.2	-0.1
Insect+	0.6	0.2	0.3	0.2	0.4	0.3	0.3	0.3	0.3	-0.3	-0.1	-0.2
Insect	0.1	0.4	0.4	0.4	0.2	0.3	0.3	0.3	-0.1	0.2	0.4	0.2
Disturbance tolerance												
Min	0.2	0.1	0.3	0.2	0.1	0.1	0.1	0.1	0.5	0.3	0.5	0.4
Mod	0.5	0.5	0.5	0.5	0.6	0.7	0.7	0.7	-0.2	-0.3	-0.4	-0.2
High	0.2	0.3	0.2	0.3	0.3	0.3	0.2	0.2	-0.1	0.2	0.1	0.1

The sample sizes given are the number of avian prey found from March to September (proportion in diet) and the number of individual birds of species or genera that screech-owls have been documented eating in the study area (proportion in environment). The number of sites where prey was detected and the number of point counts conducted are

given in brackets. Category definitions: Pass = passerine, Non-p = non-passerine, Res = resident and locally breeding species, Mig = passage migrants and winter visitors, Small = species averaging <20grams, Med = species averaging 20 – 40g, Large = species averaging >40g, Tree = predominantly arboreal or shrub level feeders, Ground = predominantly ground feeders, Grain = predominantly granivorous, Insect + = consumes a mixture of insects, fruit and/or nectar, Insect = predominantly insectivorous, Min = tolerates only minimal anthropogenic disturbance, mod = tolerates moderate anthropogenic disturbance, High = tolerates high anthropogenic disturbance.

The total niche breadth calculated by species (B) for this study was 6.5, however the true niche breadth is higher because of some of the diversity in the unidentified birds and invertebrates from this data set is masked. To facilitate comparisons between studies, I removed invertebrates except crayfish (following Gehlbach 1994) leaving 38 species (including some identified only to genus) and a niche breadth of 5.9, much lower than Ohio (69 spp, B = 16.6, VanCamp and Henny 1975) and Texas (72 spp, B = 18.0, Gehlbach 1994). The niche overlap between Manitoba and Ohio (VanCamp and Henny, 1975, Table 2) is 0.7 (70%), much higher than the overlap between Manitoba and Texas of 0.21 (21%) (Fig. 3). Gehlbach (1994) calculated the niche overlap between Ohio and Texas as 0.31. A recent study in the northeastern most portion of the species range in Québec identified 26 prey items (Richards et al. 2006). The total niche breadth In Richard's study was only 3.4 (calculated from Richards et al. 2006, Table 5); however diet was not the authors' focus and the only method used was periodic inspection of nest boxes. Almost no invertebrates were recorded in Québec due to methodology, so I calculated niche overlap with Manitoba excluding invertebrates as 0.87, indicating substantial similarities in mammalian and avian prey.

I further investigated latitudinal trends by selecting seven studies where sufficient information on prey composition was provided and calculating niche breadth, including crayfish but excluding all other invertebrates to facilitate comparison (Fig. 4.3). I found a non-significant decrease in niche breadth with increasing latitude (linear regression: $t = 3.47$, $df = 5$, $p = 0.09$, $R^2 = 0.46$). This trend would likely be significant with greater consistency in methodologies and sample sizes.

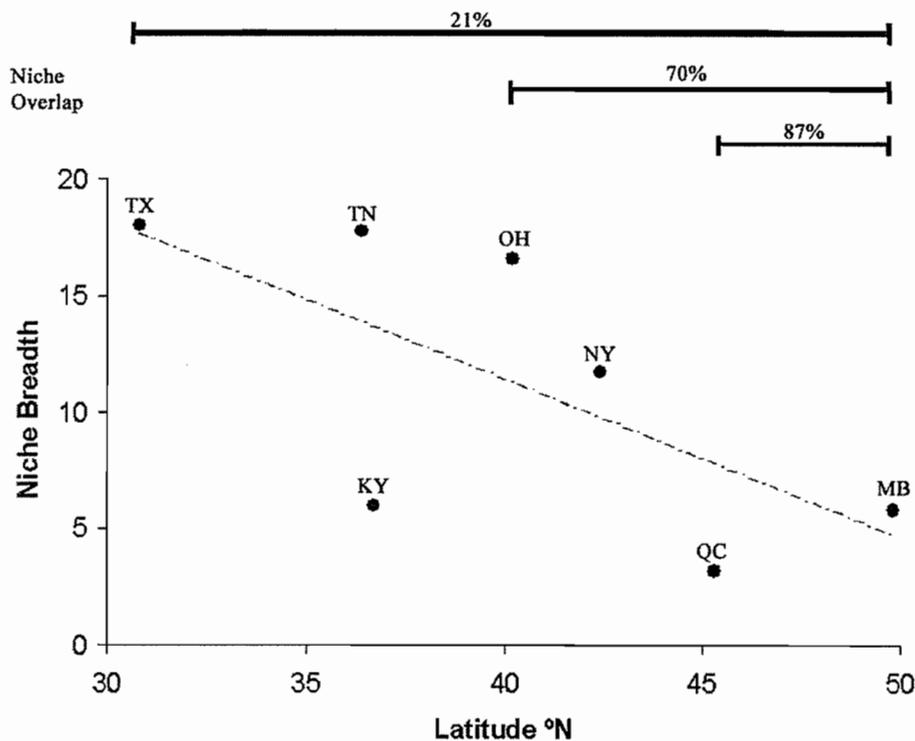


Fig. 4.3. Niche breadth (vertebrates and crayfish only) versus latitude from seven studies with niche overlap between Manitoba and Québec, Ohio, and Texas. Data from Manitoba (this study), Québec (Richards et al. 2006), New York (Allen 1924), Ohio (VanCamp and Henny 1975), Kentucky (Ritchison and Cavanagh 1992), Tennessee (Duly 1979), and Texas (Gehlbach 1994)

Some species were identified as prey items in several studies, although their relative importance differed. The meadow vole is particularly important in northern diets (68% of mammals, 13% overall and 32% of all winter captures in Manitoba; 75% of mammals

and 52% overall in Québec; and 37% of mammals, 13% overall and 23% of all captures in the non-breeding season in Ohio). The degree of specialization in Manitoba is comparatively high for a generalist predator, with the three most frequently consumed mammals (meadow vole, house mouse, deermouse) comprising at least 86% of mammalian prey (the true percentage may be higher because some prey were not identified to species and if these are excluded is 97%), and the top three birds (House Sparrow, Black-capped Chickadee, and either Cedar Waxwing or Yellow-rumped Warbler) 23% of avian prey or 48% of avian prey identified to species. These percentages are higher than Ohio (top 3 mammals 85%, top 3 birds 32%) and Texas (76%, 39%).

DISCUSSION

The high percentage of invertebrates in the diet of the Eastern Screech-Owl in the study area and the fact that 57% of invertebrates were detected using observational techniques demonstrate the need for observation in assessing prey ratios of diet generalists such as the Eastern Screech-Owl. The high consumption rate of invertebrates in the breeding season recorded in this study has only been matched by studies examining stomach contents (Duly 1979, Hanebrink et al. 1979, Brown 1989). Biases in diet information collected solely from pellets have also been demonstrated in other species that readily consume invertebrates, such as the Burrowing Owl (*Athene cunicularia*) (Haug et al. 1993, Plumpton and Lutz 1993, York et al. 2002). Nonetheless, soft-bodied invertebrate groups, such as moths, worms and caterpillars, were recorded almost only by observation. It is possible therefore that soft-bodied prey are underreported even in this study using

multiple methods and that only pure observation could determine their relative importance. The general pattern observed in the study area is that invertebrates are by far the most common prey during the breeding season, despite their relatively small contribution to biomass consumed, whereas birds and mammals become more common in the non-breeding season. This pattern is also found in southern parts of the range (Gehlbach 1994, 1995). Variation in the type of invertebrates consumed by year, e.g. the ratio of earthworms to beetles, is likely due to accessibility at the surface related to factors including humidity, soil moisture and annual variation in precipitation (Gehlbach 1994).

Fish appear to constitute a smaller proportion of the diet in the study area than elsewhere, with only a single unidentified fish found in this sample, constituting 0.05% of total prey capture in Manitoba versus 1.3% of prey capture in Kentucky (Ritchison and Cavanagh 1992), 2.1% in Texas (Gehlbach 1994), and 3.5% in Ohio (Van Camp and Henny 1975). Since screech-owls in the study area select riparian habitat (Chapter 3) and 88% of all nests were within 500m of a river or creek (Chapter 2), it remains unclear why this is the case. Screech-owls in the study area caught crayfish (0.5% of prey captures) more regularly than fish and were also observed catching frogs in shallow water.

Gehlbach (1994) noted larger birds above 41g were more likely to be cached. However, because larger items are more likely to be delivered to nests and/or cached, estimating hunting selectivity from caches may be biased towards larger items (Bull et al. 1989). The majority of birds captured in this study were small species under 20g, which were

selected for, unlike species weighing 20 – 40g and species >40g (Table 4.4), although larger species were selected in rural areas. Gehlbach (1994, 1995) suggested that male birds were captured more often than females. There was insufficient data to assess this in this study; however, an examination of the selectivity index of individual species (Appendix 1) suggests some selectivity towards colorful plumage. In this study there are only seven species with a selectivity index > 0, and these are mostly small colorful species such as American Redstart, Yellow Warbler, House Finch, and Baltimore Oriole, the exceptions being Hairy Woodpecker, Tennessee Warbler and House Wren. Gehlbach (1994, 1995) noted also noted a prevalence of ground-feeding birds over foliage-feeders. The opposite pattern emerged from this study with foliage feeders being selected for and ground feeders selected against (Table 4.4). Peculiar was the absence of Mourning Dove (*Zenaida macroura*) as a prey item in the study area because this species was a frequent avian prey item in other studies at northern locations (VanCamp and Henny 1975, Richards et al. 2006).

Niche breadth calculations suggest very different diets in the northern and southern portions of the range of Eastern Screech-Owl with narrower niches and greater specialization in the north. The northward gradient of specialization in the Eastern Screech-Owl demonstrated by a comparison of different studies is reflected in other owls, for example, Boreal Owls in Finland (Korpimäki 1986), whose total niche breadth in western Finland at 63°N is only 4.4 (from 40 species of avian and mammalian prey) and whose 3 most frequently consumed mammal species comprise 80% and the top three bird species 59% (Korpimäki 1988, calculated by Gehlbach 1994). In terms of niche breadth

and diet specialization, Manitoban Eastern Screech-Owls, with their high consumption of meadow voles and a few common bird species such as the House Sparrow, are more similar to Finnish Boreal Owls than their Texan conspecifics. The meadow vole appears to be particularly important in permitting Eastern Screech-Owls to persist in this northern study area. Although a native species, meadow voles were interestingly more commonly captured in suburban areas (9.5% of all captured prey in rural areas, 13.2% in low density suburban and 13.9% in high-density suburban areas). The trend of decreasing niche breadth with increasing latitude (Fig. 4.3), suggests that this pattern of specialization is driven by the lower diversity of prey types available at northern latitudes. The Long-eared Owl (*Asio otus*), often described as a diet specialist, has a more diverse diet in southern locations (Bertolino et al. 2001).

Eastern Screech-Owls in the study area are clearly able to shift their diet with seasonal availability. Invertebrates are unavailable and thus absent from the diet during winter, but invertebrate consumption increases steadily from pre-laying period to the post-fledging period. Conversely, mammals and birds are equally important in the winter but steadily decline in proportion through the breeding season. Although mammals, in particular rodents, were captured more than birds and contributed more to the biomass overall, birds appear to become increasingly important in late fall and the winter months in this northern study area. Mazur (1992) also reported birds and mammals in equal proportions in the late fall near Winnipeg, Manitoba. Birds were also consumed in much higher percentages during the non-breeding season than the breeding season in Texas (Gehlbach 1994) but were only slightly higher in Tennessee (Turner and Dimmick 1981) and

Kentucky (Ritchison and Cavanagh 1992) and decreased sharply in Ohio (VanCamp and Henny 1975) and Michigan (Craighead and Craighead 1956). Based on the latter two studies and Allen (1924), Ritchison and Cavanagh (1992) concluded that birds were consumed more frequently in the breeding season at northern locations perhaps due to increased availability from an influx of migrants (VanCamp and Henny 1975). This is not supported by this study; however, there is some support for VanCamp and Henny's (1975) suggestion that avian prey increases with the arrival of spring migrants, viz. birds were taken far less than mammals in the incubation period (19% versus 49%) but became dominant over mammals in the brooding period (17% versus 15%) and remained slightly higher in the post-fledging period (5% versus 3%). In Manitoba the peak arrival of Neotropical migrants is in mid- to late May during the middle of the brooding period for most Eastern Screech-Owl pairs. Furthermore, among the birds captured, the percentage of migrants increased in the breeding season and migrants had higher selectivity indices than resident and locally breeding species (Table 4.4).

The higher importance of avian prey in the winter in Manitoba is likely due to accessibility of prey with increasing snow cover. Eastern Screech-Owls have symmetrical ears (Marshall 1967) and are believed to use vision in hunting (Gehlbach 1995). They are thus less adapted to the snow-plunging technique of boreal forest species such as the similar sized Boreal Owl (*Aegolius funereus*), although even this species can be adversely affected by deep snow (Sonerud 1984). Instead Eastern Screech-Owls in Manitoba prefer to hunt mammals in winter at the base of large coniferous trees where snow cover is reduced or when they surface, for example, near bird feeders with fallen seed or when

traveling between subnivean tunnels, crossing areas such as driveways where snow has been cleared (pers. obs.). House Sparrows and other shrub roosting birds are often hunted by flushing them from roosts (pers. obs.).

Screech-owls in rural areas consume more invertebrates than do suburban screech-owls. The higher proportion of invertebrates in the diet in rural areas was also noted in Texas (Gehlbach 1994) during the breeding season. However, Burrowing Owls consumed more aerial insects at urban sites than at rural sites in Florida (Chipman et al. 2008).

Earthworms were most frequently captured in low density-suburban areas, presumably because the only species recorded, *Lumbricus terrestris*, is typically associated with human activity (Reynolds 2000). In addition, the watering of lawns at night with sprinkler systems may provide greater access to this prey item in suburban areas.

Invertebrate consumption was highest in the post fledging period when fledglings are learning to hunt and their captures are almost exclusively invertebrate (pers. obs.).

Unpaired males apparently capture larger prey items more regularly and rely less on invertebrate prey than breeding pairs, although a lack of observational data for unpaired males means that this result must be interpreted with care. Invertebrates contribute less biomass to the diet but are important when feeding chicks, as they are small, can be captured close to the nest, and delivered very frequently (as often as every 45 seconds in the case of earthworms, pers. obs.). The Eastern Screech-Owl has a higher hunting success rate for invertebrate prey (Abbruzzese and Ritchison 1997) permitting feeding at more regular intervals. Invertebrate capture is therefore important for the provisioning of broods. Consumption of invertebrates began as much as two weeks earlier in suburban

areas with the first invertebrate prey being recorded on 30 March in suburban areas as opposed to 16 April in rural area (earliest dates all occurred in 2007). The percentage of invertebrates captured in March and April against the total invertebrate capture was 1% in rural areas, 10% in low-density suburban and 4% in high-density suburban areas. Although the earlier availability of invertebrate prey is unlikely to be the sole factor permitting earlier nesting in the suburbs, there are additional dietary benefits to early nesting in that recently fledged young who leave the nest on average 5 days earlier in suburban areas than rural areas (Chapter 2), would have increased availability of avian passage migrants. Passage migrants are not only selected for, the breeding cycle of this species may be timed to coincide with maximum prey availability for hatchlings and fledglings, in particular the spring arrival of migrants (VanCamp and Henny 1975, Gehlbach 1994). The earlier availability of invertebrate prey in suburban areas may be related to factors including snow clearance, fertilized gardens, or the urban heat island, which increases invertebrate diversity in cold climates (Deichsel 2006).

Unlike in Texas where mammal consumption was higher in rural areas, in Manitoba mammals constituted the highest percentage of the diet in high-density suburban areas and were very similar in rural and suburban areas despite seasonal differences. Prey diversity and niche breadths were highest at low-density suburban sites in both breeding and non-breeding season. Rural sites had higher diversity in the breeding season than high-density suburban sites and vice-versa in the non-breeding seasons. Niche breadth was higher overall in high-density suburban areas compared to rural areas but only marginally. Seasonal differences in niche breadth in these categories reflect smaller

sample sizes. The higher diversity of prey in the non-breeding season in suburban areas may relate to the presence of bird species that, despite being uncommon in urban areas in summer, linger or overwinter in the city due in part to the urban heat island, regularly replenished anthropogenic food sources, and possibly also due to the protective benefits of planted conifers (Taylor and Koes 1995). Such birds may also be concentrated in small areas with reliable food sources, increasing their accessibility to owls. Species such as Dark-eyed Junco (*Junco hyemalis*) and White-throated Sparrow (*Zonotrichia albicollis*), as well as several other Emberizidae and Fringillidae species that are scarce in winter in the study area are most likely to occur around feeders and often in suburban/urban areas (Taylor and Koes 1995). Nonetheless, contrary to the generalized remarks of Gehlbach (1995), high-density suburban owls in Winnipeg consumed by far the greatest percentage of mammals in the non-breeding season (76%), and despite having the highest niche breadth by class in the breeding season, had the lowest niche breadth by class in the non-breeding season because of the dominance of rodents in the diet and the absence of invertebrates (niche breadth is highest when all prey classes are in equal proportions). Rodents in particular are accessible around suburban food sources. The fact that niche breadths by class are higher in the non-breeding than breeding season in both rural and low-density suburban areas may relate to the seasonal shifts in diet which render the prey classes less evenly distributed, in particular that invertebrates are nearly 4 times higher than the next nearest class (mammals) in low-density suburban areas and nearly eight times higher in rural areas in the breeding season.

Several prey species were less frequently captured in rural areas. House Sparrow, the only avian species to compose >10% of the total number of birds captured was most frequently found in the diet of owls in low-density suburban areas. In the study area, this species frequently roosts in dense shrubbery close to buildings often near feeders or grain sources (pers. obs, Lowther and Calvin 2006), and owls therefore had excellent access to this prey item in suburban areas. Another species of owl, the Tawny Owl, is known to take advantage of easy accessibility of avian prey at urban roost sites and correspondingly increase the proportion of birds in their diet in urban areas (Galeotti 1990, 1991). The house mouse was completely absent from rural diets, whereas the meadow vole was more commonly recorded as a prey item in suburban areas. These species were the two most significant individual prey items in terms of biomass contribution and were particularly important to the owls in the non-breeding season. If these capture rates are reflective of either availability or access then their apparent increased abundance in suburban areas would convey an important advantage. Since the house mouse in North America is the commensal form that lives mostly in buildings (Bansfield 1974) increased availability in suburban areas is not surprising. Meadow voles are found mostly in grassy habitats within the study area (pers. obs, Bansfield 1974). In Pennsylvania, meadow voles were more common in some suburban riparian parks than in mature riparian forest (Mahan and O'Connell 2005) and in Ontario their density increased with greater cottage development (Racey and Euler 1982). With their small home ranges, rodents like meadow vole can thrive in disturbed suburban habitats (Dickman and Doncaster 1987, Nilon and VanDruff 1987); however, rodent diversity declines with increasing amount of impervious surface and bare ground (VanDruff and

Rowse 1986) and disturbed areas such as parks surrounded by industrial sites are characterized by non-native species such as the house mouse (Nilon and VanDruff 1987). Like meadow voles, some other small mammal species such as the northern short-tailed shrew (*Blarina brevicauda*) are also most likely to occur at points of intermediate disturbance levels (Racey and Euler 1982) and in this study were only found at suburban sites. Small mammal abundance is often higher in small urban patches (Ekernas and Mertes 2006), a phenomenon that may be related to limited dispersal (Barko et al. 2003). This suggests that low-density suburban areas may offer the most diversity and abundance of prey species (Blair 1996) and the wider niche breadth and prey diversity of suburban screech-owls does therefore reflect availability. Likewise, Burrowing Owls in Florida enjoyed higher prey densities close to buildings (Millsap and Bear 2000). In addition to diversity and density, access to rodent prey in suburban areas might be higher either due to nocturnal feeding on fallen seed under bird feeders, snow clearance, and the greater number of coniferous trees under which little snow accumulates and which therefore facilitate hunting (Chapter 2).

The preference for larger birds in rural areas may be related to the increased amount of invertebrate and decreased availability of mammalian prey, i.e. the prevalence of small items and lack of mammals in the diet increasing the importance of selecting avian prey of larger biomass to meet energy requirements. Rural sites also proved different to suburban sites in terms of selectivity for both arboreal feeders and ground feeders. Ground-feeding birds are often diet generalists that may benefit from urbanization (DeGraaf 1991, Smith and Wachob 2006) and were more common in suburban areas than

rural areas. This fact and a slightly higher capture rate in rural areas (0.3 versus 0.2 elsewhere) produced the difference in selectivity. Insectivores were generally selected over granivores (Table 4.4). Foliage feeding insectivores and omnivores tended to be more colorful than ground feeders in the study area; however, roosting preferences would likely be a better indication of the ease of capture since most avian prey are not active when captured by screech-owls. The disturbance tolerance of avian prey mostly mirrored distribution with urban-adapted species selected for in suburban areas but not in rural areas, whereas urban-avoiding species were selected for. When they do occur in suburban and urban areas while migrating such species may be particularly conspicuous.

The dietary regime of the Eastern Screech-Owl at the northern periphery of its range is similar in overall composition to the diets of southerly populations. Nonetheless, niche breadth and prey diversity decrease northward corresponding to availability and seasonal shifts in invertebrate versus vertebrate consumption appear more marked. Despite their narrow niche breadth in a northern location, screech-owls in suburban areas had more diverse diets than rural owls. Rural screech-owls in the study area rely more on invertebrates and consume less vertebrate prey than suburban owls, despite the fact that invertebrate prey were available to suburban pairs two weeks earlier in the nesting season. Suburban areas, therefore, can offer small predators with a more diverse diet, especially in biologically stressful periods, than might otherwise be available.

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5. Eastern Screech-Owl hatches Wood Duck eggs

ABSTRACT.— I describe an Eastern Screech-Owl (*Megascops asio*) hatching three Wood Duck (*Aix sponsa*) eggs in a suburban nest box. Wood Duck(s) removed all five eggs of a completed screech-owl clutch, the earliest of which had already been incubated for at least 19 days, and laid three eggs in their place. The female screech-owl hatched the Wood Duck eggs, preened the ducklings, and attempted to feed them until they exited the nest box within 48 hours of hatching. Received 22 December 2005. Accepted 27 July 2006.

Wood Ducks (*Aix sponsa*) are well known to lay parasitically with conspecifics (Hartman 1972, Semel and Sherman 1986) and other cavity-nesting ducks (Bouvier 1974, Eadie et al. 1998). Wood Ducks occasionally remove conspecific eggs, however, such records usually involve damaged eggs (Semel and Sherman 1986). Wood Ducks are reported to “evict” other bird species including screech-owls from nest boxes (Bellrose and Holm 1994). However, Semel and Sherman (2001) report that when returning female Wood Ducks found boxes in which they had previously nested occupied by heterospecifics, including Eastern Screech-Owl (*Megascops asio*), they switched to another box ($n = 10$). Here I record Wood Duck(s) removing an entire clutch and laying in a nest of Eastern Screech-Owls.

While studying the reproductive ecology of Eastern Screech-Owls in suburban Winnipeg, Manitoba, I installed a miniature video camera in May 2004 inside a nest box in which a pair had successfully reared broods in two previous years. Five chicks fledged from this box in 2004. A female began laying on 3 April 2005 and by 10 April was incubating a clutch of five eggs. There was no sign of any unusual activity at the nest until 22 April,

when observers noted there were only three screech-owl eggs and one much larger egg. On 23 April, there was a second large egg and the three remaining owl eggs (Fig. 5.1a). On 24 April no change was noted; however, on the morning of 25 April, two more owl eggs had been removed and a third larger egg was present (Fig. 5.1b). Video recordings were made on a nightly basis but unfortunately did not extend sufficiently into the morning to record the removal of eggs. I monitored the nest box from 0600 to 0730 hrs CST for the next 3 days, and, on each morning, a pair of Wood Ducks landed close to the box. The female Wood Duck then flew to the roof of the box and stepped repeatedly and heavily on it before making a short circular flight and landing on the entrance hole. On each occasion I observed this behavior, the incubating owl jumped up to prevent the duck's entrance. On 27 April, a female Wood Duck was recorded gaining entrance to the nest box at 0638 hrs but was expelled by the owl which tried to bite the intruder on the back of the neck. On the morning of 2 May, the remaining owl egg was removed, though curiously no new Wood Duck eggs were added. Unfortunately egg removal was not recorded due to a technical difficulty.

I concluded the larger eggs in the box were Wood Duck eggs (confirmed upon hatching; Helgeson Nelson 1993). There was no evidence of any damaged eggs in the box and no eggs had been buried in the nesting material. The edge of the Red River was only a few meters from the base of the nest tree and, because there were no eggs or shells below the box, the removed eggs may have been dropped over water or consumed (Semel and Sherman 1986).

Despite the absence of her own eggs, the female owl incubated the three Wood Duck eggs. The first egg hatched at 2240 hrs on 25 May, the other two hatched later that evening. Shortly after hatching, the owl preened the ducklings and ate pieces of eggshell. She also brooded and attempted to feed the chicks. When the ducklings attempted to exit the box the female owl gave whinny calls, which are “elicited particularly by dispersing juveniles” (Gehlbach 1995:7). The first chick exited the box just before 2200 hrs on 26 May and the second shortly afterwards. The third chick departed the box at 0730 hrs on 27 May. The property owner took one duckling to a local nature reserve, but the other two were not located. Wood Duck chicks are highly precocial and brood merging has been recorded (Kirby 1990), but it is not known whether the chicks in question survived.

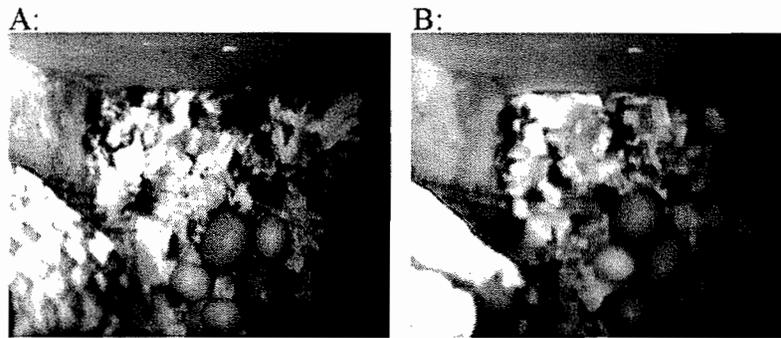


Fig. 5.1. A: Three Eastern Screech-Owl eggs and two Wood Duck eggs on 24 April 2005, B: One Eastern Screech-Owl egg and three Wood Duck eggs on 25 April 2005. In both images the wing and tail of the female screech-owl sitting at the box entrance is visible in the lower left corner; Winnipeg, Manitoba.

Raptorial birds occasionally incubate waterfowl eggs. Dawson and Bortolotti (1997) reported an American Kestrel (*Falco sparverius*) incubating a Bufflehead (*Bucephala albeola*) egg and four kestrel eggs (the Bufflehead and two kestrel chicks fledged).

Fannin (1894) reported a mixed clutch of Canada Goose (*Branta canadensis*) and Osprey

(*Pandion haliaetus*). The Black-headed Duck (*Heteronetta atricapilla*), an obligate brood parasite, sometimes parasitizes diurnal raptors (Weller 1968, Höhn 1975). Wood Duck eggs have occasionally been found in nests of Western Screech-owls (*Megascops kennicottii*) (J. M. Eadie, pers. comm.). In Winnipeg, there are several records from volunteers of the FortWhyte Alive nature center of joint use of nest boxes by Eastern Screech-Owls and Wood Ducks (e.g., on 11 April 1997, one Eastern Screech-Owl egg, five Wood Duck eggs, and seven membranes were found in one box). This does not imply synchrony of use because some may have been from the previous year or sequential nesting and it is possible that dumping or usurpation may have occurred. Eastern Screech-Owls have been recorded incubating the eggs of other species (Breen and Parrish 1996).

The average incubation periods for both Eastern Screech-Owl and Wood Duck are approximately 30 days (Gehlbach 1995, Hepp and Bellrose 1995). In this case, the female owl sat on the Wood Duck eggs for 31–34 days, within the normal range of incubation for Wood Ducks (25–37 days) (Hepp and Bellrose 1995). However, because the owl initiated egg laying much earlier than the Wood Duck(s), her eggs would have hatched approximately 3 weeks before any of the duck's had they not been removed. By accepting the Wood Duck eggs, the female owl's total incubation period was extended to 55 days. Eastern Screech-Owls have been recorded incubating infertile eggs for as long as 78 days (Gehlbach 1995).

Incidental egg dumping has been recorded in many avian species (e.g. Sealy 1989). However, the removal of host eggs over a 10-day period suggests this was not a case of egg dumping. A failed attempt at nest usurpation, however, cannot be dismissed. Unusual interspecific interactions of this nature have been attributed to competition for nest sites (Eadie et al. 1988), but several studies suggest that nest parasitism in Wood Ducks is not related to a lack of cavities (Semel and Sherman 1986). Dawson and Bortolotti (1997) argued that certain desirable qualities of the nest site might be a factor. In this case, there was a vacant nest box in the same yard with no discernable structural differences in which Wood Ducks had previously reared several broods. Semel et al. (1988) demonstrated that conspicuous placement of nest boxes increased intraspecific nest parasitism rates in Wood Ducks and the box in question was highly visible. This serves as a reminder, perhaps, of the caution required when artificial nesting structures are used as management tools (Eadie et al. 1998).

ACKNOWLEDGEMENTS

I am grateful to David and Sigrid Warrenchuk for assisting in the video recording and permitting observation on their property. Silvio E. Cascino and Barry Pomeroy produced the photographs. This manuscript was greatly improved by the thoughtful comments of Robert P. Berger, James R. Duncan, John M. Eadie, Frederick R. Gehlbach, Robert W. Nero, Spenser G. Sealy, Merlin W. Shoesmith, and an anonymous reviewer. Funding was provided by small grants from the Special Conservation Fund of Manitoba Conservation, Manitoba Hydro, and the Great Grey Owl Fund administered by Robert W. Nero.

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6. Eastern Screech-Owl in Manitoba: Evidence of historical range expansion

ABSTRACT.— A database of a total of 1954 sight records and specimens of Eastern Screech-Owl (*Megascops asio*) from 1883 to present was assembled for Manitoba, northern Minnesota, and South Dakota from numerous sources. The percentage of rufous morph Eastern Screech-Owls in these areas was calculated per decade to determine changes over the twentieth century. The percentage of rufous morph Eastern Screech-Owls in Manitoba has fallen from approximately 6-11% in the 1920s to less than 1% today. The percentage of rufous morph bird in North Dakota and northern Minnesota lies between 8 and 19% (overall averages 14%) and shows increase or decrease over time despite some short-term fluctuations. Since rufous morph screech-owls have lower survivorship in cold climates, this suggests that the Eastern Screech-Owl expanded its range into Manitoba in the late nineteenth or early twentieth century, at which time the proportion of rufous morph birds was similar to those of northern Minnesota and North Dakota but fell to present levels post-expansion due to the colder climate in Manitoba. Possible mechanisms of such expansion are discussed.

INTRODUCTION

Southern Manitoba to 52°N represents the northern range limit of Eastern Screech-Owl (*Megascops asio*); however, Manitoba may not have been a part of this species' historical range (Manitoba Avian Research Committee 2003). The first confirmed records of Eastern Screech-Owl in Manitoba are from the early 1920s. Hamilton Laing found this species at Oak Lake in 1921 (specimens CMNAV 17082 and 17193 at the Canadian Museum of Nature) and Norman Criddle recorded screech-owls at Aweme in 1922 (Taverner 1927). There is no species account for the (Eastern) Screech-Owl in Ernest Thompson [Seton]'s *Birds of Manitoba*, although he recorded other secretive small owls, e.g. Northern Saw-whet Owl, which he described as a rare resident; Boreal Owl, which he described as a probable resident and winter visitor; and Long-eared Owl, which he described as "tolerably common" (Thompson [Seton] 1890). Nonetheless, Thompson

[Seton] mentions, under the account of the Northern Saw-whet Owl, that R. H. Hunter “claims” to have seen and heard Screech-owl in Saboskong Bay and Point du Chêne in 1871, the implication being that Thompson [Seton] treated these records as hypothetical (Thompson [Seton] 1890). The lack of early records of a species that resides in close proximity to humans suggests that screech-owls were either absent or rare in Manitoba in the early twentieth century. Taverner (1927) concluded that this species was a new arrival and others noted an increased density of screech-owls in Manitoba in the 1930s, e.g. Rutherford (1935) wrote “This ‘little horned owl’ is becoming increasingly common in the greater Winnipeg district” and Cartwright (1931) stated they were “now quite common in the timber along the Red and Assiniboine Rivers”. Despite these suggestions, the possibility remains that screech-owls were initially overlooked, perhaps because they were scarce.

Within the last 50 years, Eastern Screech-Owls have expanded their range into the Swan River area of Manitoba as far as 52°N, from a previous northern limit of c. 50°N, clearly demonstrating the species’ capacity to colonize new areas in a comparatively short time (Walley and Clyde 1996). There are a few recent records in coniferous or mixed forest in areas such as Bird’s Hill Provincial Park and even as far north as the Duck Mountains (single record on 12 April 2002, B. Walley and P. Letain, pers. comm.). An extraordinary extralimital record of a gray adult seen by nine observers occurred on June 14 1998 at Pisew Falls (approximately 600km north of Winnipeg, above 55°N) (S. Clubb, pers. comm.). It is possible that this species is becoming increasingly adapted to the transition zone between the boreal biome and woodlands of a more deciduous nature. A similar

phenomenon has been suggested for Barred Owl (Boxall and Stepney 1982), a species first recorded in Manitoba in 1886 ([Thompson] Seton 1886), which may have arrived in the province at a similar time to Eastern Screech-Owl (Houston and McGowan 1999) and whose recent range expansion is well documented and dramatic (Mazur and James 2000).

One source of evidence supporting the hypothesis of range expansion may lie in the relative abundance of the color morphs: gray, rufous, and intermediate or “brown”, the former being common in Manitoba while the latter two are rare. This evidence relies on the fact that rufous morph screech-owls are more susceptible to cold temperatures and have a higher mortality, by as much as 40%, when temperatures fall to -5° and -10°C (Mosher and Henny 1976). In their study in northern Ohio, VanCamp and Henny (1975) noted a reduction of the percentage of rufous birds from 23.3% to 14.7% in the severe winter of 1951 (lowest temperatures and highest snowfall during their 30-year study). Gehlbach (1994) recorded a similar decline following a record freeze where in one study area rufous birds fell from 8.4% of the nesting population in 1983 to 4.2% in 1987 and from 23.3% to 16.1% in another. Gray plumage contains more melanin than rufous plumage and has better thermoregulatory properties and greater resistance to abrasion by dust particles (Gehlbach 1994, Gill 1995, VanCamp and Henny 1975). In other polychromatic species, e.g. Ruffed Grouse, gray morph birds also fare better than rufous ones in cold climates (Gullion and Marshall 1968.). At the northern limit of its range in Finland, gray morph Tawny Owls constitute 70% of the population and gray males have a longer breeding lifespan and higher lifetime recruitment (offspring that survive to breed) than brown males (Brommer et al. 2005). Gehlbach (1994) noted that although

gray owls are more difficult to see in full sunlight, rufous birds are more cryptic in cloudy or humid conditions because red light is filtered out in subdued lighting and scattered by water vapor. Because of the nocturnal and crepuscular habits of Eastern Screech-Owl, rufous plumage should be selected for in warm, humid environments. Rufous is dominant to gray genetically because gray x gray pairings always produce all gray offspring, whereas rufous x rufous pairing produce c. 25% gray young (Gehlbach 1994, VanCamp and Henny 1975).

I hypothesized therefore that, if the Eastern Screech-Owl expanded its range into Manitoba, then there should be a decrease in the percentage of rufous morph birds over time, as rufous morph owls, better adapted to warmer and more humid environments, would diminish in the Manitoba population due to lower survivorship. I therefore calculated the percentage of rufous morph birds in Manitoba by decade and compared these percentage with the populations in northern Minnesota and North Dakota.

METHODS

I assembled a database of Eastern Screech-Owl records in Manitoba from 1921 – 2007, and a comparative database from northern Minnesota and North Dakota from 1883 – 2007. Northern Minnesota is defined here as the area above a line across the southern border of Wilkin County to the southern border of Grant - Douglas - Todd - Morrison - Mille Lacs - Kanabec - Pine counties. This corresponds roughly in latitude to the border between North and South Dakota. I chose this area because of its location directly south of Manitoba. Records from southern Minnesota were excluded as the considerably milder climate there would be predicted to hold a higher percentage of rufous morph screech-

owls. The Manitoba database consists of over 1700 records representing 1399 individuals from numerous sources including published references, oologists' sets, museum specimens, nest cards, rehabilitated birds, applications for taxidermy permits, Christmas Bird Counts, the Manitoba Nocturnal Owl Survey, personal communication from observers, and other reliable sources. The database from northern Minnesota and North Dakota contains records of 611 individuals from a similar set of sources. The lower number of records from Minnesota and North Dakota compared to Manitoba is not reflective of lower owl densities but rather of difficulties in collecting data from afar. Care was taken to cross reference all data gathered to ensure that sightings of individual owls were not duplicated. These records were then grouped by decade and the percentage of rufous morph birds calculated per period.

RESULTS

Nearly three quarters (74%) of the records collected were sight records from either published sources or from personal communication with the author, 10% are specimens or birds found dead, and the remainder were either heard only or are banding records (Table 6.1). When the entire database is considered and records where color was not specified (the "Unknown" column) are excluded, 93% of the Manitoba population is gray and 3.5% is rufous, whereas in northern Minnesota and North Dakota 79% are gray and 19% are rufous.

Table 6.1. Break down of Eastern Screech-Owl records in Manitoba, northern Minnesota, and North Dakota from 1886 – 2007 after removal of repeat sightings.

	Adults	Juveniles	Gray	Brown	Rufous	Unknown	Totals
Manitoba							
Sight records	709	438	785 (68.4)	17 (1.5)	27 (2.4)	316 (27.6)	1147
Specimen / dead	118	6	95 (76.6)	14 (11.3)	6 (4.8)	9 (7.3)	124
Heard only	93	0	0	0	0	93 (100)	93
Banded or rehab	1	0	1 (100)	0	0	0	1
Total	945	454	887 (63.4)	32 (2.3)	33 (2.4)	445 (31.8)	1399
Nth MN and ND							
Sight records	263	81	152 (44.2)	1 (0.3)	32 (9.3)	159 (46.2)	344
Specimen / dead	80	7	59 (67.8)	4 (4.6)	21 (24.1)	3 (3.4)	87
Heard only	175	0	0	0	0	175 (100)	175
Banded or rehab	5	0	4 (80)	0	0	1 (20)	5
Total	523	88	215 (35.2)	5 (0.8)	53 (8.7)	338 (55.3)	611
TOTAL	1457	497	1053	35	84	780	1954

Numbers in brackets are percentages of the color morphs against the total for each category. Eggs are not counted per se, only individual owls reported by the oologists upon collecting. See text for definition of northern Minnesota.

A total of 783 records (39% of the database) could not be assigned a color morph either because they were heard only or because this information was not provided. This necessitated the calculation of two percentages: firstly, the number of rufous birds as a percentage of the total number of records of individual birds and secondly the number of rufous birds as a percentage of the total number of records where the morph is clearly specified (hereafter “m.s”) (Fig. 6.1). The data set for Minnesota and North Dakota suffers from a very small sample size, in particular from 1940 – 1960 and I have therefore averaged the two percentages (rufous morph birds against all individuals and rufous morph birds against individuals where color was specified) as a way of obtaining a fairer means of comparison with the Manitoba data.

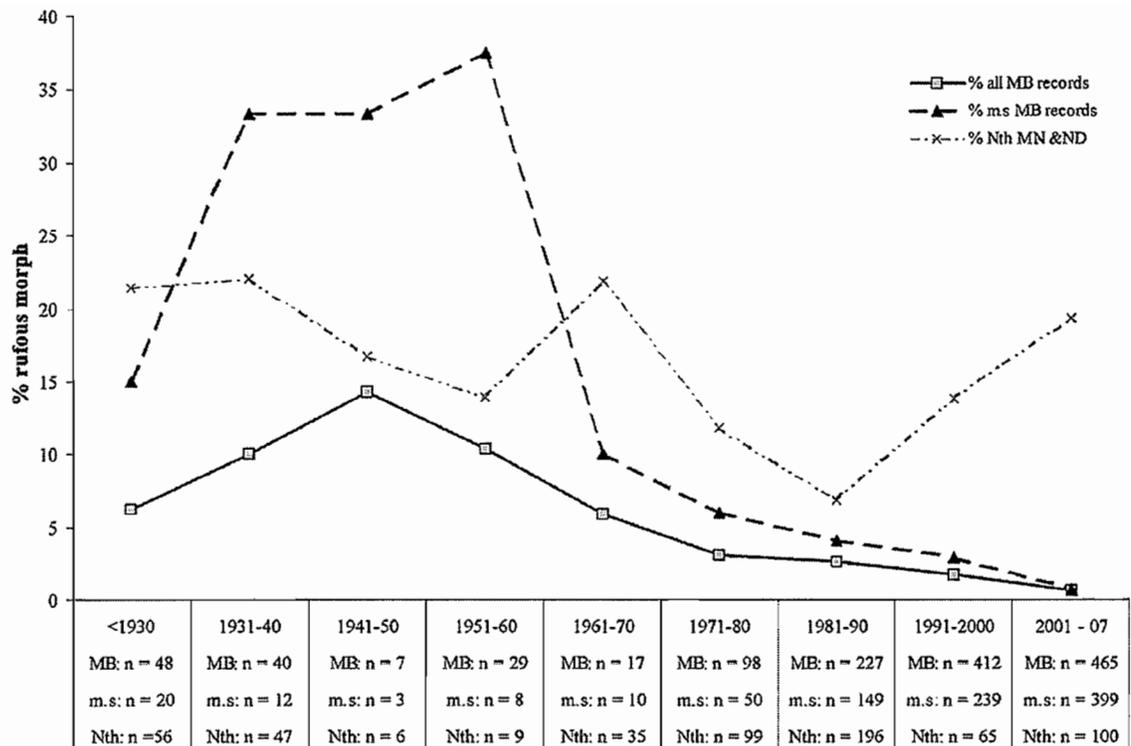


Fig. 6.1. Percentage of rufous morph Eastern Screech-Owls recorded in Manitoba by decade {% of total number of birds recorded and of total number of records where morph is specified (m.s.)} and in North Dakota and northern Minnesota (Nth) {average of the % of total number of birds recorded and of total number of records where morph is specified}.

This graph suggests that rufous morph birds have declined in Manitoba from approximately 6.25 – 10.63% (average of % all records and % ms) in the 1920s to 1% today. This decline appears steady and gradual from the 1960s to 2005, although there is an apparent increase in the percentage of rufous birds for the period 1931 – 1960. This anomaly may stem from the very low sample sizes and different data collection practices during and in proximity to WWII. During this period, specimen and egg collecting declined in popularity and the number of field observations is low. Many of the birds reported from this period were found dead or injured, often in barns or on farmsteads. Since rufous birds are more susceptible to cold, there numbers would be inflated by a

sample collected in this manner. The percentage of rufous birds from specimens only for this period is higher than the same percentage calculated from sight records only (Manitoba m.s data set: 3.2% of sight records rufous versus 5.2% of specimens, U.S. m.s data set: 17.3% of sight records rufous versus 25% of specimens). Unfortunately, the various types of records in this data set are not evenly distributed, with more specimens in the earlier part of the 20th Century and more sight records in the latter half.

Because rufous Eastern Screech-Owls are unusual in Manitoba and to a lesser extent in northern Minnesota and North Dakota, there is a tendency for observers to report their color, whereas many fail to comment on the color of gray birds. Therefore, the majority of birds in the “morph unknown” category are probably gray. I believe for this reason that a more precise figure lies somewhere in between the two types of percentages calculated, probably closer to the former (i.e. the lower end). Brown birds are also underreported, as it is difficult to distinguish this intermediate form from gray, even in specimens, where intermediate characteristics, feather wear, fading, and foxing (browns become brighter or redder over time) must be considered. In fact, most gray specimens and living screech-owls I have seen in Manitoba have had a small amount of rufous in the plumage, especially on the tarsi; as a central vertical band through the ear tufts; in the barring and cross-barring on the breast, belly, and flanks; or as a subtle wash across the underparts, nuchal collar, mantle, or wing coverts.

Despite the caveat that the percentage of rufous birds before 1960 might be slightly inflated, Figure 1 shows an unequivocal decline in the percentage of rufous morph screech-owls in Manitoba but no clear pattern of decline in northern Minnesota and North

Dakota. In the latter areas, the percentage of rufous birds appears to have fluctuated considerably but not otherwise changed greatly between the period prior to 1930 (21%) and the 2001 – 2007 period (19%). I believe the fluctuations shown here are not real but rather a product of the small sample size and the incredibly high number of morph unspecified records (53%) in the U.S data set as compared to the Manitoba data set (33%). Despite the poor quality of the data, this suggests a relatively stable percentage of rufous screech-owls in the areas south of the Manitoba border, with some fluctuations expected due to climatic variation, in strong contrast to the situation in Manitoba. These data are therefore consistent with the hypothesis that the Eastern Screech-Owl expanded its range into Manitoba in the late nineteenth or early twentieth century and that rufous morph birds then declined in number due to their poor suitability to the local climate.

DISCUSSION

If the Eastern Screech-Owl has extended its range into Manitoba, the most significant factor in this expansion is likely to be anthropogenic habitat change. Larger human settlements have brought with them the planting of trees around homesteads and shelterbelts in areas of prairie grassland formerly inhospitable to a woodland species such as Eastern Screech-Owl (Manitoba Avian Research Committee 2003). Many trees in Manitoba may now be larger than in previous centuries, especially in proximity to human habitation due to watering and heat-island effects. During the 20th century, there have been both increased plant growth at mid to high latitudes (45°N and 70°N) and a lengthened growing season (Warren et al. 2004). Tree phenology has changed with some species blooming or budding weeks earlier (Warren et al. 2004), and with some species in southeastern Manitoba becoming hardier (McKenny et al. 2001). Larger trees are more

likely to produce cavities of sufficient size for screech-owls and the open understory they prefer for hunting. Buildings on the landscape may also have assisted in range expansion, providing both shelter and access to prey, ensuring greater likelihood of winter survival in a range peripheral contexts (Adam 1989, Houston 1989, Walley and Clyde 1996). An additional benefit to Eastern Screech-Owl is the placement of nest boxes (usually for Wood Ducks), which they readily use as nest and roost sites. The earliest record of Eastern Screech-Owls breeding in a nest box in Manitoba is 1928 (nest card).

The current distribution of Eastern Screech-Owls in Manitoba is somewhat, but not entirely, linked with human settlement. Eastern Screech-Owls have higher population densities in suburban Winnipeg than in rural areas, producing larger broods and beginning breeding earlier in the year (Chapter 2). Available habitat in suburbs close to rivers or creeks with mature trees matches many of their habitat selection preferences, including a relatively open subcanopy and middle story, many potential nest sites, some planted conifers (frequently used as roost sites by breeding males), and tall trees with little shrub density below them (Chapter 3). Suburbs also have lower densities of Great Horned Owls and raccoons despite higher densities of domestic cats (Chapter 3), and a greater diversity of prey with access to invertebrate prey earlier in the breeding season (Chapter 4). Only one of 52 nests found by the author from 2004 – 2007 was in “wildlands”, i.e. <1 human resident per hectare (Chapter 2).

Another factor that may have assisted the Eastern Screech-Owl to spread northward is the introduction of certain prey items of Palearctic origin, in particular the House Sparrow (Manitoba Avian Research Committee 2003), in the late nineteenth century, first recorded

in the province in 1892 ([Thompson] Seton 1908). The strongest evidence for this is the apparent importance of the House Sparrow, and the Rock Pigeon (captured in barns presumably along with rodents) for winter survival in the Dauphin area (Walley and Clyde 1996). Nonetheless, in the Winnipeg area, no introduced prey item is consumed nearly as frequently as the native meadow vole, which comprises 35% of all vertebrate captures year round and 32% in winter (house mouse: 7% year round, 7% winter; House Sparrow: 6%, 11%; Rock Pigeon: 0.5%, 0%; and European Starling: 0.3%, 0%; n = 781, 44; Chapter 4). The introduced earthworm *Lumbricus terrestris* (commonly called “night crawler”), often captured in watered lawns and gardens, is summer prey only (5% of all invertebrates captured, n = 1542, Chapter 4). Eastern Screech-Owls are thus not dependent on introduced prey. Probably more important to screech owls are concentrations of prey, as may occur around fallen birdseed or at avian communal roosts. Human activity may increase access to birds and mammals since together they constituted 15% of the diet in the breeding season in rural areas (n = 490) versus 33% in suburban areas (n = 1611) (Chapter 4).

Eastern screech-owls appear to benefit from the urban heat islands and warmer temperatures in Winnipeg, e.g. fledging dates are significantly correlated with average March temperature and with the earlier absence of snow on the ground (Chapter 2). Climatic warming could benefit these owls by permitting earlier nesting and increased winter survival rates. In southern Manitoba, most areas have experienced a trend of increasing annual average temperature throughout the century, especially in spring (average increase of 1.7°C per century across five weather stations in Birtle, Brandon, Morden, Sprague, and Winnipeg) and winter (average increase of 1.3°C per century)

(Turner and Blair 2005). Despite gradual change over the past century, the largest increases in average temperatures across the Holarctic region have occurred since the 1970s (Mann et al. 1998). Climate change may therefore have been less significant than habitat change in promoting range expansion.

The decline in rufous morph birds in Manitoba over the course of the twentieth century from similar percentages to those found in North Dakota and northern Minnesota to near monochromatism today supports the hypothesis of historical range expansion into southern Manitoba. In addition to Eastern Screech-Owl, a number of eastern woodland species have apparently undergone similar north or northwestward expansion, including: Wood Duck, American Woodcock, Barred Owl, Red-headed Woodpecker, Yellow-throated Vireo, Purple Martin, Golden-winged Warbler, Eastern Bluebird, and Indigo Bunting (Manitoba Avian Research Committee 2003), as well as mammals such as the raccoon (*Procyon lotor*) (Larivière 2004). Many of these species have some similar habitat requirements to Eastern Screech-Owl, including cavity nest sites and/or a partially open understory for foraging. Although the causes may differ with individual species, a trend of north and northwestern expansion, possibly coupled with the disturbance of prairie habitat, is implied in the early twentieth century in southern Manitoba, and more generally in North America (Johnson 1994). The context and mechanisms of range expansion in the northern prairie region therefore warrant further investigation.

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7. Conclusion:

MECHANISMS OF SUBURBAN ADAPTATION IN THE EASTERN SCREECH-OWL

Suburban Eastern Screech-Owls (*Megascops asio*) in the Winnipeg area exhibit higher population density, larger average brood sizes, earlier average fledging, greater prey diversity, and wider niche breadth than rural screech-owls. Likewise, Gehlbach (1994) demonstrated significant differences between a suburban and a rural population of this species in Texas with the suburban population producing one and a half times more young and reaching five times greater density per unit area than the rural population because of greater fecundity and survivorship. Comparison of these two studies suggest that same processes apply across the rural – suburban gradient in Texas as in Manitoba, and that they do not appear to be more or less pronounced in either context. Gehlbach (1994) discussed various mechanisms to explain this pattern and I have presented data in this regard in the preceding chapters. In conclusion, it is pertinent to address several possible mechanisms in turn.

Urban Heat Island

The urban heat island in concert with other forms of climate buffering, e.g. the reduction of the impact of droughts through human intervention, permit higher overwinter survival and earlier nesting (Emlen 1974, Korpimäki 1978, Gehlbach 1994, Rollinson and Jones 2002, Shochat et al. 2006). Earlier nesting gives the owls a significant head start over migratory secondary cavity nesters such as Wood Ducks (*Aix sponsa*) and provides more time for the fledglings to master hunting techniques before their first winter (Gehlbach

1994). Early nesting may also facilitate the provisioning of young because the period of highest food demand, when the chicks are getting larger but the female is not yet leaving the cavity to assist the male in provisioning, would coincide with the spring arrival of Neotropical passage migrants. Among birds, screech-owls select passage migrants (Chapter 4) perhaps because their lack of familiarity with the local area makes them easier to catch. The urban heat island can increase a suburb's carrying capacity of prey populations (Emlen 1974, Rollinson and Jones 2002, Shochat et al. 2006) and may even introduce new potential prey items to an area where they were not previously found (Parris and Hazel 2005).

During this study (2004 – 2007), the mean temperature in downtown Winnipeg (The Forks) in winter (December – February) was -12.52°C , nearly 2°C warmer than the average temperature for the same period at the airport, an open area towards the outskirts of the city (-14.44°C). The mean daily minimum temperature for the same period was more than 3°C warmer at The Forks than at the airport (-16.52°C versus -19.68°C) (Environment Canada, n.d). During the breeding season of Eastern Screech-Owls (March – July), the mean temperature was 1.3°C warmer at The Forks (10.75°C versus 9.47°C) and the mean daily minimum temperature was 2.4°C warmer (5.71°C versus 3.28°C) (Environment Canada, n.d). The strongest evidence that these differences are biologically significant to Eastern Screech-Owls in the Winnipeg area is that the fledging date of the first chick in each nest is correlated with distance to the city center and with the last date with snow on the ground (Chapter 2). Suburban pairs fledge young on average five days in advance of rural pairs (Chapter 2). In addition suburban pairs had access to

invertebrate prey two weeks earlier than rural pairs (Chapter 4). Invertebrates are completely unavailable in winter in Manitoba so their early appearance in the diet of suburban screech-owls implies warmer temperatures and reduced snow cover.

Reduction in Predation

Eastern screech-owls in suburban and urban areas of Winnipeg enjoy reduced densities of predators such as Great Horned Owls (*Bubo virginianus*) and raccoons (*Procyon lotor*) than rural screech-owls (Chapters 2 and 3). On the other hand, they may live with higher numbers of domestic cats (*Felis catus*), which they avoid (Chapter 3). Screech-owls may avoid Great Horned Owls and in survey were only detected on the same transect five times (Chapter 2). Furthermore, when Great Horned Owls and Barred Owls (*Strix varia*) moved into a new area, screech-owls abandoned breeding territories soon after. This provides some anecdotal evidence for an inverse relationship between the density of larger predatory owls and screech-owls. Nonetheless, direct evidence of a causal relationship between reduced predator densities and higher screech-owl densities in medium-high density suburban areas is lacking.

Nesting success was correlated to distance to building in Texas (Gehlbach 1994), as has also been documented for other bird species (Møller 1988). In this study, screech-owls avoided potential nest sites close to buildings; however, the average distance of a successful screech-owl nest to a building was <50m. This behavior may facilitate the avoidance of certain predators. Rural screech-owls used cavities with a smaller entrance on average, suggestive of higher nest predation pressure (Sonerud 1985, Belthoff and

Ritchison 1990, Yetter et al. 1999). In Texas, suburban screech-owl chicks stayed longer in the nest presumably due to the reduced threat of nest predation (Gehlbach 1994).

Although cause and effect are difficult to determine, predation risk appears to influence the habitat selection of Eastern Screech-owls.

Habitat Change

Many urban and suburban areas offer suitable habitat to Eastern Screech-Owls in Winnipeg and they show their highest breeding success and population density in these areas. Older suburbs in particular have large deciduous trees along streets and in yards and parks, with open lawns beneath them. This habitat greatly suits the screech-owl's hunting style and habitat selection (Chapter 3). In Winnipeg, suburban areas afford screech-owls another luxury with a higher percentage of coniferous trees than rural areas, which the owls select for on breeding territories (Chapter 2) and which males in particular use as roost sites in the early stages of breeding before deciduous trees have foliated when they need to be close to the nesting cavity (Chapter 2). Conifers and buildings offer screech-owls excellent roost sites to avoid detection as well as for thermoregulatory purposes. Buildings are also a factor in the habitat selection of Barn Owls at the northern periphery of their range (Andrusiak and Cheng 1997).

Shrub density around suburban nests is also lower than in rural areas, in part because many gardens and parks are manicured (Chapter 3). Shrub density was negatively correlated with breeding success. The middle story of suburban areas is also less dense than in rural areas (Chapter 3). The less dense, but mature, vegetation with an open

understory found in suburban areas improves the ease of detecting predators and defending nests. This also allows the owl to approach or leave the nest by flying very low to the ground to avoid detection (Gehlbach 1994). A final advantage of suburbia is the placement of nesting boxes for Wood Ducks, often along rivers and close to houses, which screech-owls readily use for both nesting and roosting. Because screech-owls are polyterritorial, nest boxes may improve the quality of territories or even make some areas suitable for breeding that would otherwise lack sufficient cavities. They may therefore contribute to the higher densities of screech-owls in suburban areas. There was no evidence of nest-boxes creating an ecological trap since brood sizes from nest-boxes did not differ significantly from those of natural cavities (Chapter 2).

Prey Availability

Suburban screech-owls showed broader niche breadth and higher prey diversity than their rural counterparts (Chapter 4). They were also able to consume more birds and mammals and were less dependent on invertebrate prey in the breeding season (Chapter 4). This suggests greater prey availability in suburban areas. Rodents in particular are accessible to screech-owls around bird-feeders with fallen seed, and feeders also attract birds providing greater concentrations of prey in a small area (pers. obs). Well-watered and fertilized lawns provide screech-owls with another concentrated food source in earthworms and beetles that are most active at the surface after rains or watering (pers. obs). Suburban areas thus provide these owls with an increased abundance, variety, and accessibility of prey.

Eastern screech-owls have several important pre-adaptations to highly fragmented and disturbed habitats such as suburban areas. As discussed above, their preference for open habitat makes them well suited to the suburbs and their small spatial requirements enable them to exploit small habitat patches (Gehlbach 1995). Their small body size, inconspicuous perch hunting style, and cryptic plumage enable them to live in close proximity to humans with less persecution than larger predators (Gehlbach 1995). They are diet generalists and can therefore capitalize on fluctuating food supplies (Gehlbach 1994). They have large broods (range 2 – 6, average 4.2 fledglings) and breed annually (as opposed to being dependent on prey cycles as are more stenophagous owls) and at an early age (one year old) (Gehlbach 1994). Their comparatively short incubation and nesting period combined with their polyterritoriality and the fact that they are residents and can commence breeding in the early spring facilitate reneating when disturbance is encountered (Gehlbach 1994). Consequently, Eastern Screech-Owls in suburban Winnipeg have reached higher densities, achieved larger brood and earlier fledging, and enjoy more diverse diets than owls in rural areas on the outskirts of the city with lower human density. There is also evidence to suggest that it was this pattern of exploiting the advantages of proximity to humans and their structures, as well as the changes they brought to habitat and climate, that enabled the Eastern screech-owl to expand its geographical range northward into Manitoba over the course of the late nineteenth and twentieth centuries (Chapter 6). In terms of climate and diet, this expansion has propelled them to the biogeographical edge, further from the core range and characteristics of their predominantly tropical, insectivorous genus than any of their congenitors.

PREDICTIONS AND FINDINGS

At the outset of this research, I predicted that suburban and urban Eastern Screech-Owls in the Winnipeg area would have advanced breeding phenology and higher reproductive success than screech-owls in rural areas. I expected that in Manitoba's northern temperate climate, at the periphery of the range of Eastern Screech-Owl, any differences in breeding phenology and brood size between rural and suburban pairs would be even greater than in Texas (Gehlbach 1994). The first of these predictions has been clearly demonstrated.

Eastern Screech-Owls have denser populations, advanced breeding, more offspring per nesting attempt and a more varied diet in suburban areas than less densely populated areas. Breeding phenology is correlated with distance from the city center implicating the urban heat island. There are also differences in the habitat available to the owls in more densely populated versus less densely populated areas, e.g. high density suburban areas have a more open canopy with trees and shrubs spaced farther apart, more conifers, more American elm and Manitoba maple (the two most commonly used tree species for nesting). Suburban owls have to contend with fewer raccoons and Great Horned Owls but more domestic cats and live in greater proximity to buildings with more pedestrian activity (possible predator deterrents).

The second prediction, that such differences would be more pronounced in Manitoba than Texas, was not supported. The difference in breeding phenology was in fact slightly greater in Texas than Manitoba (6 versus 5 days). Likewise, suburban owls in Texas produced 0.9 chicks more per nesting attempt than rural birds (Gehlbach 1994), compared to a difference of 0.3 chicks per nesting attempt in Manitoba. Unfortunately, it has proven difficult to assess the significance of these results due to methodological

differences (gradient approach in Manitoba versus comparison of two study sites in Texas). In both Manitoba and Texas, the evidence suggests that the same suite of interacting mechanisms combine to provide an advantage to suburban screech-owls. These are the urban heat island, lower densities of natural predators and nest predators, some buffering of predator activity due to human presence, greater and more varied prey availability, and suitable open habitat that facilitates hunting. In Manitoba, the addition of certain habitat features such as coniferous trees and human structures for roosting is also important.

The data suggest that screech-owls in Manitoba occur in much lower densities than elsewhere in the geographical range, as predicted by the abundant center hypothesis (Brown 1984, Brown et al. 1995) and also found in other owl species (Sunde et al. 2001), though not always realized in other birds (Blackburn et al. 1999). This is despite the fact that they produce more young per nesting attempt than elsewhere in the range, following a trend of increasing clutch size with increasing latitude (Murray 1976). This suggests that winter mortality is very high in Manitoba, due at least in part to this species' limited tolerance to cold (Mosher and Henny 1976). In this study, 84% of survey detections and 83% of nests found were in suburban areas (>10 p/ha) and 65% of survey detections and 60% of nests found were in medium – high-density suburban areas (>20 p/ha). The range-wide trends discussed above and the fact that such a large portion of the nests and territories were in suburban areas strongly suggest that the various suburban advantages discussed above play a significant role in the maintenance of this species in this northern

study area, and, given the similarities with other studies (Gehlbach 1994), possibly across the range.

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

With close to half of the human population now living in cities (United Nations 2006), the effect of urbanization on the world's fauna is highly significant and the management of wildlife in urban areas is of increasing conservation importance. Urban areas are important both in their own right for the plants and animals that live with them and also in terms of the way they are connected to the surrounding landscape, enhancing or limiting the dispersal of wildlife (Marzluff 2001, 2005). Human activities can make common species rare (or even extinct) and vice-versa. In addition to threatened species, species that are common today therefore warrant monitoring and research to understand how human activities can benefit or disadvantage them. The distribution of the Eastern Screech-Owl in Winnipeg affords several important lessons in management to ensure that cities and towns maintain their biodiversity and reasonably intact food chains.

The Eastern Screech-Owl's strong association with riparian habitats in the study area suggests that protecting riparian areas and preventing removal of trees from these areas in cases where new development is planned is key to ensuring a healthy population of Eastern Screech-Owl in the city. Screech-owls breed in some areas where the riparian buffer strip, e.g. behind a row of houses, is little more than 50m wide, as long as there are also mature trees in the surrounding yards and along streets. The size requirements in summer of this species appear to be small, most pairs occupying territories of a radius of

<500m; however, these birds appear to utilize a much greater area in winter. Following literature on the importance of patch size and connectivity (Bunnell 1999, Clergeau et al 2001, Alberti and Marzluff 2004, Bierwagen 2005, Donnelly and Marzluff 2006), ensuring that riparian corridors are intact on both sides of rivers through the city, with minimal breaks in connectivity, would go a long way to maintaining high biodiversity and ensure that owls born in suburban areas have territories they can occupy.

The city of Winnipeg has been dealing with the problem of the loss of American elms (*Ulmus americana*) due to Dutch elm disease. The nesting data of Eastern Screech-Owls in Winnipeg suggest that this native riparian cavity species is a key component of the riparian community. American elm was in fact the tree species that was used most often by nesting screech-owls. The work to preserve the elm in the city is therefore extremely valuable for wildlife. As a significant cavity-producing tree, the American elm is important for many species in addition to the Eastern Screech-Owl.

Survey data (Chapter 2) indicate that, although screech-owls in moderate density suburban areas possess many advantages, their population densities may peak in the upper suburban zone of 20 – 30 p/ha. Unfortunately the survey design in this study proved insufficient to assess whether screech owl populations may decrease above a certain high human density, e.g. 50 p/ha. This raises a fundamental question about how different levels of human density affect wildlife and how best to optimize space for wildlife in human population centers. At least one pair of Eastern Screech-Owls nested successfully in an extremely densely populated area (99 p/ha) close to downtown Winnipeg with

several high-rise condominiums. Conversely other areas along the very same river, both inside and outside of the city, where trees and shrubs were removed to create a view of the water, had no resident pair of screech-owls over the four years of this study. Those urban owls were able to raise young in that area because, in addition to all the impervious surfaces surrounding those high-rises, the area contained a wooded riparian green space and streets lined with tall, mature native cavity-bearing trees. Other areas, with fewer residents but farther from a river and without a designated greenspace per se, also held a resident pair of screech-owls. In these cases, the streets and most yards contained mature cavity-bearing trees such that if viewed from the air, they would give the impression of reasonably contiguous canopy cover. In these cases the small interconnected “greenspaces” that are private yards provided enough food and shelter, as well as a nesting resource (many natural cavities) for the owls. This suggests that even densely populated areas can support native predators if certain spatial requirements and basic habitat needs are met. The simplest recommendation arising from this thesis therefore must be that, even in densely populated cities, riparian corridors should be protected as greenspaces. This would not prevent humans from using such riparian corridors for recreation. In fact, many have argued that such corridors in cities improve the quality of life or urban residents (Worster 1973, Niemelä 1999, Shutkin 2000). Secondly, greenspaces should be arranged spatially so as to enable wildlife to persist in all areas and designed so as to maximize native vegetation matching the natural ecosystem of the region. Furthermore, wherever possible, residential areas should match those areas specifically designed for wildlife in basic habitat characteristics, thereby permitting both occupancy and animal movements. In a city such as Winnipeg, this would require careful

consideration, since several ecosystems are, or, at least historically, were present. This thesis has not dealt with native grasslands, which were once present in certain parts of the city, and which also warrant consideration in urban planning.

Much recent discussion in ecology has focused on the notion of ecological traps and sink populations (Best 1986, Remes 2000, Battin 2004, Baker et al. 2005, Mannan et al. 2008). It is therefore possible that providing nest-boxes may entice wildlife into areas where their productivity will be low or where high mortality or parasitism may create sinks. At least in the case of the Eastern Screech-Owl in Winnipeg, there is no evidence of any decoupling of population density and reproductive success, i.e. the areas of highest population density also have the highest reproductive success, regardless of whether nest-boxes are supplied or not. Nest-boxes do not appear to be creating a problem for screech-owls and the broods they raise in them are of the same size as those in natural cavities (larger broods are produced in boxes on average but the difference is not statistically significant). Nonetheless, this research has demonstrated a different problem with nest-boxes, viz. that the conspicuous placement of many boxes in close proximity can lead to increased dump-nesting from Wood Ducks, which even has an impact on screech-owls (Chapter 5). I would therefore recommend that nest-boxes be monitored and their positioning on the landscape be considered, ideally overseen by a local authority, so as to complement the distribution of natural cavities but to minimize the risk of dump nesting (Semel et al. 1988, Semel and Sherman 2001) and interspecific competition (Artuso 2007).

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8. Appendices

APPENDIX 1: PREY ITEMS

Prey by species of Eastern Screech-Owl from March 2004 – February 2008. The selectivity index (s) for certain species of birds are also given

Prey Item	Total Captured	Biomass
BIRDS	n = 344	9601g
<i>Passerines</i>	282 (82%)	5984g (62%)
<i>Non-passerines</i>	11 (3%)	1444g (15%)
<i>Unidentified bird</i>	51 (15%)	2173g (23%)
Unidentified small passerine	90 (26%)	1782g (19%)
House Sparrow	43 (13%) s = -0.2	1204g (13%)
Unidentified sparrow or finch	33 (10%)	662g (7%)
Black-capped Chickadee	30 (9%) s = -0.2	330g (3%)
Unidentified warbler	19 (6%)	190g (2%)
Cedar Waxwing	9 (3%) s = -0.5	288g (3%)
Yellow-rumped Warbler	9 (3%) s = -0.1	111g (1%)
American Redstart	7 (2%) s = 0.8	58g (1%)
Yellow Warbler	6 (2%) s = 0.3	57g (1%)
House Finch and <i>Carpodacus</i> sp	6 (2%) s = 0.1	128g (1%)
White-breasted Nuthatch	4 (1%) s = -0.8	84g (1%)
Rock Pigeon	4 (1%) s = -0.4	1080g (11%)
American Robin	3 (1%) s = -0.9	231g (2%)
<i>Catharus</i> sp	3 (1%) s = -0.1	93g (1%)
Hairy Woodpecker	3 (1%) s = 0.2	198g (2%)
Downy Woodpecker	3 (1%) s = -0.6	81g (1%)
Tennessee Warbler	3 (1%) s = 0.2	30g (0.3%)
Northern Shrike	2 (1%)	130g (1%)
Blue Jay	2 (1%) s = -0.5	170g (2%)
American Goldfinch	2 (1%) s = -0.7	26g (0.3%)
European Starling	2 (1%) s = -0.7	164g (2%)
House Wren	2 (1%) s = 0.5	22g (0.2%)
Dark-eyed Junco	2 (1%) s = -0.6	38g (0.4%)
Virginia Rail	1 (0.3%)	85g (1%)
White-throated Sparrow	1 (0.3%) s = -0.3	26g (0.3%)
Baltimore Oriole	1 (0.3%) s = 0.2	33g (0.3%)
Pine Grosbeak	1 (0.3%)	56g (1%)
Rose-breasted Grosbeak	1 (0.3%) s = -0.3	45g (0.5%)
<i>Regulus</i> sp	1 (0.3%) s = -0.4	6g (0.1%)
MAMMALS	n = 429	17698g
<i>Rodent</i>	418 (97%)	17276g (98%)
<i>Non-rodent</i>	11 (3%)	422g (2%)
Meadow vole and unidentified vole	292 (68%)	14308g (81%)
House mouse	55 (13%)	1128g (6%)
Unidentified small mammal	26 (6%)	780g (4%)
Deermouse	24 (6%)	480g (3%)

Unidentified rodent	21 (5%)	580g (3%)
Little brown bat	6 (1%)	240g (1%)
Short-tailed shrew	4 (1%)	82g (0.5%)
Red squirrel (young)	1 (0.2%)	100g (1%)

AMPHIBIANS AND FISH

n = 8

119g

Unidentified frog	3 (38%)	45g (38%)
Leopard frog	2 (25%)	40g (34%)
Wood frog	2 (25%)	24g (20%)
Unidentified fish	1 (13%)	10g (8%)

INVERTEBRATES

n = 1542

3277g

<i>Hard (detectable in pellets)</i>	690 (45%)	1425g (43%)
<i>Soft (not detectable in pellets)</i>	179 (12%)	338g (10%)
<i>Unidentified invertebrate</i>	673 (44%)	1514g (46%)
Beetle: Scarabidae	554 (36%)	1108g (34%)
Beetle: family unknown	76 (5%)	152g (5%)
Beetle: Carabidae	29 (2%)	58g (2%)
Beetle: Staphylinidae	3 (0.2%)	6g (0.2%)
Beetle: Coccinellidae	3 (0.2%)	3g (0.1%)
Earthworm (mostly <i>Lumbricus terrestris</i>)	79 (5%)	158g (5%)
Caterpillar sp	56 (4%)	112g (3%)
Moth (mostly Noctuidae)	36 (2%)	54g (2%)
Winged insect	12 (1%)	42g (1%)
Crayfish sp	7 (0.5%)	37g (1%)
Dragonfly sp	5 (0.3%)	15g (0.5%)
Larvae or pupae	4 (0.3%)	8g (0.2%)
Slug sp	2 (0.1%)	2g (0.1%)
Spider sp	2 (0.1%)	4g (0.1%)
Cockroach sp	1 (0.1%)	4g (0.1%)

Twenty "*Microtus* sp" are all most likely to be Meadow voles hence combined. Beetle identifications are imperfect and the number of Scarabidae may be inflated due to other families with similar head or leg shapes. Most of the unidentified invertebrates were observed and were most likely small beetles or other very small prey. The most common Scarabidae prey are in the genus *Phyllophaga*, the most common Carabidae prey are in the genus *Calosoma*.