DISTRIBUTION AND MOVEMENT PATTERNS OF AFRICAN WILD DOGS AND RED FOXES IN RELATION TO HABITAT STRUCTURE AND ANTHROPOGENIC INFLUENCE.

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ABSTRACT

Diversity and spread of habitat types (i.e. heterogeneity) within a landscape have important implications for the distribution of resources (e.g. prey species) and subsequently the distribution and movement patterns of animals. Human activities often directly disrupt the natural environment, fragmenting it into patches of natural habitat interspersed with human-use areas that are not suitable for many animal species. Other phenomena, like climate change, can gradually change the structure of a landscape, resulting in changes in biological community structure. The study of animal movement through diverse and patchy landscapes can thus be a valuable tool for understanding the effects that human activities and natural change (e.g. weather patterns) can have on animals.

The primary goal of this research was to investigate the interaction of important predatory mammals with their environments using different techniques in order to discern potential anthropogenic effects on the species. Two species of mammalian predator, the African wild dog (*Lycaon pictus*) and the red fox (*Vulpes vulpes*) were examined. Movement data obtained from field studies were compared with predictions made from theoretical movement models. Computer simulations were performed using an individual-based movement model to explore fundamental movement patterns in fragmented landscapes and to permit some comparisons between the two species in light of the fact that the wild dog is considered a specialist (limited in landscape use by specific requirements) and the red fox, a generalist (flexible in landscape use)

Radio-collared African wild dogs were tracked as a pack for 19 months in South Africa to provide locational fixes used in this study to examine home range and habitat selection over different seasons. Red foxes were snow-tracked for two winter seasons on Prince Edward Island (Canada) to obtain detailed movement paths, which were compared among geographically distinct study sites in terms of habitat selection, path shape, displacement, and interaction with local habitat variables such as snow depth. Mapping software was used to relate movement and distribution of both species to their respective habitat characteristics.

The African wild dog pack selected some habitats consistently, indicating some specialization, but the home-range size and location were inconsistent and extended to the reserve boundaries (and beyond on a number of occasions), suggesting that the enclosed area did not contain all the resources required by the pack. Simulated specialist movement path shape was affected by increasing fragmentation (decrease of good habitat), becoming straighter (or more directed) in less suitable habitats. Wild dogs, consistent with their status as specialist predators, showed some specialist tendencies in this study and extended their range beyond the reserve, similar to the way in which simulated specialists extended their paths directly through unsuitable habitat.

Although red foxes had similar movement patterns at all study sites, habitat selection differed across study sites with few consistencies among sites that were more heterogeneous or human-impacted. Thus, fox movement does not appear to be impacted by fragmentation or heterogeneity. Foxes demonstrated versatility, which is consistent with a generalist definition. Simulated generalists, like the foxes studied here, were not affected by fragmentation as indicated by similar shape at all fragmentation levels (or percentages of good habitat). Fox movement had dispersal consistent with that expected from a Lévy walk model which is indicative of an optimal foraging strategy.

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The completion of this thesis and maintenance of my sanity, for the most part, would not have been possible without the support and assistance from so many people in my life. It is probably an impossible feat to thank everyone that has a hand in this work, but I will attempt to do my best to name and appreciate them.

My co-supervisors Marina Silva and Sheldon Opps were a tremendous positive influence on me and helped guide what turned out to be a very large and diverse project of projects. Despite having a lot going on in their lives (and new life together), they always made an effort to be available. I learned more than I could ever have imagined from them and from the work that resulted from the research of this thesis. I would like to thank them for their patience with me and for opening doors for me through the exploration of different technologies used to examine animal movement. Their extensive comments on drafts taught me a lot about writing and about my own strengths and weaknesses. I also must thank my two committee members, Pedro Quijon and Javier Sanchez who also shared specific expertise for pieces of this project.

A large part of this thesis was based on research done in Mkhuze Game Reserve, South Africa, and I would like to thank Operation Wallacea and the University of Prince Edward Island for making that intercontinental trip possible. However, once in South Africa, all did not go smoothly and wild dogs disappeared from the reserve. As a result, Chris Kelly and the Priority Species Monitoring Project of Ezemvelo KwaZulu-Natal Wildlife Conservation allowed me to use a previously-collected dataset, for which I am deeply grateful. I felt extremely privileged to work in iSimangaliso Wetland Park (a world heritage site), and I did participate in cheetah radio-tracking for the majority of my time there in addition to analyzing the wild dog data. Eventually, near the end of my stay, two wild dogs did return to the reserve and I was on the team that captured one of them to remove a snare and apply a radio-collar, an experience that words cannot describe. To touch Africa's most endangered carnivore was beyond a privilege. I would also like to thank Den Kelly, Xander Combrin, Beka Nxele, and Paul Havemann for supplying me with local information required to complete the study. Bella Davies and Victoria Hobbs were invaluable sources of knowledge regarding, and patience in teaching about, GIS and all of its intricacies. Janet Edwards, a fellow Masters student (from the University of Pretoria, South Africa) working on genetic studies of wild dog populations provided many fun anecdotes of the African bush and shared my interest in this species. Thank you also to the numerous safety officers that accompanied us in vehicles and on foot through the bush and taught us some essential survival skills. My field supervisor in South Africa, Mike Perrin was also of great assistance in the analysis of data as he has had many publications on the distribution of African wildlife in the area.

Back on Prince Edward Island, the study of red fox movements and diet was a task that required the assistance of many eager volunteers and a keen summer student. Stephany Maslis was hired on to help for a summer and she and I spent countless hours at field sites searching for elusive fox scats and getting way too excited when we found anything that resembled feces, then sorting them back at the lab finding all sorts of interesting things. Kerry-Lynn Atkinson, Shillaen Watts, Frank Dickson, Whitney Kelly-Clark, and Nikki Lewis also were willing to lend a hand in scat collection. Dr. Gary Conboy and his parasitology lab at the Atlantic Veterinary College were extremely helpful in teaching me to identify various parasites from fecal samples. Live-trapping efforts, as can be attested to by other field biologists, require patience and volunteers that are willing to work at all hours of the day or night. Attempting to live-trap an intelligent species such as the red fox did indeed test my patience but I was blessed with many who were interested in lending a hand. I would like to thank Kerry-Lynn Atkinson, Whitney Kelly-Clark, Hailey Lambe, Nikki Lewis, and Stephany Maslis for forgoing showers and accompanying me to set and check live-traps early in the mornings and late at night. Karen Johnson, a student who had previously studied red foxes in our lab, was a valuable source of information on fox behaviour and live-trapping. Unfortunately, though we caught some raccoons, skunks, and cats, and I watched frustrated as a fox explored but did not go into a trap, we did not capture or process any foxes for this study. Carl Polsar and Clarence Ryan provided post-hoc recommendations for future efforts. However, snow-tracking was conducted to gather some movement information and Kerry-Lynn Atkinson, Frank Dickson, and Nikki Lewis frequently accompanied me in the field. No field work could have been completed without collaboration and permission from local landowners and Parks Canada, and I thank them for their willingness to participate, share stories, and learn more about wildlife. Special thanks to Phil McCabe (PEINP Park Ecologist) for his help and suggestions, not to mention awesome stories about his Park experience in other areas of Canada.

When it came down to analyzing collected data, Henrik Stryhn was always willing to discuss statistical procedures, and Raphael Vanderstichel, Brad Potter, and Joshua Mailhiot got me through frustrations with ArcView GIS. Special thanks are in order for the Government of PEI for allowing me to use the GIS layers of PEI from the 2000 Corporate Land Use survey for data analysis.

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Though not directly involved in this research, many of the other biology department students were supportive and for that I am very grateful. In particular, the other graduate students empathized with the stresses and joyous discoveries. My friends and family did their very best to understand what I was doing and my sister, Belinda, and my mum especially put up with my rants and frustrations. Thank you for the ice cream and fast food trips to calm me down! The other faculty and staff at UPEI always had a friendly face and some kind advice whenever I was in positive or negative spirits. Thank you to my landlady, Eleanor for not complaining about my late night work habits and field trips and for always inquiring with genuine interest about the research.

I need a whole new paragraph to thank my best friend and partner, Frank Dickson, for his unending patience and willingness to listen and tell me over and over that it was going to turn out well and that I was smart enough and had worked hard enough. Frank has only known me as a graduate student and if he can put up with me under those pressures, we are in it for the long haul!

I would like to dedicate this thesis to my late Grampy (John A. MacLeod), who passed away last summer. He was very proud of the pursuit of education, although I will always remember him telling me that there was nothing more annoying than someone acting uppity about their education. Thanks to him, I will try to never think I am better than anyone no matter how much education I achieve.

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GLOSSARY

The definitions for the following terms refer to their use in the context of this research and may differ from definitions found in other disciplines.

Anthropogenic (adj): Describing something that is caused or created by humans

Autocorrelation (n): Cross-correlation or dependence (see definition for correlation below) of something with itself.

Conservation (n): The practice of protecting something from loss or harm.

Correlation (n): Similarity of observations as a function of time or distance, or dependence of an observation on the previous observation.

Directional Bias (n): Something (i.e. a cue) in the external environment that causes preference for movement in a certain direction.

Directional Persistence (n): An influence for movement in a certain direction that is inherent, or comes from within the animal itself.

Endangered (adj): A species that is present in such small numbers that it is in imminent danger of extinction without conservation or management measures.

Extirpation (n): In an ecological context, the loss of a species from a specified area, but not from the entire world (extinction).

Fragmentation (n): The act or process of breaking a large quantity of something into smaller fragments or pieces. In the context of a landscape, fragmentation splits large natural tracts of land into patches, potentially of differing qualities.

Generalist (n): One with a wide set of skills or knowledge. In an ecological context: an animal that is versatile in its use of habitats and resources.

Geographic Information System (GIS) (n): A system of hardware and software used for storage, retrieval, mapping, and analysis of geographic data. A GIS layer is spatial data that describe the characteristics of specific locations

Global Positioning System (GPS) (n): A navigational unit that locates and stores geographical positions by using satellite signals.

Habitat Selection (n): The differential use (i.e. preference or avoidance) of habitat types by an animal in a landscape. Considered here to be synonymous with habitat use.

Heterogeneous (adj): Something is heterogeneous when it is composed of units that are different in nature. A landscape is considered heterogeneous if it has a variety of different habitat types as opposed to a tract of land that is uniform in quality. Heterogeneity (n) is the quality of the state of being heterogeneous. For example if a landscape has higher heterogeneity than another, it is more heterogeneous in nature.

Home Range (n): The area used by an animal in a specified time period that provides resources needed on a daily basis.

Keystone species (n): A species that has a disproportionate effect on its biological community through interconnected roles with other species through predator/prey or competitor interactions.

Lag (n): A specified distance or time period away from the origin. (v): to delay or fall-behind by a specified distance or time period.

Management (n): In an ecological context, the process of actively handling, controlling or supervising individual animals or populations in the interest of crisis prevention.

Model (n): A hypothetical description of a complex entity or process, often with the use of mathematical equations. Models are useful not only for description, but for interpretation and predicting future consequences.

Move (n): The change in position from one point to another.

Movement (n): The basic physical process of changing position.

Net Displacement (n): The shortest distance covered from point A to point B, regardless of the shape of the route that might occur in between.

Patch (n): In an ecological context, a fragmented portion of habitat.

Path (n): In the context of movement, the route followed by an animal through a landscape.

Perceptual range (n): The maximum distance at which an animal perceives its surroundings.

Reintroduction (n): The process of moving animals into an area (i.e. introducing) where they previously existed.

Simulation (n): The technique of representing real-world processes by a computer program. Monte Carlo simulations are a class of computational algorithms that rely on repeated sampling to compute results to simulate physical and mathematical systems.

Spatial scale (n): A relative magnitude of length at which something is observed. For example, observations from a helicopter are done at a larger spatial scale than observations by a person walking through a habitat.

Specialist (n): In an ecological context: an animal that requires a specific set of conditions or resources and cannot adapt to use others.

Step (n): Each point at which a measurement of position was made along a movement path. This is not equivalent to a biological move, in which an animal consciously decides to move in a certain direction for a specified distance.

Tortuosity (n): The quality or condition in which a movement path is twisty, crooked, or compact in nature. A tortuous path is the opposite of a straight and direct path.

Translocation (n): The process of moving individuals to another area.

Turning angle (n): The angle at which the direction of movement changes from that of the previous move.

1. INTRODUCTION

1.1. BACKGROUND

Landscape heterogeneity is based on the diversity of elements such as habitat types, and the size, shape, spatial configuration, and interaction among them (Mimra 1993 in Sklenicka and Lhota 2002). The natural environment is spatially heterogeneous (i.e. diverse in habitat types), allowing different species to coexist and use resources differentially. Heterogeneity in the landscape can be altered by natural phenomena like climate change, ice flows, storms and earthquakes but also by anthropogenic activities. Fragmentation has been defined as the anthropogenic process of increasing landscape heterogeneity by the breakup of natural habitat into pieces or patches (Wilcox 1980). Thus a fragmented landscape is usually also a more heterogeneous one. Fragmentation results in a loss of some habitat, alteration in quality or structure of others, an increase in edge habitat, loss of some species and a change in community structure (Diamond and May 1976; Krishnamani et al. 2004; Kruess and Tscharntke 1994). Biotic and abiotic changes associated with habitat fragmentation can also alter animal movement patterns. As an example, Silva et al. (2005) found a decrease in the species richness of small mammals in agricultural landscapes without connecting corridors for movement, although some species actually benefitted from the fragmentation. Agriculture, urban development, mining, and intensive forestry have resulted in the loss and fragmentation of natural habitats (Riley et al. 2002). Studying the response of animals to spatial heterogeneity that may be naturally occurring or the result of human activities can help us to understand the impact and damage of human actions on an ecosystem. In particular, movement patterns of animals are influenced by this spatial heterogeneity (Johnson et al. 1992; Turchin 1998) and animal response to habitat alteration and loss can be quantified using movement data (Diffendorfer et al. 1995).

Mammalian carnivores interact with other species through predation and competition and as such, are important to biological communities (Palomares and Caro 1999; Treves and Karanth 2003). As top predators in many terrestrial communities, carnivores can control the numbers and activities of other animals responsible for high levels of predation on other species (Crooks and Soulé 1999). In this way, they are acting as keystone predators in their role in structuring the community and maintaining diversity (Paine 1969; Pimm 1980; also see Mills et al. 1993). For this reason that it is important to look at the role of these carnivores and how they are interacting with their environment when studying biological communities. Unfortunately, many top carnivores are under pressure of habitat loss and other forms of persecution and are at higher risk of becoming endangered (see Clark et al. 1996), which could put entire communities at risk of destabilization. Some carnivores also interact closely with people, resulting in potentially dangerous situations. For example, in Uganda, interactions with leopards and lions have killed hundreds of people over the past few decades (Treves and Naughton-Treves 1999). Coyote aggression and their direct attacks on people have recently become a major problem in many areas of North America (e.g. Timm et al. 2004). These examples are just a few of many that emphasize the importance of studying carnivores in order to manage and conserve populations effectively (Gese 2001; Treves and Karanth 2003). In order to develop management plans, we must first understand the ecology and behavior of the species. Whether a species is of concern from a conservation point of view or is a nuisance, the movement of individuals is an important field of study. Furthermore, the manner in which animals utilize the available area has been recognized for some time as an important component of ecological studies (Kernohan et al. 2001). Understanding how animals use space and move within it will help us better understand the requirements of these animals.

In this thesis, two very different species of mammalian carnivore were studied: the African wild dog (*Lycaon pictus*) and the red fox (*Vulpes vulpes*). The wild dog was studied in Mkhuze Game Reserve (South Africa) while the red fox was studied in Prince Edward Island (Canada), both areas that represent diverse and patchy landscapes. The African wild dog is an endangered species and conserving and managing remaining populations in small fenced reserves is a huge challenge. Understanding the movements and use of resources within these reserves can help prevent extirpations and, ultimately, extinction of the species. The red fox is a commonly found species on Prince Edward Island (PEI) and is distributed widely around the world. PEI is subject to erosion, fragmentation, climate change, and anthropogenic activities. Despite increasing fragmentation of natural landscapes for agricultural and urban land use, and the close proximity to people on PEI, the fox is adapting and spreading its distribution over the island, even establishing in urban areas. Fox habitat selection and movement patterns are of interest to us as tools for understanding how the species is impacted by human activities on PEI.

Two of the original components of this thesis research are detailed only in the appendices due to limited data collected. The first is GPS-tracking of red foxes, from which it was hoped home range estimates and a greater dataset of fine-scale movement data would be obtained. This was not successful because no foxes were caught in live-traps, although the prepared protocols for handling and immobilization are outlined in the appendices. Ultra high-performance liquid chromatography (UHPLC) and mass spectrometry (MS) were used in an attempt to analyze the molecular components of fox scats to identifying important nutrients and food items. The goal was to look at diet more specifically than possible with basic macroscopic sorting of scat. Although this was a novel approach for scat analysis, sufficient molecular baseline information on compounds of interest was lacking. However, the protocol for extraction is included in the appendices as a reference for possible future endeavors in this direction. A microscopic survey of parasite content and macroscopic analysis of diet were successfully completed on fox scat samples and are outlined in the appendices as a complementary study to fox movement and the influence of human activities.

1.2. RESEARCH OBJECTIVES

The main goal of this study was to explore the effects of differing landscape characteristics and human influence on animal movement.

Objectives:

1. To examine habitat selection and home range patterns in African wild dogs reintroduced to a game reserve in South Africa using radio-telemetry data.
2. To investigate habitat selection and movement patterns of red foxes inhabiting PEI using snow-tracking data and theoretical models.
3. To perform basic computer simulations with a simplified model to examine the movement patterns of random animals in fragmented landscapes.

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2. LITERATURE REVIEW

2.1 ANIMAL MOVEMENT

Movement is a basic physical process influenced by many factors including social interactions, reproduction, landscape structure, and distribution of food resources. Animal movement occurs as a result of inherent and external cues acting on an animal, either independently or in combination. Landscape structure (Johnson et al. 2002; With 1994a) and resource availability (Edwards et al. 2001; Ciucci et al. 2003) are examples of external biases (or *directional biases*) acting on animal movement, while an animal's perceptual range (Chust et al. 2003; Mech and Zollner 2002), body size (Mech and Zollner 2002; With 1994b), and spatial memory (Atkinson et al. 2002; Benhamou 1994; Ramos-Fernández et al. 2004) are examples of inherent biases (*directional persistence*) or constraints on movement. Animals make biologically important 'moves' based on decisions and interactions with their surroundings. Each move has a length, a turning angle, and a direction (Turchin 1998, see Fig. 2.1). A turning angle is the angle formed between subsequent move directions (Whittington et al. 2004). Moves together make up a movement path (also referred to here as 'path'), which has a total length, a net displacement, an absolute direction, and a tortuosity (Turchin 1998, see Fig. 2.1). Net displacement is the shortest distance between the beginning and end of a path, and tortuosity is a measure

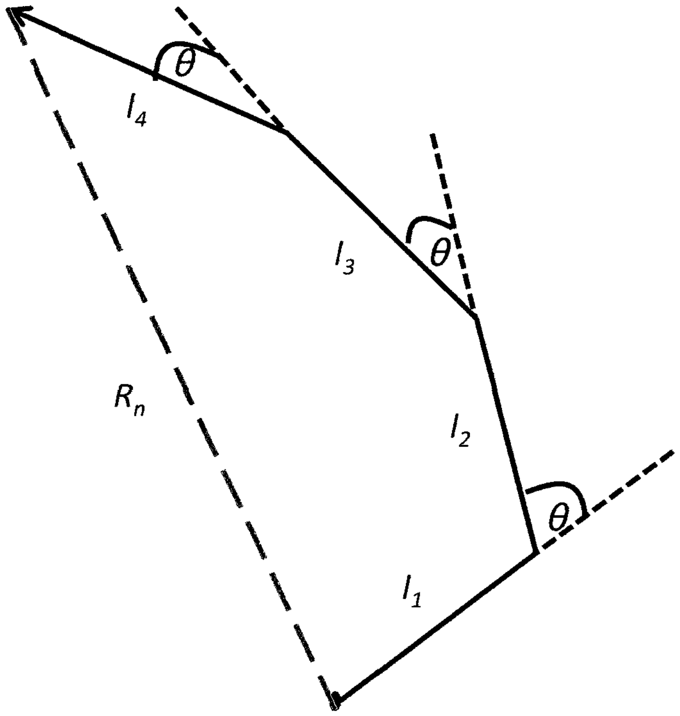

FIG. 2.1.—Schematic representation of an animal movement path. Solid lines represent the actual move with length, l_n, short-dashed lines represent the direction, of the previous move, θ represents the turning angle, and the long-dashed line represents the net displacement of the path (R_n). Modified from Kareiva and Shigesada (1983) and Crist et al. (1992).

of how twisted, or compact a path is (Claussen et al. 1997; Nams 1996). A more tortuous path is winding and compact and involves greater exploration of the area in a plane, while a less tortuous path is straighter (Doerr and Doerr 2004; Whittington et al. 2004). The analysis of these movement paths is one of the most powerful ways to quantify animal movement (Turchin 1998). Movement parameters can vary with the species, individual, environmental conditions, physical landscape and spatial scale considered (Turchin 1998). For example, when animals are restricted in a small search area or a good patch of resources, they decrease move lengths and increase turning angles (Bell 1990; Benhamou and Bovet 1989; Crist et al. 1992).

The study of animal movement can improve our understanding of species ecology, including inter- and intraspecific interactions and spatial distribution (Turchin 1998). For instance, knowledge of movement patterns can help identify spatial requirements of species, and allow the development of more effective strategies to conserve rare or endangered species (e.g. lynx—Ferreras 2001; moths—Betzholtz 2002). Modeling animal movement patterns also has application to the field of human health and prevention of disease spread; especially as human populations continue to expand, increasing contact with wild animals that can be important vectors of disease (Daszak et al. 2000).

Spatial scale, or the level of magnification at which an object or process is viewed, is a fundamental concept in movement analysis (Turner et al. 2001). Since underlying biological processes of animal movement patterns may be scale-dependent, the spatial scale at which observations are made may influence the patterns observed (Doerr and Doerr 2004; Rettie and McLoughlin 1999). For example, at a broad spatial scale a path may look very linear but at the scale of the animal's perception, it may be very tortuous. This is the result of scale-dependent activities and physical constraints (Bergman et al. 2000; Fritz et al. 2003; Johnson et al. 2002). Since movement has implications for foraging strategies, habitat selection, reproduction, and other social behaviours (Bascompte and Vilà 1997; Benhamou 2004; Doerr and Doerr 2004), it is most appropriate to study it based on the perception scale of the species (Nams 1996; With 1994a). The way or level at which an animal perceives its landscape, or its perceptual ability or range, will determine the spatial scale at which it moves from one area or patch in its habitat to another and will vary for different species and among different landscape types (Morris 1987; Olden et al. 2004; Zollner 2000; Zollner and Lima 1999; Zollner and Lima 1997). As an example, Zollner (2000) found that in a fragmented agricultural landscape gray squirrels had a perceptual range of 300-400 m while chipmunks had a perceptual range of only 120-180 m.

2.1.1 Home Range

The concept of home range has been defined and redefined many times over. Burt (1943) first defined home range as "that area traversed by an individual in its normal activities of food gathering, mating and caring for young." However, this definition has been challenged because the word "normal" is difficult to interpret and lacks a temporal component (Cavallini 1996b; White and

Garrott 1990). A less ambiguous definition of the home range of an animal is the limited area within which it can be found during a specified time period (Harris et al. 1990; Kernohan et al. 2001). A home range can be flexible, varying with season and overlapping with conspecifics (Harris et al. 1990). In contrast, a territory, a term commonly used interchangeably with home range, is defined as an area that is occupied by an individual or group to the exclusion of other animals of the same species (Begon et al. 1990; Burt 1943; Mech 1970). Animals may or may not be territorial, but will still have a home range. Quantifying an animal's home range size and shape allows researchers to gain information on foraging behaviour, habitat selection, and inter- and intraspecific interactions (Harris et al. 1990). Animals use the area within their home range with varying intensity, and most often there will be at least one part of it used with a much higher frequency. The term *core area* has been introduced in the literature, and refers to those areas within the home range where individuals are found with greater probability (Hodder et al. 1998; Kaufmann 1962). While home ranges of different animals have been found to overlap (e.g. Boitani et al. 1984; Kolb 1986; Lovari et al. 1994), overlap of the core areas does not commonly occur (Samuel et al. 1985). Thus, the identification of core areas is important in studying intraspecific interactions, as well as the animal's responses to the environment (Samuel et al. 1985).

A variety of methods have been developed to estimate home ranges including minimum convex polygon, probability ellipse, cluster analysis, harmonic mean, and kernel methods (see Harris et al. 1990 and/or Kernohan et al. 2001 for a review of these methods). With the exception of the minimum convex polygon, these methods are also useful for core area identification. While each method has disadvantages and advantages, the minimum convex polygon and kernels are currently the most widely used in home range estimation of animals (Kernohan et al. 2001). Therefore, brief introductions of these methods are provided below.

Minimum Convex Polygon.—The oldest and most widely used method for estimating home range is the minimum convex polygon (MCP) (Harris et al. 1990). The MCP estimates the home range of an animal by connecting the outermost locations and calculating the area of the resulting convex polygon (Fig. 2.2) (Mohr 1947; White and Garrott 1990). There are several advantages to using the MCP in home range analysis, including simplicity, flexibility of shape and ease of calculation (White and Garrott 1990). This method is particularly sensitive to outliers, points that may represent excursions not typical of everyday movements, extending beyond the true boundaries of the home range (Kernohan et al. 2001). An option to minimize outliers in the MCP is to use a polygon that uses only 90% or 95% of the data points (e.g. Cavallini 1996b; Harris et al. 1990; Woollard and Harris 1990). MCP is also sensitive to sample size and it has been suggested that for an accurate home range estimate, upwards of 100-300 locational data points are required (Kernohan et al. 2001; Seaman et al. 1999;). While the use of GPS collars can result in a large data set, obtaining this amount of data with VHF radio-tracking may not be possible

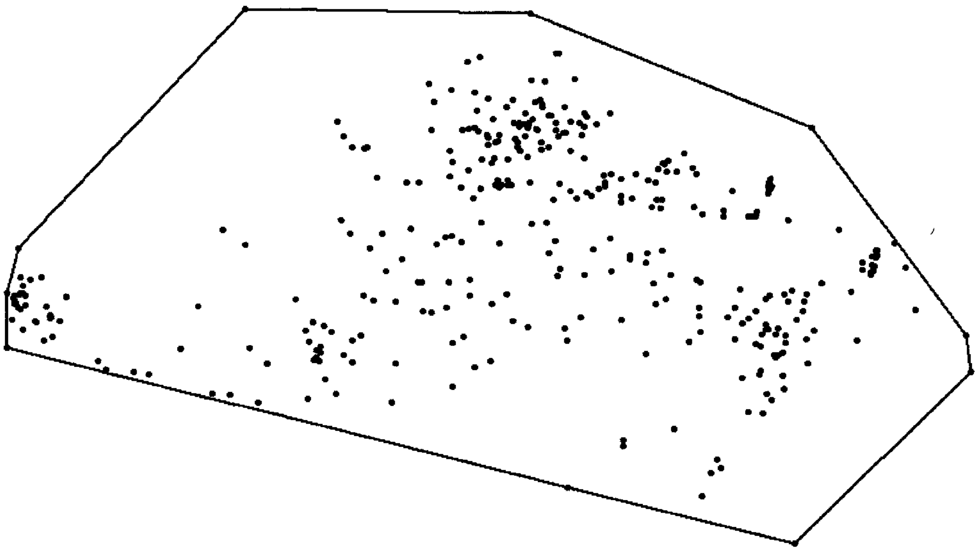

FIG. 2.2.—Example of a home range calculated using the 100% MCP method. Animal locations are represented by black circles. Created with ArcView GIS 3.3.

(Kernohan et al. 2001). Despite its limitations, it has been argued that the MCP must always be used to permit comparison with other studies due to historically high levels of reliance on this method (Harris et al. 1990; Kernohan et al. 2001).

Kernel Methods.—Using smoothed density estimates can allow for more robust comparisons of home-range use among animals or areas (Bowman and Azzalini 1997). Worton (1989) first applied kernel methods to estimate the utilization distribution (UD: the name given to the distribution of an animal's position in the plane) and the related home-range size. In contrast to the MCP, kernel density estimators (KDE) calculate the UD boundary based on the complete distribution of the animal's location points, rather than just the outermost points (Kernohan et al. 2001). This permits the exclusion of some outliers (Marzluff et al. 2001), and allows the identification of core areas of use (Samuel et al. 1985; Fig. 2.3). A contour of a specified percentage of the UD volume can be traced as the home range boundary.

The kernel method is based on placing a probability density function, called a kernel, over every location data point in the sample (Seaman and Powell 1996). The utilization estimate for each point is calculated by spatially summing the volume of all overlapping kernel values (Worton 1989). Therefore there will be a peak in the resulting utilization distribution in areas where there is high overlap of the kernels. Kernel methods smooth out locational data and the amount of smoothing is controlled by the choice of bandwidth (or smoothing parameter, *h*), of the kernel (Bowman and Azzalini 1997; Wand and Jones 1995). The bandwidth controls the width of the individual kernel that determines

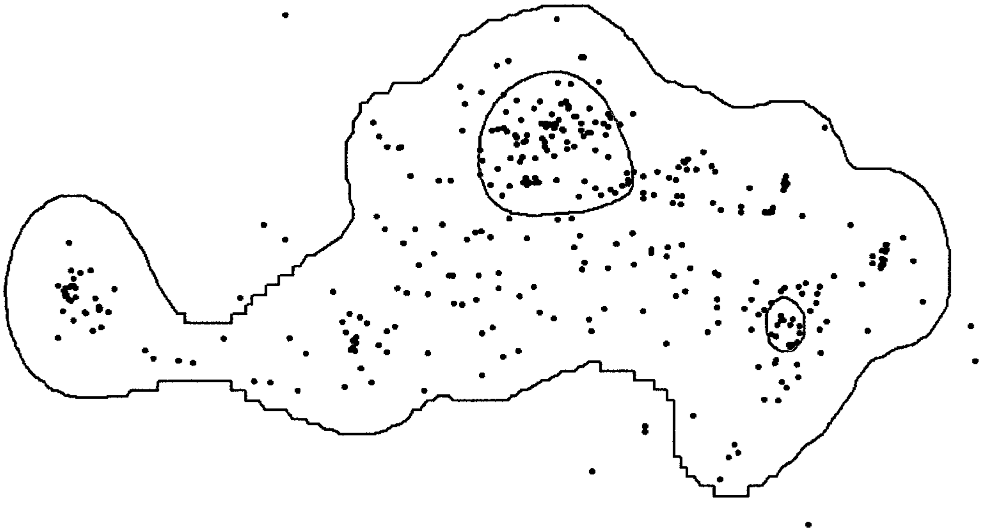

FIG. 2.3.—Estimation of the home range using the fixed-kernel technique. Animal locations are represented by black circles. The red outline represents the 95% contour (home range) and the green outline the 50% contour (core area). Created with ArcView v. 3.3.

the amount of smoothing of the data. If a small value of *h* is used, fine detail of the data will be observed while using a larger value of *h* will obscure all but the most prominent features (Kernohan et al. 2001; Rosenblatt 1971; Worton 1989) (Fig. 2.4). The bandwidth value therefore is critical and researchers must be cautious in their choice of an appropriate value (Kernohan et al. 2001).

Two widely used methods for bandwidth estimation are least squares cross-validation (LSCV) and normal optimal smoothing (Kernohan et al. 2001; Bowman and Azzalini 1997; Seaman and Powell 1996). The least squares method does not assume a particular underlying distribution (e.g. Gaussian) and calculates a bandwidth that minimizes the integrated squared error of the kernel, or the difference between the estimated density and the true density (Kernohan et al. 2001, Silverman 1986). Though the LSCV is currently the recommended bandwidth selection method (Seaman et al. 1999), it can bias toward small clusters of data and provide poor estimates for KDE on animal location data (Blundell et al. 2001; Bowman and Azzalini 1997; Hemson et al. 2005). As a result, the UD may be undersmoothed and highly variable (Kernohan et al. 2001). Normal estimation of bandwidth is a more conservative measure as it smoothes out the data to a much higher degree, minimizing the importance of smaller isolated patches of data compared to concentrated areas of use (Bowman and Azzalini 1997). Bandwidth selection using an 'ad hoc' method for a bivariate normal distribution has also been used for home range estimation (Seaman et al. 1998; Silverman 1986; Worton 1995).

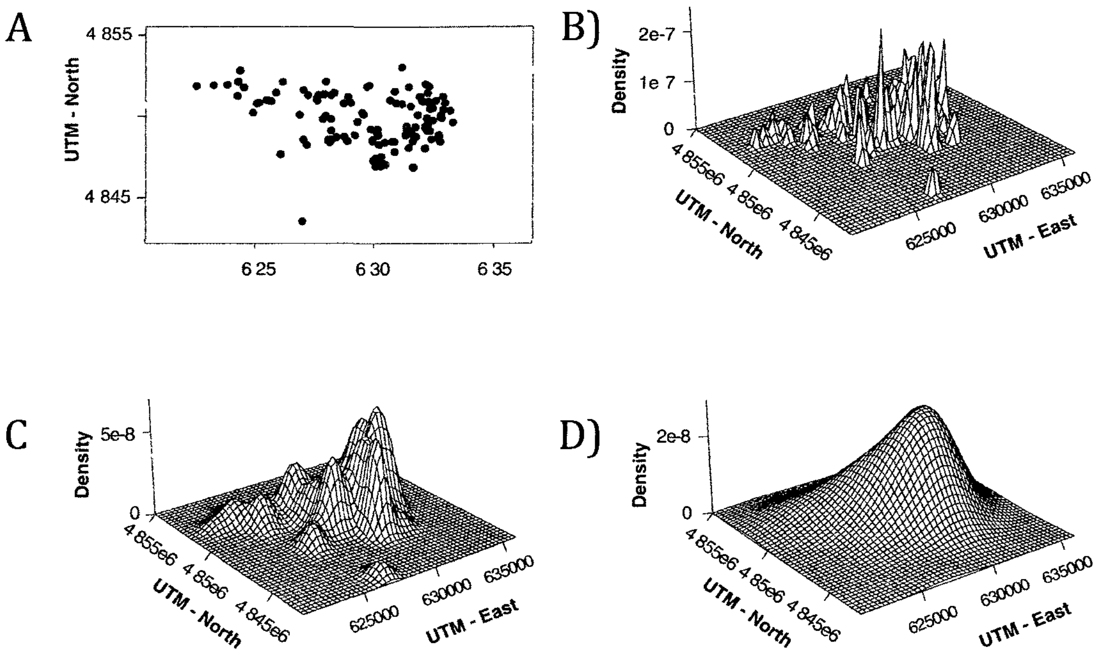

Fig. 2.4.—Illustration of the effect of different bandwidths on kernel UD estimates in home range analysis. Animal locations are represented as a utilization distribution (A), and are smoothed with different bandwidths (B) *h*=150, C) *h*=500, D) *h*=1500). Adapted from Kernohan et al. 2001.

Alternatively, smoothing values can be estimated based on the biology and behaviour of the animal (Bowman and Azzalini 1997). An animal moving less on average should have a lower smoothing factor (i.e. a smaller bandwidth) because it is more likely to be located close to the observed location. The appropriate bandwidth will be different for each species and is the most critical parameter when using kernel density estimation (Silverman 1986).

Estimation the home range using the kernel method can be accomplished using either fixed or adaptive kernels. The fixed kernel approach involves the use of the same bandwidth value over all data points (Worton 1989). In contrast, the adaptive kernel approach involves varying the bandwidth for each location. The local bandwidth is larger in areas with fewer observations than in areas with many observations (Kernohan et al. 2001; Seaman and Powell 1996).

2.1.2 Habitat Selection

Johnson (1980) defined habitat selection as the disproportionate use of habitat compared to its availability. It is presumed that animals use (or select) a habitat because it has some advantage to them, and avoid other habitats because of risk or lack of resources. Not all animals will select habitat in the same way and this allows them to coexist and occupy different ecological niches (Rosenzweig 1981). Levins (1968) suggested that there are generalist-type animals that use habitat in proportion to its abundance, and specialist-type animals that use some habitats more than expected. For certain purposes, it is beneficial to simplify the classification of animals into one category or the other, but most animals fit in the gray area between generalist and specialist animal types, neither choosing any and all habitats nor limited to only one specific type. The spatial distribution of habitats and resources (including prey) is the most important factor affecting how most animals select habitat (Arthur et al. 1996, Kennedy and Gray 1997; Manley et al. 2002). In a patchy environment, habitats will differ in their suitability so animals will move and select habitat differently than they would in a more homogenous landscape (Johnson et al. 1992). Density of conspecifics and/or competitors can also limit the selection and defense of habitats (Grant 1975; Owen 1972; Peek 1986; Stamps 1991).

Habitat selection, like movement, can be a spatially scale-dependent process. Animals may select habitat at a large spatial scale based on some appealing conditions, than locally based on more specific conditions (Fustec et al. 2001; Morris 1987; Wiens 1986). For example, an animal might select for forest, and within the forest, select for grassy clearings.The concept of home range is based fundamentally on selection of habitat at a broad spatial scale by animals for regular use (Fustec et al. 2001). The study of habitat selection allows us to understand individual and population requirements and distribution in a landscape, which can be useful for management practices (White and Garrott 1990). As mentioned previously, the perceived quality of habitat can be seen in changes of movement parameters such as tortuosity (e.g. Crist et al. 1992; Whittington et al. 2004). Thus habitat selection and use are closely linked with fine-scale patterns of movement in addition to large-scale distribution of animals.

Habitat use is most commonly measured by superimposing animal locations over maps of a geographical area of interest and counting how many observations are found in each general habitat type. Based on the availability of habitat types (the expected use) and the observed use, the selection (preference or avoidance) of the habitat by the animal can be calculated. Habitat selection of categorical data can be analyzed with preference indices (e.g. Strauss 1979), hypothesis testing (e.g. Aebischer et al. 1993; Johnson 1980; Neu et al. 1974; Pendleton et al. 1998), and regression approaches (e.g. Keating and Cherry 2004). There is no general consensus on the best overall statistical method to use, and they often report different results (McClean et al. 1998). However, McClean et al. (1998) found that a simple χ^2 goodness-of-fit test with simultaneous confidence intervals (sensu Neu et al. 1974) gave results most consistent with known requirements of young turkeys. Selection of areas based on specific landscape characteristics such as elevation can also be done using maps and observed locations or probability distributions (e.g. Mace et al. 1999).

There are some potential issues with habitat selection analyses. Aebischer et al. (1993) groups these into dependence of observations, dependence of habitat proportions, nonavailability of habitats, and differential selection by similar groups of animals. Dependence of observations can increase type 1 error, or a “false positive” where selection is detected but may not be real (Swihart and Slade 1985). Dependence of habitat proportions does not allow for absolute preference to be calculated since the avoidance of one habitat will mean that others have a higher chance of being preferred (Aebischer et al. 1993). Inclusion of habitats that are not really physically or biologically available to the animal will not represent true selection (Johnson 1980). Pooling selection information of individuals behaving differently in different landscapes may change the overall results and lead to erroneous conclusions (Aebischer et al. 1993). It is also important to note that although habitat selection is often considered a static characteristic, it will vary based on what an animal needs and is doing at a particular moment (Matthiopoulos 2003).

2.1.3 Models for Studying Animal Movement

Models of animal movement can allow the quantitative description, interpretation, and prediction of movement behaviours. Random walk models based on diffusion equations can be used to describe movement (Skellam 1951; Turchin 1998). Random, or diffusive, movement is the most basic of all types and has no bias, so movement is equally likely to occur in any direction with no memory of the previous position (Turchin 1998). This type of movement is what one would expect of ink particles diffusing in water or of a simple tumbling bacterium. However, it has been argued that it does not represent movement of more complex animals (e.g. mammals) due to a lack of bias to forward movement (Austin et al. 2004). The model for simple diffusion of a random agent of movement (or walker) in one dimension is as follows:

$$\partial u/\partial t = D\,\partial^2 u/\partial x^2 \qquad (1)$$

where $\partial u/\partial t$ = rate of change of position (partial derivative), u is the probability of an individual being found at location x, at time t, and D = a diffusion constant (Turchin 1998).

The inclusion of bias, or some factor that causes an animal to favour movement in a particular direction, is important when considering models of movement of animals. The incorporation of a bias term into equation (1) results in the Fokker-Planck model as follows (Turchin 1998; see Fig. 2.5):

$$\partial u/\partial t = -(\partial/\partial x)\,(ßu) + (\partial^2/\partial x^2)\,(\mu u) \qquad (2)$$

where $\partial u/\partial t$ = rate of change of position, ß = bias (proportional to the difference between the probability of moving left versus right), μ = motility (proportional to the probability of moving) (Turchin 1998). The bias here could be the result of either a directional bias such as forest edge acting as a cue to the animal (Schöne 1984), or of directional persistence such as a tendency to move east. This model assumes one-dimensional space, fixed move length, and uncorrelated moves (not dependent on previous moves) (Turchin 1998). This model is still simple, but does allow for directional bias and parameters that can vary in space and time, making it a more realistic model than simple diffusion.

The correlated random walk (CRW) model is the usually the most basic model used in description of search strategies of animals that show a degree of directional movement (e.g. Bergman et al. 2000; Bovet and Benhamou 1988; Mårell et al. 2002; Turchin 1996). Move lengths and turning angles are

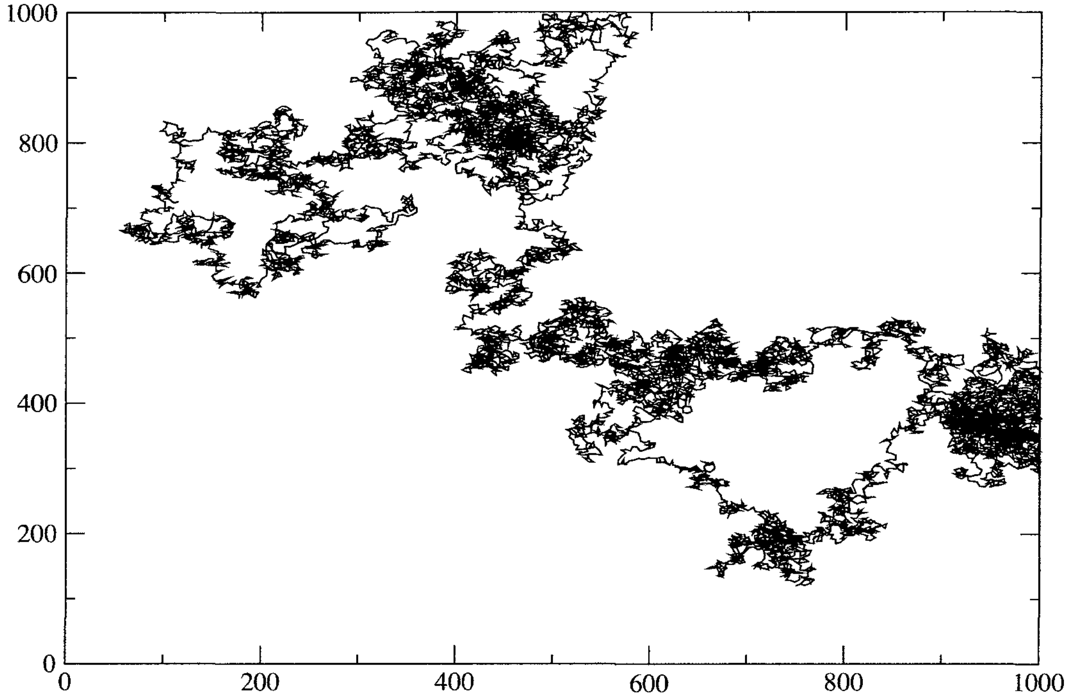

Fig. 2.5.—An example of a random walk movement path in a heterogeneous environment (XY axis). Plotted using Grace and created using a simulation from Chapter 4.

assumed non-autocorrelated, but there is directional persistence (Doerr and Doerr 2004; Fig. 2.6). The model for classic CRW in a homogenous landscape is given by the Telegraph equation (Goldstein 1951):

$$\partial^2 u/\partial t^2 + 2\partial u/T\partial t = v^2\ (\partial^2 u/\partial x^2) \tag{3}$$

where T = time of directional persistence (a higher value for straight, smooth paths), and v = speed of movement. One of the most important characteristics of the CRW model is its scale-dependence. At a small spatial scale, it appears linear, but at a large scale, broader view, it appears more random (Turchin 1996). In cases where the move direction is influenced not only by the previous direction but also by an absolute direction (external or directional bias), a biased correlated random walk occurs (Turchin 1998). The resulting path is even more directed and linear than that observed with a CRW (Turchin 1998).

Lévy walk (LW) results in paths with patches of small random moves separated by fewer longer moves (Viswanathan et al. 2000, see Fig. 2.7). Mean squared displacement (a classic measure of dispersal—Kareiva and Shigesada 1983; Okubu 1980; Skellam 1973) is not a linear function of time for LW (Ramos-Fernández et al. 2004), and is greater for the same period of time as other random walks (Weeks et al. 1995). This means that a Lévy walker is more likely to move forward to new sites in an environment of randomly distributed resources than to backtrack, as an animal moving with CRW or BRW might (Viswanathan et al. 1999). For this reason, LW is often used to describe efficient foraging of animals when resources are scarcely and randomly distributed (Viswanathan et al. 1999). LW has been observed in search

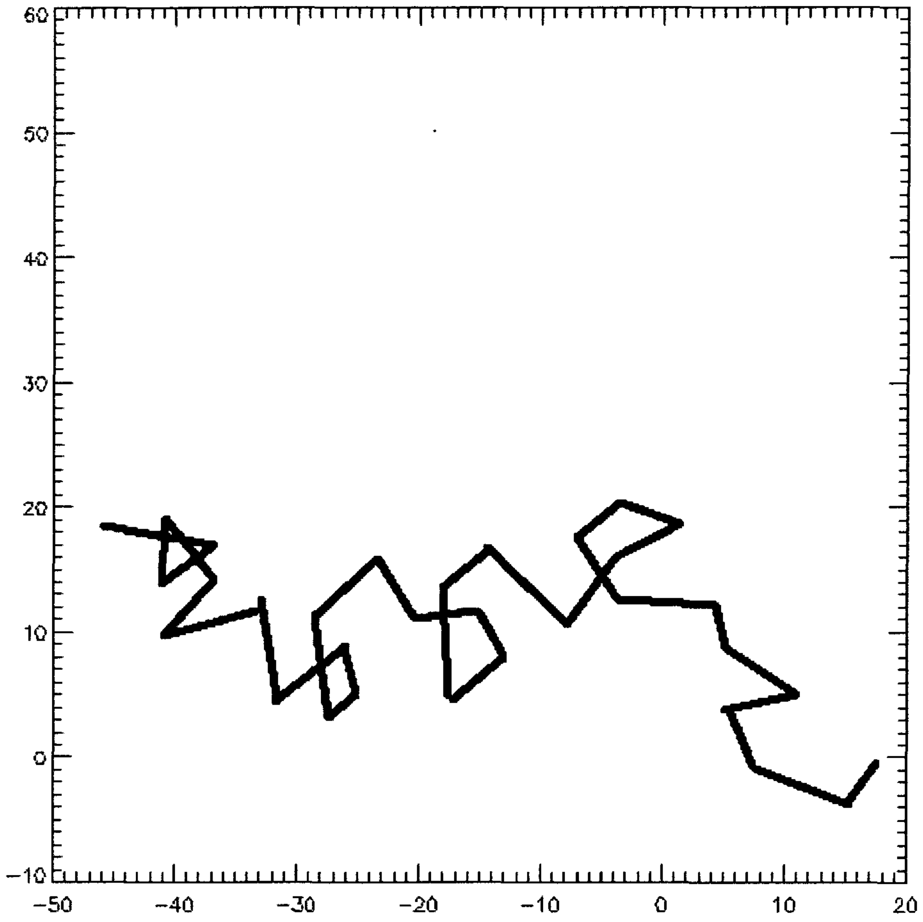

Fig. 2.6.—An example of a correlated random walk path (XY axis) (adapted from MacKenzie 2008).

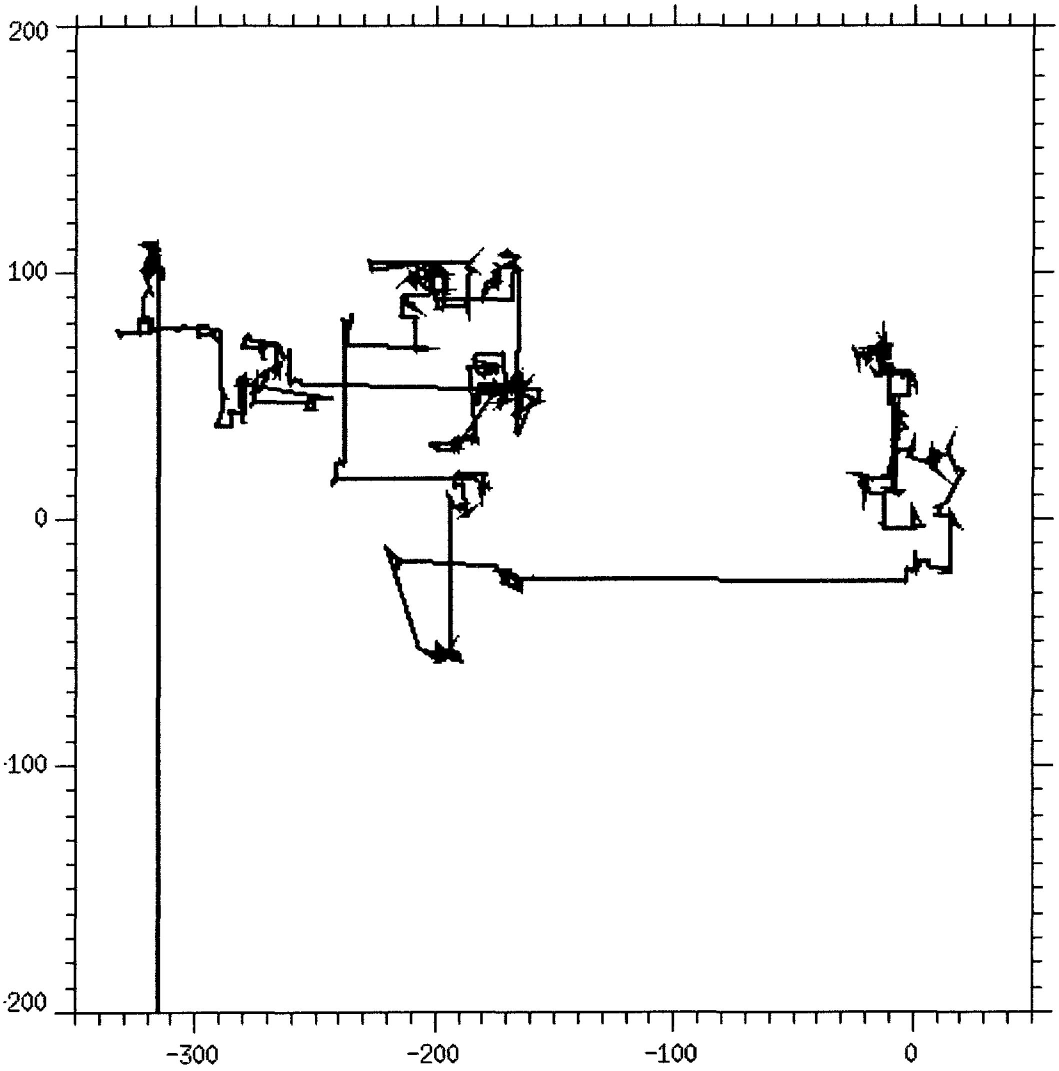

FIG. 2.7.—An example of Levy walk (XY axis) (adapted from MacKenzie 2008).

patterns of foraging jackals (Atkinson et al. 2002), spider monkeys (Ramos-Fernández et al. 2004), reindeer (Mårell et al. 2002), and wandering albatrosses (Viswanathan et al. 1996). Unlike CRW, LW has scale-independent properties, and thus appears to have the same patterns over small and large spatial scales (Shlesinger et al. 1993).

Animal movement patterns vary between species and even individuals, so no one model will fit them all. As a result, the construction of very specific models, and the use of computer-based simulations to artificially obtain movement data have become increasingly commonplace. Computer simulations are programs can be used to simulate animal movement through artificial landscapes based on a basic theoretical or customized model of movement (e.g. Carter and Finn 1999; Gardner et al. 1989; Zollner and Lima 1999). Simulations can help to identify underlying mechanisms of movement and to make predictions. For example, Carter and Finn (1999) used an individual-based computer simulation to look at the effects of landscape pattern on movement and to test a model of red fox foraging and nest predation. In this way, simulations can complement field data and help answer hypotheses that may be difficult to test with field experiments. Random walk models are most often employed, and CRW models provide more realistic predictions (e.g. Byers 2001; Schippers et al. 1996; Schumaker 1996; Zollner and Lima 1999). Often movement is tested with more than one model, such as both correlated random and levy walk models to see which has a better fit (e.g. Bartumeus et al. 2005; Mårell et al 2002).

2.2 FIELD TECHNIQUES

2.2.1 Telemetry

Telemetry is a system of technologies used to determine an animal's location and potentially other information, such as status, from a remote location (Priede 1992). Radio-tracking is the classical way to use telemetry to obtain both spatial and temporal information on animals, especially wide-ranging or elusive species (Kernohan et al. 2001). There are two distinct types of radio-tracking: continuous and discontinuous. Continuous radio-tracking involves estimating an animal's position at short and regular intervals. The timing of these intervals depends on the species being studied and the research goals. For example, in the case of the red fox, the interval is typically the time required for an animal to traverse its entire home range (about 15 minutes) (Cavallini and Lovari 1994; Lucherini and Lovari 1996; Macdonald et al. 1999). The use of continuous radio-tracking can provide data that are useful in studying movement patterns, habitat selection and interactions between animals (if information for individuals is gathered concurrently) (Harris et al. 1990). Discontinuous radio-tracking involves locating the animal at either discrete or random time intervals (e.g. once or twice per day or per week during the study period). This type of tracking has typically been used for the estimation of home-range size (Harris et al. 1990). It also allows for the concurrent study of a larger number of animals when a study has limited resources (Harris et al. 1990).

The standard field technique used for to obtain data used in estimating home-range size and centers of activity of larger mammals is very high frequency (VHF) radio-tracking (frequencies within 30-300 MHz). A radio-collar or radio-tag attached to an animal emits short pulses of specified VHF. A researcher picks up these pulses with an aerial and a receiver unit that in turn emits louder signals with proximity to the transmitter. There are two ways to track animals using VHF radio-tracking. The first method involves “homing in” whereby the researcher uses the VHF signal to physically locate the animal (Mech 1983). As the signal becomes stronger, the researcher can manipulate the receiver and aerial to gain a more accurate bearing until the animal can be visually located (White and Garrott 1990). In studies of animal behaviour, this type of tracking has the potential to greatly bias the results, as most animals will behave very differently in the presence of humans (Schwartz and Arthur 1999; White and Garrott 1990). However, for animals that can be observed from quite a distance (e.g. large animals or those that are easily visible in open habitats), this type of tracking may provide valuable information. Homing in can also allow the researcher to visually locate areas of important use such as dens or food caches (Gese 2001). Alternatively, VHF radio-tracking can be used to locate animals through the collection of directional bearings from two or more known locations (White and Garrott 1990). Using biangulation (in the case of two fixes) or triangulation (for three), the intersection of these bearings gives an estimated location for the animal (Fig. 2.8). Triangulation can be done by hand using topographical maps (Bowen 1982), or with computer software (reviewed in White and Garrott 1990 and Larson 2001). The manner in which directional bearings are obtained (point locations or sequential locations) may introduce

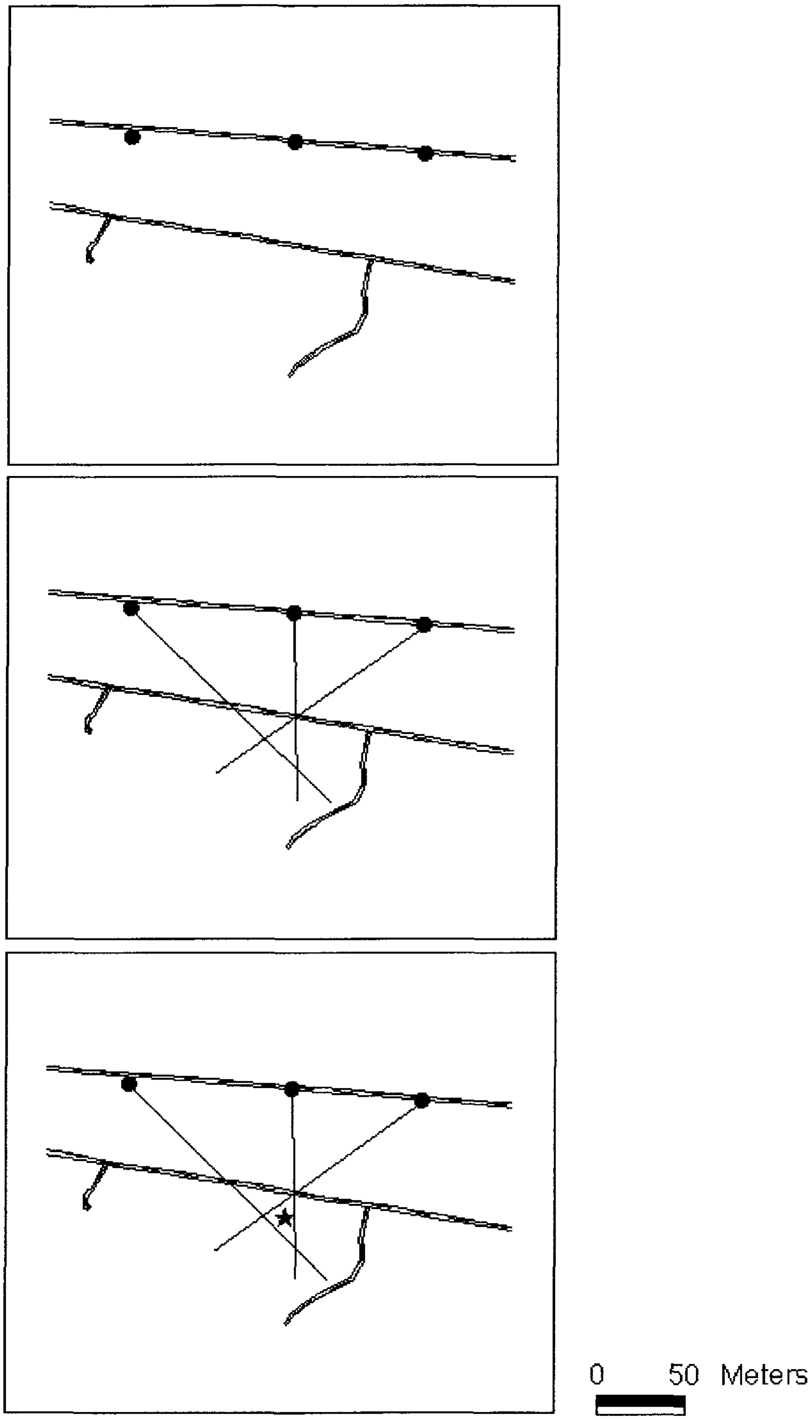

FIG. 2.8.—Diagram illustrating triangulation using three bearings. A) Locations where signals were obtained (as indicated by circles). B) Bearing estimates from each location (as indicated by lines). C) Estimated location of the animal (as indicated by star). Created using ArcView GIS 3.3.

error into the triangulation process. In the case of point locations, fixes are taken by several people (each with an error) at predetermined synchronized times. On the other hand, sequential locations are taken by one researcher who attempts to obtain fixes from a variety of locations around the animal (Schmutz and White 1990). For terrestrial animals, this is typically done by driving to locations in close proximity and taking directional bearings within a limited time window. Bearings are usually obtained within 15 minutes of each other (for mobile medium-sized animals) to reduce error due to animal movement (Chamberlain et al. 2003; Chamberlain and Leopold 2000), and within an angle of 45 and 135 degrees of each other to reduce location error (Springer 1979). This method can become flawed if the animal is moving to a new location at each bearing, and the result would be an average location of the animal (White and Garrott 1990). The only way to eliminate the error introduced by a moving animal is to take simultaneous bearings (Schmutz and White 1990).

Other errors associated with triangulation can be classified into those relating to variance around the bearing (error arc), to distance between the transmitter and receiver, and to the intersection of the triangulated bearings (Rogers et al. 1996; Saltz 1994). Although the importance of estimating these errors is recognized, many researchers do not quantify the errors by repeating measurements and calculating variation in bearings. White and Garrott (1990) provide comprehensive guidelines for the implementation of such a system to test the accuracy of triangulation. They suggest that a researcher place transmitters at various locations in different habitat types, while another researcher attempt to locate them (White and Garrott 1990). Bearing error can then be estimated from this experiment and used in the triangulation process to quantify the error.

Global positioning system (GPS) technology is changing the way animals are located with telemetry. GPS-collars and tags can estimate animal location by using signals from satellites to give latitude and longitude (Rodgers 2001). GPS-collars can take frequent locational fixes, store data on board, and even automatically detach from the animal at a specified time (Rodgers 2001). However, this technology remains relatively expensive and has reduced battery life in comparison to traditional VHF radio-transmitters (Kenward 2001). Due to the higher locating power of GPS technology, there is a need for more components, including extra battery, and the increased weight has limited their use in smaller animals (Markov and Markov 2005; Rodgers 2001). Electronic detachment of collars, though beneficial over recapture required with many VHF collars, does not always function properly (Merrill et al. 1998).

Autocorrelation (spatial and temporal self-dependence of data; often difficult to distinguish) is an issue of concern with respect to telemetry data because most statistical analyses assume independent observations. When successive observations are dependent, they are considered to be autocorrelated. Swihart and Slade (1985) argue that there must be a minimum amount of time between the acquisitions of locational data to eliminate autocorrelation. However, recent research has suggested that eliminating autocorrelation reduces the biological relevance of home-range estimates (De

Solla et al. 1999; Millspaugh and Marzluff 2001; Otis and White 1999). For example, Reynolds and Laundre (1990) determined the sampling time interval required for spatially-independent fixes in their study on coyotes. However, they found that using statistically independent data resulted in the underestimation of home-range size and distance traveled. Other researchers have evaluated the time to independence of successive locations by a biological rather than statistical method (e.g. Cavallini and Lovari 1994; Lucherini and Lovari 1996; Macdonald et al. 1999). For example, Lucherini and Lovari (1996) determined the time to biological independence of observations (time for animal to cross its home range) to be 15 minutes for red foxes. However, if looking at fine-scale movement patterns with detailed movement paths, a degree of autocorrelation between moves is expected and acceptable. Correlated random walk models incorporate a correlation in move directions (Doerr and Doerr 2004; Kareiva and Shigesada 1983), and if autocorrelation was removed, detail in animal behaviour at a fine-scale would be lost and models could lose predictive ability.

Location error and bias caused by collaring and tracking study animals can also affect resulting home-range estimates and habitat selection data and vary depending on the type of telemetry used and specific experimental design (reviewed in White and Garrott 1990). It is important to note that statistical significance is not always an appropriate measure of biological significance in telemetry studies, and some ecological questions can still be addressed from statistically insignificant trends (Garton et al. 2001). Though it is not an exact art, telemetry allows us to gather location information of animals which, in conjunction with geographic information systems (GIS), can be used to gain distribution data for use in monitoring, conserving, and managing animals.

Telemetry is a technology that is widely used to study animals directly, but there are some limitations of direct studies. Mainly, they are invasive, and involve the capture and modification of an animal. In some cases, the application of a tracking device alters the natural behaviour such as foraging (e.g. Hamel et al. 2004; Ross and McCormick 1981). As well, the presence of people in close proximity during VHF homing can bias the movements of the animals to either avoid or come into closer contact with the researcher (Schwartz and Arthur 1999; White and Garrott 1990). For these reasons, and where live-trapping and tracking are difficult, indirect methods of study can be a more appropriate method, and sometimes the only one, for studying movement depending on the species.

2.2.2 Snow-tracking

An indirect method of studying animal movement is the tracking of snow trails, during which information is recorded at regular intervals. This method is only applicable in the winter, and then only where is sufficient snowfall and the weather conditions allow for tracking in a timely fashion after snowfall. With snow-tracking, we can reconstruct movement paths and gather information on habitat use (Ciucci et al. 2003; Edwards et al. 2001; Silva et al. 2009). Because it is indirect, the behaviour of the animal is not altered by direct tracking, and because it results in exact locations (as opposed to triangulations), the data is more accurate and detailed. Detailed current landscape characteristics (e.g. land cover, terrain specifics) can also be recorded along the movement paths. These data are particularly valuable because surveys used to create GIS layers may have been done many years ago and at too large a spatial scale. Since snow-tracking can only be performed in the winter, the movement data obtained will only be valid for generalization during that season. As with most indirect methods of study, data cannot be compared on a temporal or individual level as it is not known exactly when the animal was there, nor the sex or age of the individual.

2.3 THE AFRICAN WILD DOG

2.3.1 Taxonomy, Description, and Distribution

The African wild dog (herein 'wild dog') belongs to class Mammalia, order Carnivora, family Canidae, and subfamily Caninae. The wild dog was originally classified as *Hyaena picta* (Temminck 1820), with *picta*, painted, referring to the unique blotched coat of the animals. It was later reclassified as *Lycaon pictus*, the only member of the genus *Lycaon* diverged from *Canis* but this taxonomic position is still uncertain (Wayne et al. 1997). The wild dog is also known as the painted hunting dog or cape hunting dog. Wild dogs have large rounded ears, very long legs and bushy tails with white tips, and every individual has a unique patchy mix of black, brown, yellow, and white fur. They are 0.75 m high at the shoulder and weigh 20-30 kg (Mills and Hes 1997), averaging 27 kg over both sexes (Skinner and Chimimba 2005). This makes the wild dog the smallest of the large African carnivores (Creel and Creel 2002). Wild dogs have a short life span, averaging 10 years in captivity (Frantzen et al. 2001), and a maximum of only 6-8 years in the wild (Mills and Hes 1997; Somers et al. 2008).

Historically, the wild dog was found over most of sub-Saharan Africa in all habitats except rainforest and desert (Skinner and Chimimba 2005). However, the species has faced dramatic abundance fluctuations resulting in steep declines and, in some cases, extirpations from vast areas (Fig. 2.9). The wild dog was originally classified as vulnerable in 1986 by the International Union for Conservation of Nature (IUCN) (IUCN 2006). In 1990, the wild dog was classified as endangered by the IUCN and it has retained that status since then (IUCN 2006; McNutt et al. 2008). In South Africa, the wild dog is protected provincially (Friedmann and Daly 2004). Currently, there are currently only 3,000 - 5,500 animals left in an estimated 600-1,000 packs in Africa, about half of which are found in southern Africa (Fanshawe et al. 1997). The largest remaining populations are in northeastern Namibia, northern Botswana, western Zimbabwe, Zambezi Valley, and Kruger National Park (South Africa) (Mills and Hes 1997; Skinner and Chimimba 2005). Based on sightings, it is estimated there are about 33 packs remaining in South Africa (Friedmann and Daly 2004). Two of these packs occur in Hluhluwe-Umfolozi Park, 25 in Kruger National Park (KNP), 2 in Madikwe Game Reserve, 2 in Pilanesberg National Park, and 2 in Venetia-Limpopo Nature Reserve (Friedmann and Daly 2004). In KNP, photographic surveys are conducted every 5 years and 5 packs are monitored

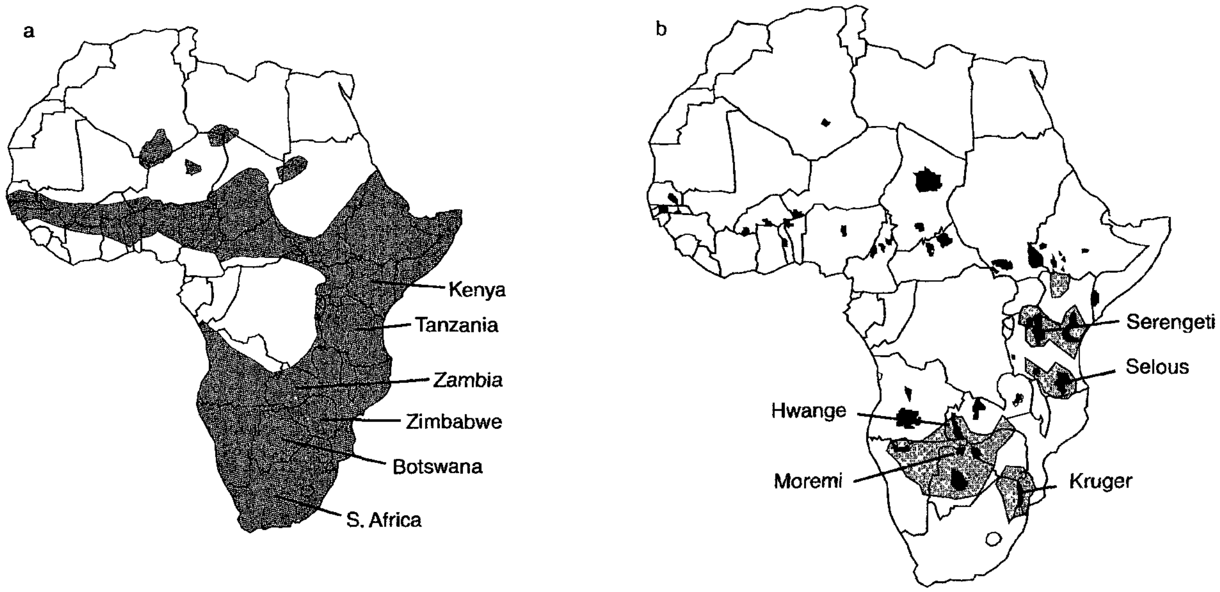

FIG. 2.9.—Map of wild dog distribution. (a) Historical range of wild dogs with countries that currently have larger populations indicated, (b) Current range of wild dogs based on sightings in the past 15 years. Modified from Creel and Creel 1998 (data from Fanshawe et al. 1991, Woodroffe et al. 1997, unpublished survey by L. Frame and J. Fanshawe, and reports from Tanzania).

on a monthly basis, while at the other 4 locations, all animals are monitored weekly (Friedmann and Daly 2004). The reason for such intensive monitoring is a tendency for population numbers to drop rapidly, even in KNP, where the population is considered viable (Fanshawe et al. 1991). In KNP in 1989 there were an estimated 30 packs with 357 animals (Maddock and Mills 1993). In 1995, the number rose to 434 animals, before plummeting to only 177 in 2000 (Davies 2000).

2.3.2. Population Dynamics and Behaviour

Wild dogs are considered the most social of the canids and the pack forms the basic social unit (Fox 1975). There is very little aggression or fighting within the pack or even between packs due to social appeasement rituals, such as submissive posture and lip-licking (Estes and Goddard 1967). Packs size can range from a pair up to 50 wild dogs (Mills and Hes 1997). Pack size, like populations size, can vary over time; in Kruger National Park it has varied from averages of 13.7 (Maddock and Mills 1993) to 7.1 wild dogs per pack (Davies 2000).

Wild dogs reach reproductive age at about two years (Frantzen et al. 2001) and have litters that average 10-11, but that can be as large as 21 pups (Fuller et al. 1992). As a result of such large litters, wild dogs are obligate cooperative breeders. Although typically only the alpha male and female mate (Van Heerden and Kuhn 1985), the other pack members are needed to help in pup raising (Courchamp et al. 2002; Malcolm and Marten 1982). The breeding (including mating and pup-rearing) season varies slightly by location, but generally occurs in the dry season (March-September) (Mills and Hes 1997; Pienaar 1963; Reich 1981). Dens can be created as holes in the ground or from old aardvark burrows or old warthog or hyaena dens (Skinner and Chimimba 2005). Gestation is approximately 72 days and there is usually one litter per year (Skinner and Chimimba 2005). Denning occurs for about 13 weeks (Mills and Hes 1997), although weaning from milk begins at only two weeks when other pack members begin to regurgitate food for the begging pups (Skinner and Chimimba 2005). At about a year and a half of age, same-sex groups leave their natal packs, dispersing up to 250 km away to find unrelated groups of the opposite sex to bond with to form a new pack (Frame and Frame 1976; Girman et al. 1997; Skinner and Chimimba 2005). Because of this innate inbreeding-avoidance behaviour, wild-dog genetic variability is high, although inbreeding is still a risk in one-pack populations (Girman et al. 1997, McNutt 1996).

In addition to breeding success, wild dog sociality and cooperation have also been linked to their hunting success (Creel 1997; Creel and Creel 1996; Creel and Creel 1995; Scheel and Packer 1991), and defense of kills (Fanshawe and Fitzgibbon 1993). Wild dogs have a diversity of prey species that they consume at different rates depending on location and availability. Most studies consistently show that impala (*Aepyceros melampus*) is one of the most important prey species in terms of biomass consumed (Fuller and Kat 1990), ease of kill (especially in smaller packs--Creel and Creel 2002), and percentage of total kills (Childes 1988). In Hluhluwe-Umfolozi Park (South

Africa), the preferred prey of wild dogs (in order of decreasing percent biomass consumed) are nyala (*Tragelaphus angasi*), impala, wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus ellipsiprymnus*), reedbuck (*Redunca arundinum*), kudu (*Tragelaphus strepsiceros*), red duiker (*Cephalophus natalensis*), and grey duiker (*Sylvicapra grimmia*) (Kruger et al. 1999). Many of these species are also favored prey of the lion (*Panthera leo*) and of the spotted hyena (*Crocuta crocuta*), common competitors of the wild dog (Creel and Creel 1996). Wild dogs can hunt cooperatively in open areas by sight, and individually (with sharing of kills) in wooded areas (Skinner and Chimimba 2005). Wild dog hunting is successful up to 85% of the time, with higher success in larger packs (Skinner and Chimimba 2005).

Wild dogs are found at very low densities over their range (e.g. Mills and Biggs 1993; Schaller 1972), which is unexpected for a small carnivore (Peters and Raelson 1984). Fuller et al. (1992) show that even where wild dogs are well protected, they have a density of only 2-35 per 1,000 km^2. In parks with a large portion of open woodland, the species averages 17-20 adults per 1,000 km^2 (Fuller et al. 1992; Maddock and Mills 1993). For instance, in KNP where there is a viable population, the density is 16.7 per 1,000 km^2 (Maddock and Mills 1993). Creel and Creel (1996) found that the density of wild dogs is negatively correlated with competition intensity from both hyaenas and lions. Mills and Gorman (1997) found that wild dogs in KNP did not always favour habitats that were preferred by prey like impala, but instead were found more frequently in areas avoided by competitors like lions and hyenas. Hyenas steal food from wild dogs in open areas, reducing their intake (Fanshawe and Fitzgibbon 1993). This loss is significant and costly to the wild dogs since hunting costs so much energy (Gorman et al. 1998). Thus, it should not be a surprise that wild dogs often prefer more closed habitats, such as open areas with understory growth, or bushveld (e.g. Andreka 1996; Creel and Creel 2002; Mills and Gorman 1997). Lions compete for prey as well, but more importantly they prey on wild dogs (Van Heerden et al. 1995). In a study of 57 deaths in KNP, 33% were caused by lions (Van Heerden et al. 1995).

Home range size of wild dogs (as a pack) will depend on the metabolic needs of its pack members (Gittleman and Harvey 1982), prey availability and seasonal movements (Frame et al. 1979; Malcolm and Van Lawick 1975) and physical constraints like reserve size (Woodroffe and Ginsberg 1998). Pack home ranges can overlap, although the members themselves of different packs rarely meet (Mills and Gorman 1997). Home-range size of wild dogs has been shown to vary from only 242 km2 (Andreka et al. 1999) up to 2,000 km2 (Frame et al. 1979). Home range size is typically reduced during denning when caring for pups takes priority (Skinner and Chimimba 2005). In KNP, home range during denning was 80 km^2 compared to 885 km^2 outside of the denning period (Gorman et al. 1992), and could get up to 1,110 km^2 outside of the breeding season (Fuller et al. 1992).

2.3.3 Other Threats and Conservation Efforts

Wild dogs are in serious decline due to a vast array of natural and anthropogenic factors. Some of the major factors leading up to its current endangered status are direct competition with other carnivores (Creel and Creel 1996; Scheepers and Venzke 1995), road casualties, and direct persecution by people (Bere 1955). Among the major current factors affecting wild dog persistence are its low density, potential inbreeding in small isolated populations and subsequent loss of genetic diversity, environmental and disease-related catastrophes, and habitat and population fragmentation (Woodroffe and Ginsberg 1997). Although many of these risk factors are found in nature, anthropogenic persecution and the loss and alteration of habitats play a major role in wild dog mortality, imposing limits on the persistence of packs and subpopulations (Woodroffe and Ginsberg 1997). Direct persecution now occurs only in private areas, where wild dogs have an undeserved bad reputation for preying on livestock and are persecuted directly by ranchers (Rasmussen 1999; Lindsey et al. 2005b; Woodroffe et al. 2005).

Despite this, it appears that even indirect anthropogenic activities are still a threat to wild dogs. Using mortality data from a number of sites where wild dogs were studied using telemetry, the anthropogenic extinction risks for the species were identified as road accidents, snaring, and shooting (Woodroffe et al. 2007). In that same study, up to 68% of mortality was anthropogenic in cause (Woodroffe et al. 2007). Anthropogenic activities should only truly threaten a species if wild dogs would have continued to persist without them, in spite of natural threats, but Woodroffe et al. (2007) found an additive effect, emphasizing that people are a true threat to the species. It is perhaps because of human-related threats to the wild dog that an estimated 3/5 of the remaining wild dogs in all of Africa are found in protected areas (Fanshawe et al. 1991). Some carnivores in areas with high negative human impact remain in higher numbers but this is not the case with the wild dog. To illustrate, snaring was a major issue for spotted hyenas in the Serengeti National Park (Hofer et al. 1993); however their numbers remained much higher than those of wild dogs for a long period of time (Creel and Creel 1996).

In South Africa, there is a single viable population of wild dogs that inhabits KNP (Fanshawe et al. 1991). According to Lindsey et al. (2005a), this is also the only area in South Africa that can support another viable population in its entirety. However, in the interest of maintaining wild dogs in a diversity of natural locations and increasing genetic diversity, reintroductions are being conducted into smaller fenced game reserves, so that they might be managed as parts of a larger population (Ezemvelo KZN Wildlife 2007; Lindsey et al. 2004; WAG 2005). This is classically known as a metapopulation, in which subpopulations are separated geographically but are connected by dispersing individuals (sensu Levins 1970; Lines 2006; Wells and Richmond 1995).

Reintroductions (introduction of individuals to an area where they previously existed) and translocations (movement of individuals to another area) of wild dogs are costly, but without them it is probable the species would soon be extinct (Lindsey et al. 2005a; Lines 2006). Funds for wild dog conservation often come from ecotourism and associated education initiatives on public and private game reserves (Lindsey et al. 2005c). Some extra measures to ensure ecological success of these management operations include moving animals to areas with lower densities of competitors (Creel and Creel 1996) and sufficient food and other resources (Lindsey et al. 2004), as well as bonding dogs from different areas into a single pack gradually over time (Gusset et al. 2006; McCreery 2000). In addition to human intervention in conservation, sometimes nature restores the balance of species. Wild dogs wander widely and as a result sometimes wind up in areas where they have been extirpated for some time (Skinner and Chimimba 2005). For example, wild dogs have recently returned to the Serengeti National Park (Tanzania) since their extirpation in the 1990s (Wildlife Direct: http://baraza.wildlifedirect.org/2010/02/08/serengeti-first-sighting-of-wild-dogs-in-20-years/).

2.4. THE RED FOX

2.4.1. Taxonomy, Description, and Distribution

The red fox, *Vulpes vulpes* (L., 1978), herein also referred to as 'fox,' belongs to the class Mammalia, order Carnivora, and family Canidae. It is the most widely distributed member of Carnivora (Fig. 2.10) (Macdonald and Reynolds 2004). The fox is a medium-sized mammal, the largest in its genus, and weighs 3-14 kg (Macdonald and Reynolds 2004). The fox typically has a red coat with white on the neck and underbelly, black legs and feet and a white

Fig. 2.10.—Map of native red fox range (shown in red). Australia and New Zealand are also populated but by entirely non-native subspecies. (http://www.iucnredlist.org/apps/redlist/details/23062/0)

tip on the tail. The morphological characteristics, such as weight, measurements, and fur color can vary geographically. As an example, foxes in North America are lighter and lankier than elsewhere (Macdonald and Reynolds 2004). "Silver" foxes, with black fur with silver tips, as well as "cross" foxes, with grey-brown fur and black across the shoulders and down the back, are both color variations of the red fox (Johnson and Hersteinsson 1993). There are many subspecies of the red fox (see Lariviere and Pasitschniak-Arts 1996), but their ecological significance is uncertain (Macdonald and Reynolds 2004). European subspecies of red fox were introduced to North America in the 17th century and to Australia in the 19th century (Macdonald and Reynolds 2004).

2.4.2. Population Dynamics and Behaviour

The social system of the fox is difficult to define as there is a lot of variation (Cavallini 1996a; Doncaster and Macdonald 1991; Macdonald 1981; Voigt and Macdonald 1984). The basic social unit is either a male-female pair or a group, with young of the year (Cavallini 1996a; Macdonald 1981; Preston 1975). Forming a group may alert members to prime foraging areas and increase success in pup-rearing (Poulle et al. 1994). Despite being found in groups, foxes are solitary foragers for the most part (Doncaster and Macdonald 1992). Foraging and reproductive success are also important factors behind the formation of groups in other social carnivores (e.g. African wild dog—Malcolm and Marten 1982). Intra-group encounters are mainly non-aggressive and occur frequently (Poulle et al. 1994; White and Harris 1994). Inter-group interactions rarely occur and are mainly aggressive, occurring between males during breeding season (White and Harris 1994). Territoriality, or the exclusion of conspecifics from an area (Fretwell and Lucas 1969), between groups is more likely to occur in areas where food resources are restricted to few rich patches (Macdonald 1987).

The mating pair has one litter in early spring and pups disperse in their first year (Macdonald and Reynolds 2004; Storm et al. 1976). Foxes can occasionally cooperate in raising young, with non-breeding females (helpers) aiding in parental care (Adkins and Stott 1998; Cavallini 1996a; Macdonald 1979; Vergara 2000; von Schantz 1984). In some cases, barren or lactating vixens feed the young of dominant females while non-breeding females may adopt the young on the death of the biological mother (Cavallini 1996a). In cases where more than one vixen bred within a territory, communal denning and nursing are sometimes observed (Macdonald 1979; Voigt and Macdonald 1984).

The red fox is often considered a generalist (an animal that depends on a wide range of environmental resources—sensu Caroll 1985) due to its ability to adapt to a variety of changing environments. Foxes can occur in forest, tundra, agricultural land, desert, and urban areas (Doncaster and Macdonald 1991; Hersteinsson and Macdonald 1992; Macdonald et al. 1999). They are more abundant in heterogeneous, fragmented landscapes (Ables 1975, Lloyd 1975), and tend to select mixed or shrub cover areas over continuous forest or open areas (Catling and Burt 1995; Jones and Theberge 1982, Lloyd 1980;

Macdonald and Reynolds 2004). In these mixed mosaic habitats, there is a greater amount of "edge" than in continuous tracts of one habitat type, and foxes prefer to use these edges, as well as railway corridors and roads for traveling between habitats (Adkins and Stott 1998). Denning occurs in areas with fewer disturbances while resting usually occurs in areas with densest cover (Cavallini and Lovari 1994). Foraging activities may take place in a wide variety of habitats depending on the availability of food (Saunders et al. 1997). Foxes can also be established in urban and agricultural areas (Macdonald and Reynolds 2004).

The home range size of the red fox depends largely on the habitat type and population density. For example, foxes in the rural suburbs of Oxfordshire (UK) have a home range of only 0.1 km^2 while in rural farmland in Ontario (Canada), they have a home range of 20 km^2 (Voigt and Macdonald 1984). A literature review by Trewhella et al. (1988) revealed that at higher population densities, foxes tend to have smaller home ranges. The home range location and size of foxes can also vary with population structure, reproduction, and trophic changes (Cavallini 1996a, b). For example, after the death of a neighbour, foxes can move into previously occupied areas (Cavallini 1996a). Many studies have found overlap in red fox home ranges, indicating a lack of territoriality (Cavallini 1996b; Lovari et al. 1994; Poulle et al. 1994; Macdonald et al. 1999; Voigt and Macdonald 1984). However, there is usually no overlap in core areas (Poulle et al. 1994; Woollard and Harris 1990) that may represent the true territories of foxes. Generally, the red fox is a nocturnal animal, with periods of activity similar to those of its available prey (Ables 1969; Doncaster and Macdonald 1997; Lovari et al. 1994). Male foxes have been found to travel nearly twice as far as females during a 24-hour period (Servin et al. 1991). This difference is most likely related to females spending more time near dens caring for pups, while males are engaged in territory defense and management (Doncaster and Macdonald 1997). During the winter, there are more hours of activity during the day for both sexes than in other seasons (Ables 1969; Doncaster and Macdonald 1997). Timing of activity can also be limited by human activities (Doncaster and Macdonald 1997).

The red fox is an omnivore, incorporating invertebrates, mammals, birds, fruit, scavenged meat and anthropogenic foods into its diet (Macdonald and Reynolds 2004). Foxes frequently cache away extra food and return for it later (Macdonald 1976, 1977). Because of the similarities between fox diet and that of other canids such as the coyote (*Canis latrans*), interference competition can occur where those species coexist (Macdonald and Reynolds 2004). As a result, foxes usually establish territories outside those of coyotes (Harrison et al. 1989; Sargeant et al. 1987) and avoid areas preferred by coyotes (Dekker 1989; Van Etten et al. 2007; Voigt and Earle 1983).

2.4.3. Interactions With Human Populations

Human attitudes towards red foxes vary worldwide. The most common types of human-caused mortality of foxes are trapping, shooting, and traffic (Allen and Sargeant 1993; Harris and Smith 1987; Storm et al. 1976). In areas where red foxes are potential carriers of the rabies virus, they are considered nuisance animals and are subject to population control (Doncaster and Macdonald 1997; Heydon and Reynolds 2000). In some areas like Australia, the fox is considered a pest since it has contributed to the collapse of the mammal fauna on a continental scale (Kinnear et al. 2002). In contrast, in Prince Edward Island (Canada), foxes are considered a likeable species and are often fed on a regular basis.

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3. AFRICAN WILD DOG HOME RANGE AND HABITAT SELECTION IN MKHUZE GAME RESERVE, SOUTH AFRICA

3.1 ABSTRACT

The African wild dog, *Lycaon pictus*, is a highly endangered species and in South Africa, there is only one remaining viable population. Reintroduction and management of the wild dog are of high priority and knowledge of the species' ecology is crucial to success. GPS locations of an African wild dog pack reintroduced into the Mkhuze Game Reserve in South Africa, collected by Ezemvelo KwaZulu-Natal Wildlife Conservation, were used to examine the home-range area (using minimum convex polygon and Kernel methods) and habitat selection of the species. Home-range size varied over the study period and the composite home-range size was greater than the area of the reserve. Pearson's correlation analysis showed delayed negative relationships of temperature and evapotranspiration with range area ($P < 0.05$ for most estimation methods). There was no difference between home-range area in breeding and non-breeding seasons, but there was a marginally-significant difference between wet and dry seasons (Mann-Whitney U-test; $P = 0.063$). *Acacia* low closed woodland was consistently preferred by the wild dogs while riverine forest was consistently avoided. Seasonal differences were observed for selection of other habitat types. Although in principle Mkhuze Game Reserve

is large enough to support a viable wild-dog pack, the introduced pack persisted only from their release in May 2005 to June 2008. Human influence, in the forms of habitat alteration and snaring, also came into play and must not be forgotten when considering future reintroductions.

3.2 INTRODUCTION

The African wild dog (*Lycaon pictus*), herein called the 'wild dog', is the smallest of the large African specialist carnivores (Creel and Creel 2002). It is classified as endangered by the International Union for Conservation of Nature (IUCN 2006). According to Fanshawe et al. (1997), there are an estimated 3,000-5,500 wild dogs left in 600-1000 packs, more than half of which are in southern Africa but most populations are too small to be viable in the long-term. In South Africa, there is a single viable population that inhabits Kruger National Park (KNP) (Fanshawe et al. 1991) and that has fluctuated greatly between 177-434 dogs in 21-32 packs during the last couple of decades (Davies 2000; Maddock and Mills 1994). According to Lindsey et al. (2005), KNP is also the only area in South Africa that can support another viable population. However, in the interest of maintaining wild dogs in more natural locations and increasing genetic diversity, efforts are underway to reintroduce wild dog packs into multiple smaller reserves and manage these reserves as a meta-population (sensu Lines 2006 and Wells and Richmond 1995; Ezemvelo KZN Wildlife 2007; Lindsey et al. 2004; WAG 2005). A 10-year plan, completed with success in 2007, focused on creating this meta-population and managing smaller isolated fenced reserves in South Africa (Mills et al. 1998).

Reintroduction is defined as the introduction of a species to an area where it previously existed to aid conservation efforts (IUCN 1998). Translocation is defined as the movement of animals from one part of their habitat to another with established conspecifics (Lines 2006). Both of these management methods are costly and can be both ecologically and politically difficult (Lindsey et al. 2005; Lines 2006), but without them it is probable the species would soon be extinct. Therefore, it is imperative to improve our knowledge of the factors affecting home range and habitat selection of reintroduced animals if we want to increase the viability of reintroduced packs. Some proactive measures include ensuring lower densities of competitors (Creel and Creel 1996), sufficient food and other resources (Lindsey et al. 2004), and bonding dogs from different areas into a solid pack with the use of fenced areas, or *bomas* (Gusset et al. 2006; McCreery 2000).

Wild dogs are highly social, forming packs of 2-27 individuals (e.g. Burrows 1993). Their sociality has been linked to hunting success (Creel 1997; Creel and Creel 1996; Creel and Creel 1995; Scheel and Packer 1991), defense of kills (Fanshawe and Fitzgibbon 1993) and breeding success (Courchamp et al. 2002; Malcolm and Marten 1982). The spotted hyaena (*Crocuta crocuta*) and lion (*Panthera leo*) are two competing species that restrict wild dog access to resources and subsequently may affect their home range, habitat selection, and movement patterns (Creel and Creel 1998; Fanshawe and Fitzgibbon 1993;

Mills and Gorman 1997; Vucetich and Creel 1999; Woodroffe et al. 2004). Lions prey on wild dogs, while hyaenas are mainly a threat through stealing of kills (Gorman et al. 1998). Wild dogs achieve densities lower than those of competitor species, even on large natural landscapes (e.g. Creel and Creel 2002; Mills and Biggs 1993; Schaller 1972; Soulé 1987). This is important to note because based on body size exclusively, we would expect that the wild dogs would maintain higher densities (Peters 1983). A lower population density is associated with an increased risk of extinction (Purvis et al. 2000), and so this is a natural extinction risk for the wild dog.

When attempting to conserve and manage animal populations, it is essential to identify the factors affecting home-range area and habitat selection. Burt (1943) defined home range as the area covered by an animal on a day-to-day basis for food collection, reproduction, and care of young. There is also typically a 'core area' that is used more extensively and is defended from conspecifics (Burt 1943; Mech 1970). Wild-dog packs usually maintain a large home range, exposing them to threats along boundaries of protected areas unless they are situated in a very large reserve (Creel and Creel 1998; Woodroffe et al. 2004). Woodroffe and Ginsberg (1999) estimated that a home-range area of up to 10,000 km^2 is needed for a viable population of wild dogs. In Kruger National Park, the mean observed home range of a pack of wild dogs is 537 km^2 (Mills and Gorman 1997), but in other areas individual packs may have ranges from 500-2,000 km^2 (see Fuller et al. 1992 for a review). Aside from competition, some reasons for potentially large range areas include satisfaction of high daily energy requirements (Gorman et al. 1998; Nagy 2001), and inbreeding-avoidance behaviour (Frame et al. 1979; Girman et al. 1997).

Within the home range, the distribution of resources is uneven and animals prefer certain habitats while avoiding others (Manley et al. 2002). Habitat selection is dependent on the needs of the species being studied, the landscape and vegetation structure (e.g. Danielson 1992; Karr and Freemark 1983), the distribution of resources (Manley et al. 2002), interspecific interactions (e.g. Danielson 1992), and also environmental variables (e.g. Connell 1978; Karr and Freemark 1983). For example, climatic variables like precipitation, temperature and evapotranspiration can change vegetation structure and, therefore, could in turn change prey distribution (Andrews and O'Brien 2000). Competitor distribution, human influence, and habitat structure will also affect home range and habitat selection of an animal such as the wild dog. As there is such large variation in home-range areas and little information on habitat selection of the wild dog, it is possible that conservation efforts in differing areas are inefficient. In areas where wild dogs are being reintroduced, it is important to study the needs of the species in specific areas to determine success of the effort.

Mkhuze Game Reserve (MGR) was established in 1912 (Gush 2000) and is currently part of the meta-population plan for South Africa (Mills et al. 1998). It is part of the larger iSimangaliso Wetland Park (a World Heritage Site, formerly the Greater St. Lucia Wetland Park) in the KwaZulu-Natal province on the East coast of South Africa (Fig. 3.1). Wild dogs were present until extirpated from the

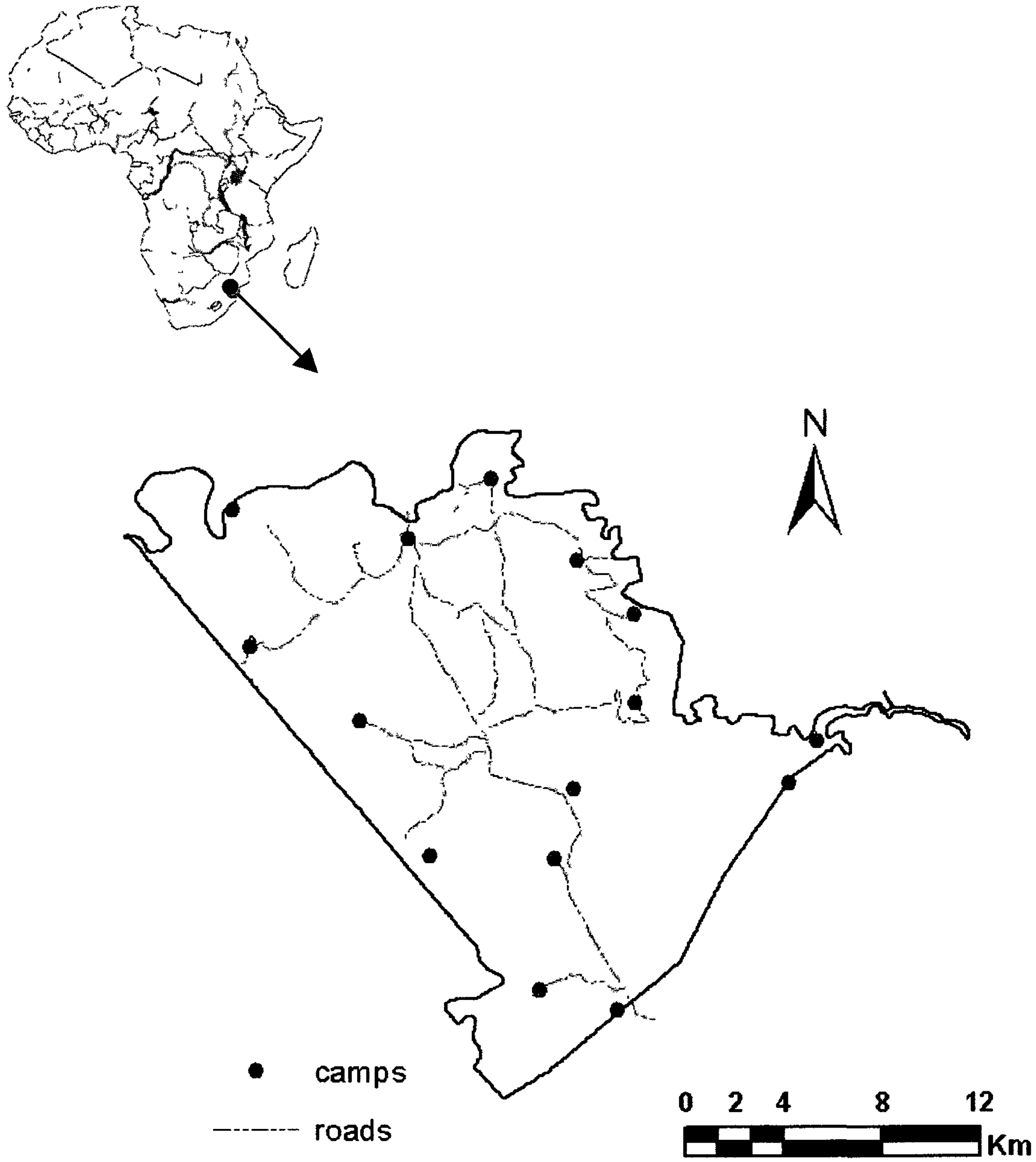

FIG. 3.1.—Outline map of Mkhuze Game Reserve, drawn out from its location in South Africa.

area in the 1930s. The conservation and management of wild dogs in the reserve falls under the Priority Species Monitoring project and in 2005 one pack of 13 wild dogs was reintroduced to MGR.

In an effort to improve the success of future wild dog reintroduction programs into MGR, and other similar areas in South Africa, I conducted a "forensic" study of a pack of collared wild dogs that persisted in MGR for 19 months after this study began. In 2004, thirteen wild dogs originating from Marakele National Park and Madikwe Game Reserve (both in South Africa) were placed together in adjoining bomas (fenced areas) for 5 months at MGR to bond them into one pack. Following this, in May of 2005, the pack was released from the boma (Ezemvelo KZN Wildlife 2007). The main goal of this study was to investigate the home-range area and habitat selection of wild dogs in MGR. In addition to habitat selection, the proximity of wild dogs to known snare locations, roadways, and tourist and ranger camps was quantified to explore the human impact on wild dogs within the reserve. It is expected that a better knowledge of home range size and habitat preference or avoidance within MGR will help to identify what conditions are critical for the persistence of wild dog packs in this and other small reserves. I also expected that the home range and habitat selection would vary seasonally and that wild dogs would use roadways, but avoid campsites. This is one of only a few studies that look at the habitat selection of this endangered species and is the only one done to date in MGR.

3.3 MATERIALS AND METHODS

Study Site.—MGR is located between 32°06'25" to 32°56'46" E and 26°51'26" to 28°29'07" S in the subtropical zone, characterized by warm, wet summers and mild, dry winters. This area receives about 1,200 mm of rain annually, 60% of which falls in the summer. The reserve is approximately 357.4 km^2, and is surrounded by electric fencing. It has been classified into 13 categories of habitat type (Van Rooyen 2004) based primarily on vegetation type and slope. For this study, three smaller vegetation types were clumped into an "other" category, resulting in 11 categories as follows (and detailed further in Appendix 1): *Acacia nilotica* low closed woodland, *Acacia* tall open woodland, *Acacia tortillis* low open woodland, dry closed woodland, Lebombo wooded grassland, low thicket, Lebombo open woodland, river floodplains and seasonal streams, riverine forest, *Terminalia sericea* savanna, and other (lakes and pans, human habitation, and palm savanna). MGR has four of the five big game animals: leopard (*Panthera pardus*), African elephant (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*), and buffalo (*Syncerus caffer*). However, it lacks lions (*Panthera leo*) that are found in some neighbouring reserves, such as the private reserve, Phinda, to the South.

Data Collection.—Two individuals from the pack were collared at one time, one as a backup in case of death or a malfunctioning collar. The Priority Species Monitoring team performed the anesthesia and collaring of animals. Darting was done with either fentanyl with xylazine, or Zoletil (Kreeger 1996) under supervision of Dr. Dave Cooper of Ezemvelo KZN Wildlife. The radio-collars applied were Sirtrack VHF Model V5C181 (width = 40 mm, circumference = 420 mm, weight ~ 420 g; Sirtrack, Hastings, New Zealand) with activity and mortality signals and anti-snare plates.

The wild dogs were radio-tracked from December 2006 (after bonding, collaring, and habituation) to June 2008. Tracking was discontinued in June 2008, because at this point all the wild dogs had been found dead or had disappeared from the park. Two dogs did return shortly after with one of them pregnant, but they were removed since packs of two seldom breed successfully. Wild dogs were tracked as a pack with Telonics aerials (Telonics, Arizona, USA) and Sirtrack receivers (Sirtrack, Hastings, New Zealand) with frequency capacities of 148-152 m Hz, capable of receiving signals up to 15 km away. Though two animals were collared at a time, the first signal located was used as the pack location. Effort was made to locate the pack once at dawn and once at dusk (periods of higher activity) according to field procedure guidelines of the Priority Species Monitoring Project. Cheetah monitored in a similar fashion in MGR have one fix per day, but two were obtained for the wild dogs due to their dispersive nature and greater range. Two were sufficient and practical to fulfill the requirements of this study since the focus was not fine-scale movements, but dispersal and overall use of the reserve. A Garmin eTrex GPS device (Garmin Ltd., Olathe, Kansas, USA), accurate to within 10 m or less (Wing et al. 2005), was used to measure the locational fix of the pack. In this study, there were three types of locational fixes: A-sightings consisted of a close and accurate positional fix where the pack was seen directly; B-sightings were the presumed location of the close, but elusive, pack where a strong signal was present but the landscape prevented direct viewing; and C-sightings resulted from two to three compass bearings and a computer-tabulated biangulation or triangulation. Directional bearings for biangulations and triangulations were taken within 40-150° of each other, with about 80% within 80-100°. For C-sightings, LOAS software (v. 4.0.3.1) was used and the estimated locations were accurate to within 50-100 m (as determined by LOAS, Ecological Software Solution www.ecostats.com Copyright 1998-2007). This research project followed ASM guidelines on animal care (*Journal of Mammalogy* 88:809–823, 2007) and was approved by both Ezemvelo KwaZulu-Natal Wildlife Conservation and iSimangaliso Wetland Park Authority.

Data Analysis.—ArcView GIS software (v. 8.1 and 9.3, Environmental Systems Research Institute, Inc., Redlands, California) was used to analyze the locational fixes. Minitab v.15.1.0.0 was used for statistical testing.

In order to compare our findings with other studies, I calculated monthly home ranges using two commonly used methods. First, I calculated home ranges as 100% minimum convex polygons (MCPs) drawn through the points at the furthest extent of a dataset so as to contain all of the points and construct a home-range area (Mohr 1947). 95% and 90% MCPs were also calculated to exclude possible outliers (sensu Jennrich and Turner 1969). These were done with the area added method, which calculates the 100% MCP then removes points one-by-one that change the area the most. Second, I estimated utilization distributions (UD) using fixed Kernel density estimates (bivariate normal), which give the probability of use of an area around fixed points and can reveal core areas of use or familiarity (Burgman and Fox 2003; Worton 1989). Optimal bandwidth (h) for each kernel was determined using the *ad hoc* method for the bivariate normal UD as follows (using R, Worton 1989, Seaman et al. 1998):

$$h = \sigma \left(n^{(-1/6)}\right) \tag{1}$$

where n = sample size, and

$$\sigma = 0.5 \left(\sigma_x + \sigma_y\right) \tag{2}$$

In order to get an estimated area for home range based on the utilization distribution, percent volume contours (PVCs) enclosing 50% (considered here as the 'core area' sensu Heupel et al. 2004; Shannon et al. 2006), 90%, and 95% of the Kernel utilization distributions were used. 90% and 95 % contours were chosen to compare with other studies and with the MCPs calculated previously. The home-range size was tested for significant difference between seasons (both climatic and reproductive) using Mann-Whitney U-tests. Based on Mills et al. (1998) and observed mating in MGR, the breeding season was defined as March through June and the non-breeding season, July through February. The dry season (based on climate data from Ezemvelo KZN Wildlife) was between May and September inclusive and the wet season, between October and April inclusive. The effects of temperature, rainfall, and evapotranspiration were examined with Pearson's correlation (*r*). Each climatic variable was also lagged by one and two months to detect delayed effects (sensu Koenraadt et al. 2004; Thompson and Ollason 2001). Multiple linear regressions tested for a combined effect of all variables on home-range areas. Minitab (v. 15) was used for statistical analyses unless indicated otherwise.

A digitized version of a habitat map from 2004 (Vanrooyen 2004) was used to determine the relative availability of the different types of habitat and thus the expected use. This was acceptable since development in MGR has been very limited due to its role in conservation of numerous species. The observed, or true, usage of a particular habitat type was defined as the ratio between animal locations in each habitat type and the total number of locations recorded in the study area. Expected usage of a habitat type was defined as the ratio of the area of the particular habitat to the total area of the study site. The study site was delineated by the extent of MGR and thus our GIS data. Habitat selection was examined by comparing use and availability of habitat types within a study area using the Neu Method (Byers et al. 1984; Neu et al. 1974). The Neu method is a straightforward application of the χ^2 goodness-of-fit test, and is usually used to compare the overall distribution of use to that expected if habitats were used in proportion to their availability. If there is a difference, simultaneous confidence intervals (Bonferroni Z-statistic) are calculated around the observed proportions to determine whether the expected proportion of usage in each habitat is significantly from observed. If the expected use value falls within the observed interval, the habitat is used as expected (no significant difference), if it falls above the interval, it is avoided, and if it falls below, it is preferred. 95% simultaneous Bonferroni confidence intervals were calculated around the observed use for each of the 11 habitat types based on the formula:

$$p_i - Z_{\alpha/2k}[\sqrt{(p_i(1-p_i)/n)}] \leq p_i \leq p_i + Z_{\alpha/2k}[\sqrt{(p_i(1-p_i)/n)}] \qquad (3)$$

where p_i is the observed proportion of use, $Z_{\alpha/2k}$ is the upper standard normal table value with a probability of $\alpha/2k$, α is the significance level (0.05 here), k is the number of habitat types, and n is the total number of observations. This was done for all data and also separately for wet, dry, breeding, and non-breeding seasons. To determine the proximity of the wild-dog pack to human influence, buffers were arbitrarily drawn around three types of infrastructure based on physical landscape, observed distribution of other species, and estimated risk (e.g. proximity to a snare or roadway more likely presents an immediate risk): roadways (50 m), camps (200 m) and known illegal snare locations (100 m), then the number of sightings within these buffers was recorded.

3.4 RESULTS

847 locational fixes of the wild dog pack were used for this study. Seventy-one percent were A-sightings, 14% were B-sightings and 15% were C-sightings. Seventeen fixes were located outside of the reserve boundary. About 10 of these fixes were an escaping group of dispersing males that looped continually in and out of the reserve, and about five were from the main pack exiting the reserve for one to two days at a time. These outside fixes could not be used for habitat selection (due to lack of habitat data outside MGR), although

they were used for calculation of home-range area. Including these outside fixes, the wet season had 506 fixes, the dry season, 341, the breeding season, 382, and the non-breeding season, 465. Over the study period the pack size was decreasing due to emigration and deaths, notably due to snares (at least 4 out of the 13) or related injuries, road death (1 wild dog), hunting injuries, and disease. Unfortunately, the cause of death was not certain in many cases, often due to delay in finding the bodies.

Home Range.—When all points (N = 847) were plotted on the habitat map, they appeared scattered throughout the entire reserve and a 100% MCP yielded a home range of 383.94 km^2, an area larger than the total area of the reserve (Fig. 3.2), and even a 95% PVC yielded an area of or 377.79 km^2. Fig. 4 shows the fluctuations of the home-range area with different estimators and of the core area. Monthly home ranges (Table 3.1) did not show any significant differences between reproductive seasons (Mann-Whitney U-tests: $P > 0.05$), although home range was marginally smaller in the dry season than in the wet seasson (100% MCP, Mann-Whitney U-test: $W = 97.5$, $P = 0.0629$). It appeared that overall the core areas of use were concentrated in the Southern area of the reserve (Fig. 3.3). Temperature and evapotranspiration lagged by one and two months did have significant correlations with home-range size (see Table 3.2). Temperature lagged by one month had a significant relationship with home-range area with all MCPs and PVCs used (see Table 3.2). Temperature lagged by two months was significant for both 90% and 95%

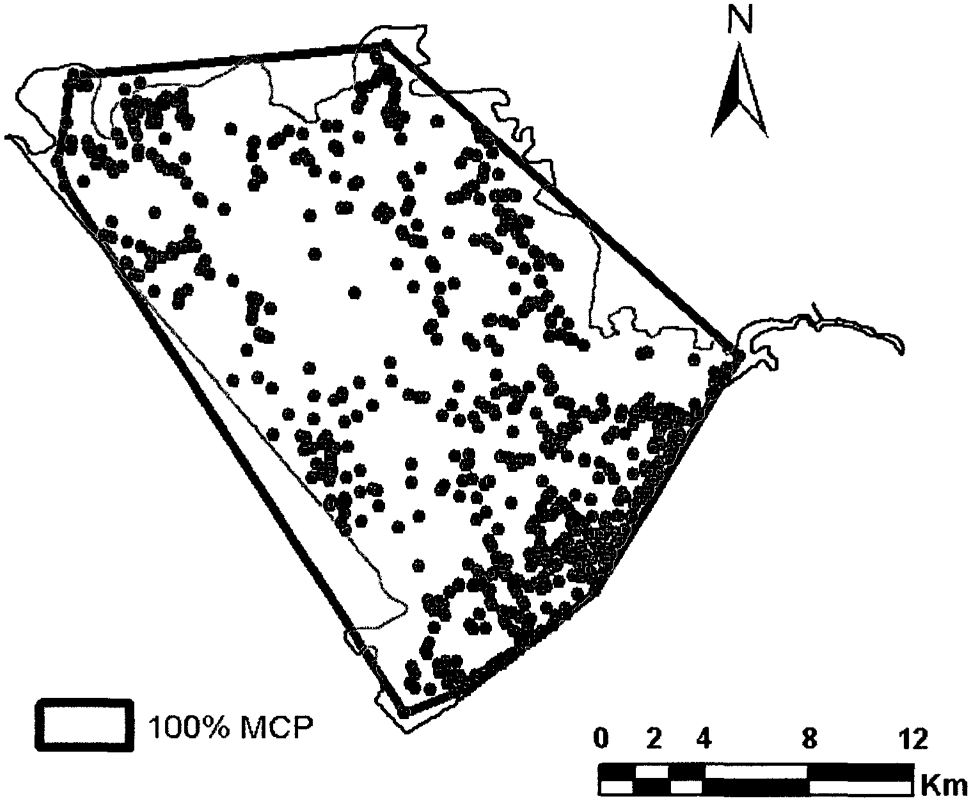

FIG. 3.2.—Mkhuze map showing all 847 sightings (●) and the 100% MCP outline in yellow.

TABLE 3.1.—Home-range sizes (km^2) of an African wild dog pack in Mkhuze Game Reserve. * Indicates months with fewer recorded fixes. MCP is minimum convex polygon and PVC is percent volume contour.

Month	Year	N	100% MCP	95% MCP	90% MCP	50% PVC	90% PVC	95% PVC
December*	2006	24	39.82	34.69	31.42	16.60	67.79	87.09
January	2007	39	110.12	106.98	103.53	71.03	176.25	208.13
February	2007	41	103.38	85.51	76.45	61.18	196.64	244.35
March	2007	50	85.64	61.70	55.77	34.73	108.30	133.08
April	2007	46	101.10	95.21	92.01	56.22	176.52	211.80
May	2007	57	191.17	166.04	141.95	77.20	240.20	293.66
June	2007	52	256.74	238.71	189.29	130.08	361.48	439.47
July	2007	54	295.70	254.80	214.19	124.47	382.91	467.07
August	2007	54	282.12	248.74	230.55	151.52	410.69	486.35
September	2007	45	318.92	252.45	193.55	103.04	378.01	468.01
October	2007	51	294.68	263.25	241.40	149.07	439.56	519.84
November*	2007	22	256.26	229.12	212.21	152.42	456.79	552.20
December	2007	41	184.28	147.90	136.10	92.22	320.88	405.55
January	2008	52	232.41	208.23	120.12	81.18	274.69	349.66
February	2008	42	252.67	223.16	200.55	98.89	395.27	486.38
March	2008	55	177.12	156.00	76.88	46.82	175.03	224.73
April	2008	43	241.75	192.78	170.76	112.73	403.68	504.36
May	2008	52	313.12	255.17	219.16	146.98	492.89	599.22
June*	2008	27	31.90	22.84	18.52	17.85	62.76	79.47
All data	--	847	383.94	--	--	103.59	320.35	377.79

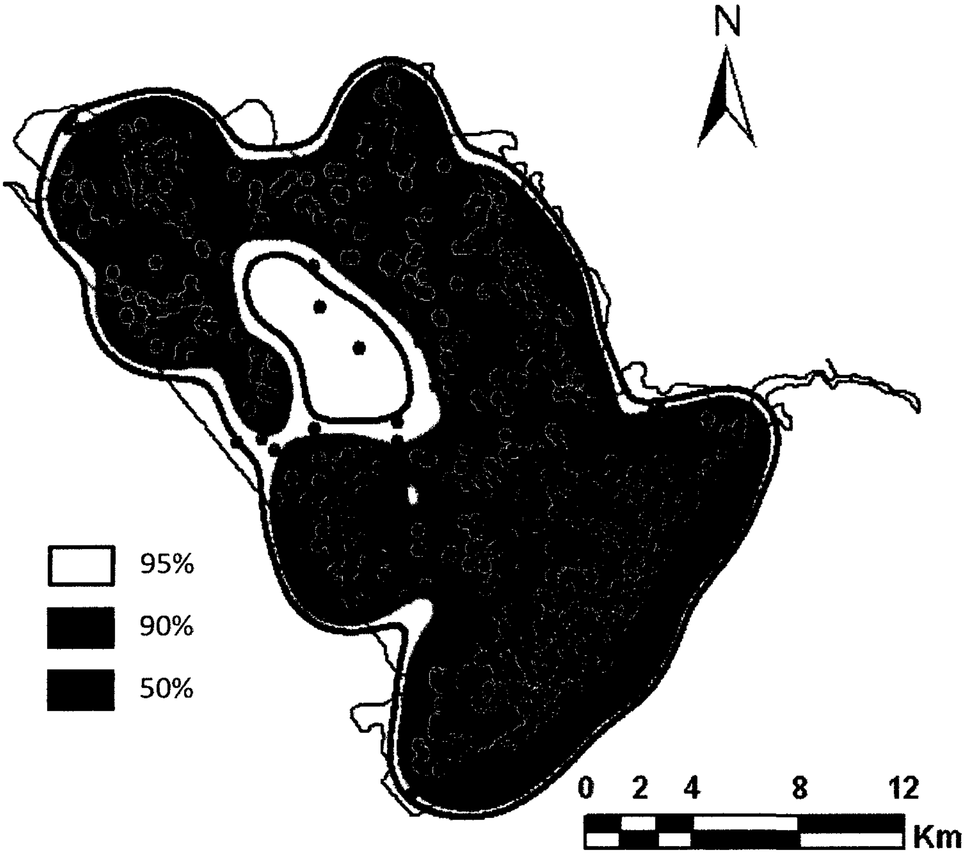

Fig. 3.3.—MGR map showing all data (N = 847) with 50%, 90%, and 95% PVCs for Kernel utilization distributions.

TABLE 3.2.—Significant correlations between home-range area and climatic variables. MCP is minimum convex polygon and PVC is percent volume contour.

Home-Range	**Variable[3]**			
Estimator	**Temp – 1**	**Temp – 2**	**Evap – 1**	**Evap – 2**
90% MCP	*r*[1]= -0.519	*r* = -0.545	*r* = -0.488	*r* = -0.586
	P[2] = 0.027	P = 0.024	P = 0.040	P = 0.013
95% MCP	*r* = -0.535	*r* = -0.493	*r* = -0.522	*r* = -0.544
	P = 0.022	P = 0.044	P = 0.026	P = 0.024
100% MCP	*r* = -0.550	*r* = -0.468	*r* = -0.496	*r* = -0.580
	P = 0.018	P = 0.058*	P = 0.036	P = 0.015
50% PVC	*r* = -0.521	*r* = -0.555	*r* = -0.486	*r* = -0.545
	P = 0.027	P = 0.021	P = 0.041	P = 0.024
90% PVC	*r* = -0.480	*r* = -0.461	*r* = -0.463	*r* = -0.467
	P = 0.044	P = 0.062*	P = 0.053*	P = 0.059*
95% PVC	*r* = -0.476		*r* = -0.454	*r* = -0.457
	P = 0.046		P = 0.058*	P = 0.065*

[1] Pearson correlation coefficient, [2] P-value (significant at ≤ 0.05, marginally significant if 0.05 < P <0.07), [3] Temp means temperature, Evap means evapotranspiration, –1 designates a lag by one month, and –2, a lag by two months. * Indicates marginally significant results at the α = 0.05 level.

MCPs as well as the 50% PVC, and marginally significant for the 90% PVC and 100% MCP. Evapotranspiration lagged by one month was significantly correlated with 90%, 95%, and 100% MCPs and 50% PVC, and marginally correlated with 90% and 95% PVCs. Evapotranspiration lagged by two months was significantly correlated with 90%, 95%, and 100% MCPs and 50% PVC and marginally with 90% and 95% PVCs. Correlations were all negative indicating a delayed decrease in home-range size is occurring with an increase in temperature and evapotranspiration. There were no significant correlations of home-range size with rainfall lagged by one or two months, or with temperature, evapotranspiration, or rainfall without a temporal lag (P-values all > 0.05). Insignificant regression coefficients were found for all variables included in multiple linear regression analyses (P > 0.05).

Habitat Selection.—Wild dogs were found to use many habitats as expected, but they did select habitats differently from expected in some cases (Table 3.3-3.4). The observed distribution over habitats differed in the wet (P < 0.001), dry (P < 0.001), breeding (P < 0.001), and non-breeding (P < 0.001) seasons as well as overall (P < 0.001). Low closed woodland was consistently preferred and riverine forest was consistently avoided regardless of season. River floodplains and seasonal streams were mainly avoided and *Terminalia sericea* savanna was preferred most of the time. Depending on season, other habitat types were used differently as well. Twelve and a half percent of wild-dog fixes used (total N = 830) fell within a 50 m buffer around main roadways

TABLE 3.3.—Comparisons of use and availability of various habitat types used by wild dogs based on radio-tracking data.

Habitat Type	Exp. Use	Obs. Counts	Bonferroni Interval	Use
Wet Season				
Acacia nilotica low closed woodland	0.049	87	$0.126 < p < 0.224$	+
Acacia tall open woodland	0.160	57	$0.074 < p < 0.156$	--
Acacia tortillis low open woodland	0.064	25	$0.022 < p < 0.078$	0
Dry closed woodland	0.167	77	$0.108 < p < 0.202$	0
Lebombo wooded grassland	0.071	32	$0.033 < p < 0.097$	0
Low thicket	0.096	28	$0.026 < p < 0.086$	--
Open woodland	0.084	54	$0.069 < p < 0.149$	0
River floodplains and Seasonal streams	0.127	44	$0.052 < p < 0.126$	--*
Riverine forest	0.076	6	$0 < p < 0.026$	--
Terminalia sericea savanna	0.093	78	$0.110 < p < 0.204$	+
Other[2]	0.014	8	$0 < p < 0.032$	0

Continued

TABLE 3.3—Continued.

Habitat Type	Exp. Use	Obs. Counts	Bonferroni Interval	Use
Dry Season				
Acacia nilotica low closed woodland	0.049	47	$0.086 < p < 0.196$	+
Acacia tall open woodland	0.160	49	$0.091 < p < 0.203$	0
Acacia tortillis low open woodland	0.064	24	$0.031 < p < 0.113$	0
Dry closed woodland	0.167	45	$0.081 < p < 0.189$	0
Lebombo wooded grassland	0.071	20	$0.023 < p < 0.097$	0
Low thicket	0.096	21	$0.025 < p < 0.101$	0
Open woodland	0.084	18	$0.018 < p < 0.090$	0
River floodplains and Seasonal streams	0.127	24	$0.031 < p < 0.113$	--
Riverine forest	0.076	7	$0.015 < p < 0.027$	--
Terminalia sericea savanna	0.093	77	$0.165 < p < 0.297$	+
Other[2]	0.014	2	$0 < p < 0.018$	0

Continued

TABLE 3.3.—Continued.

Habitat Type	Exp. Use	Obs. Counts	Bonferroni Interval	Use
Breeding Season				
Acacia nilotica low closed woodland	0.049	61	$0.1075 < p < 0.2170$	+
Acacia tall open woodland	0.160	45	$0.0715 < p < 0.1679$	0
Acacia tortillis low open woodland	0.064	14	$0.0091 < p < 0.0653$	0
Dry closed woodland	0.167	45	$0.0715 < p < 0.1689$	0
Lebombo wooded grassland	0.071	24	$0.0275 < p < 0.1001$	0
Low thicket	0.096	20	$0.0199 < p < 0.0865$	-
Open woodland	0.084	16	$0.0126 < p < 0.0725$	-
River floodplains and Seasonal streams	0.127	34	$0.0479 < p < 0.1330$	0
Riverine forest	0.076	10	$0.0027 < p < 0.0505$	-
Terminalia sericea savanna	0.093	102	$0.2053 < p < 0.3373$	+
Other[2]	0.014	5	$0 < p < 0.0303$	0

Continued

TABLE 3.3.—Continued.

Habitat Type	Exp. Use	Obs. Counts	Bonferroni Interval	Use
Non-Breeding Season				
Acacia nilotica low closed woodland	0.049	73	$0.1112 < p < 0.2104$	+
Acacia tall open woodland	0.160	61	$0.0883 < p < 0.1804$	0
Acacia tortillis low open woodland	0.064	35	$0.0411 < p < 0.1131$	0
Dry closed woodland	0.167	77	$0.1189 < p < 0.2203$	0
Lebombo wooded grassland	0.071	28	$0.0292 < p < 0.0942$	0
Low thicket	0.096	29	$0.0308 < p < 0.0969$	0
Open woodland	0.084	56	$0.0789 < p < 0.1678$	0
River floodplains and Seasonal streams	0.127	34	$0.0393 < p < 0.1104$	-
Riverine forest	0.076	3	$0 < p < 0.0176$	-
Terminalia sericea savanna	0.093	53	$0.0734 < p < 0.1601$	0
Other[2]	0.014	5	$0 < p < 0.0251$	0

Continued

TABLE 3.3.—Continued.

Habitat Type	Exp. Use	Obs. Counts	Bonferroni Interval	Use[1]
Pooled Data				
Acacia nilotica low closed woodland	0.049	134	$0.124 < p < 0.198$	+
Acacia tall open woodland	0.160	106	$0.095 < p < 0.161$	0
Acacia tortillis low open woodland	0.064	49	$0.035 < p < 0.083$	0
Dry closed woodland	0.167	122	$0.112 < p < 0.182$	0
Lebombo wooded grassland	0.071	52	$0.039 < p < 0.087$	0
Low thicket	0.096	49	$0.035 < p < 0.083$	-
Open woodland	0.084	72	$0.059 < p < 0.115$	0
River floodplains and Seasonal streams	0.127	68	$0.055 < p < 0.109$	-
Riverine forest	0.076	13	$0.003 < p < 0.029$	-
Terminalia sericea savanna	0.093	155	$0.148 < p < 0.226$	+
Other[2]	0.014	10	$0.001 < p < 0.023$	0

[1] Bonferroni confidence intervals shown ($\alpha = 0.05$) were placed on observed use. "+" indicates used more than expected; "-" indicates used less than expected; "0" use according to availability or non-significant difference between expected and available. *Indicates marginally significant results. [2] Other includes lakes, pans, human habitation, and palm savanna.

TABLE 3.4.—Summary of habitat selection[1] by wild dogs in Mkhuze Game Reserve.

	Climatic Season		**Reproductive Season**		
Habitat Type	**Wet** (N = 496)	**Dry** (N = 334)	**Breeding** (N = 376)	**Non-Breeding** (N = 454)	**All Data** (N = 830)
Acacia nilotica low closed woodland	+	+	+	+	+
Acacia tall open woodland	--	0	0	0	0
Acacia tortillis low open woodland	0	0	0	0	0
Dry closed woodland	0	0	0	0	0
Lebombo wooded grassland	0	0	0	0	0
Low thicket	-	0	--	0	--
Open woodland	0	0	--	0	0
River floodplains and seasonal streams	--*	--	0	--	--

TABLE 3.4.—Continued

	Climatic Season		Reproductive Season		
Habitat Type	**Wet** **(N = 496)**	**Dry** **(N = 334)**	**Breeding** **(N = 376)**	**Non-Breeding** **(N = 454)**	**All Data** **(N = 830)**
Riverine forest	--	--	--	--	--
Terminalia sericea savanna	+	+	+	0	+
Other (lakes, pans, human habitation, palm savanna)	0	0	0	0	0

[1]"+" indicates used more than expected; "-" is less than expected; "0" is use according to availability. *Indicates marginally significant results.

(and they were frequently observed travelling along roadways), 1.4% of fixes were found within 200 m of ranger and tourist camps, and 0.4% were found within 100 m of recorded illegal snare locations.

3.5 DISCUSSION

After wild dogs were bonded into one pack, and were reintroduced into MGR in 2005, they remained until June 2008. By June 2008, all of the dogs had been found dead (snares, and unknown causes of death such as predation, hunting injuries, disease) or had dispersed from the park (fences are intended to keep large game inside the park, and although they limit wild dogs and other similar species, they are not complete barriers). The purpose of this study was to explore the home range and habitat selection of this pack in the hopes of providing information and recommendations to make future reintroductions to MGR and other reserves more successful.

The composite home-range size of the wild-dog pack over the study period was 383.94 km^2 (100% MCP) or 377.79 km^2 (95% Kernel), which is larger than the area encompassed by MGR. Wild dogs used the entire reserve and beyond in the study period. Home range included area outside the reserve partly due to the escape of wild dogs on several occasions, and partly due to the home range estimators used. A MCP often contains area not used by animals by its nature of using only points at the edge of the distribution (sometimes those outside the reserve), and the Kernel method places probabilities of use around observed locations and when these locations are at the edge of the reserve, the animals are expected to use area outside the reserve. However, due to some escape and use of areas around the edge of the reserve provides some evidence for use of area beyond MGR fences. The home range did not appear to be stable, fluctuating in area and in position within the park over the study period, and this seems to indicate a lack of establishment in the park. Because wild dogs are obligate cooperators and pack size is linked with reproductive and hunting success, some of the variation was likely due to pack size decrease over the study period. This is also a limitation for statistical comparison of home range over time and of correlation with climatic factors, but unfortunately, adequate records are not available to correlate home-range size with pack size. Core areas were relatively large and were concentrated in the Southern region of the park as shown by the 50% Kernel 'core area.' South of MGR is Phinda, a private game reserve which has all of the same wildlife (including wild dogs), with the addition of lions. There was also a pack of wild dogs in the Northern part of Phinda. Because dispersal of yearlings is so important (inbreeding avoidance—Girman et al. 1997), it is possible that wild dogs were attracted to and beyond the periphery of MGR as a result of an attempt to bond with this unrelated pack. It is typical for large carnivores to require large areas due to wide-ranging behavior (Woodroffe and Ginsberg 1998), but interestingly other studies have shown minimum home ranges for viable packs to be much less than the area of Mkhuze. For example, Lindsey et al. (2004) found that a minimum viable pack size of 5 adults and 5 yearlings in Eastern South Africa would require an area of 144 km^2 to ensure enough prey.

In Hluhuwe-Umfolozi Park, the home range is 242.35 km^2, a very small part of the 900 km^2 available (100% MCP—Andreka et al. 1999). It is important to note that these home ranges are likely varying as a result of the quality and perception of the habitat by the wild dogs on a local scale (i.e. in each reserve). Frame et al. (1979) found where prey was scarce, wild dogs traversed the home range more frequently than when prey was more available. It may be the case that in Hluhluwe-Umfolozi, the prey distribution is more clumped in a smaller area or competition is limiting the wild dogs to a smaller area. Resource distribution is the most commonly used explanation for animal distribution but it is important to note that other factors such as the distributions of conspecifics, competitors, and predators most likely play important roles as well. Same-sex groups of yearlings or adults disperse from their pack and find other unrelated groups of the opposite sex to bond with and form a new pack (Girman et al. 1997; Skinner and Chimimba 2005), which is essential to avoiding inbreeding in a species with low density (Girman et al. 1997). There were no other packs in the park and so dispersing members of the pack could not encounter any packs to bond with. This could be one reason that the home range continued to expand. This tendency to continue emigrating out of a reserve is a typical one-pack population problem in wild dogs and has also been observed in Hluhluwe-Umfolozi Park before the addition of another pack (Maddock 1999). In many of the areas where home-range studies were done, there were multiple packs and pack interactions likely affected the home range and habitat selection (e.g. Kruger National Park—Mills and Gorman 1997, Hhluhluwe-Umfolozi Park—

Lines 2006). Pack interactions likely divide up reserves into sections for packs even though wild dogs are not territorial and are very social (Mills et al. 1998).

The wild-dog pack had a marginally smaller home-range size in the dry season. During dry seasons, there is less water available and a decrease in abundances of grazing species, such as ungulates (Ogutu et al. 2008) that serve as prey for higher order mammals like the wild dog. This would result in a decrease in potential intake. Also, during the dry season, animals are concentrated around watering holes and this would make for defined food sources in a more limited area. It is also worth noting that breeding in some areas (like KNP—Pienaar 1963) occurs during the dry season (March-September) for wild dogs. As well, impala also tend to breed at this time (sensu Brown et al. 1991), resulting in vulnerable males during rut and young of the year, both favored prey of wild dogs (Pole et al. 2004). Therefore, in addition to potential decrease in intake, food sources are more vulnerable and concentrated in the dry season, likely resulting in a concentration of the predator as well. The lack of change in home-range size between breeding and non-breeding seasons in MGR was expected, since they did not breed during the study (although mating occurred, and litters were born in 2005 and 2006 prior to the study), and therefore the pack did not den to care for a litter of pups. Reproductive state was expected to affect home range, as during the breeding season (especially during the denning period) wild dogs stay closer to the den to care for pups (Creel and Creel 2002). Climatic factors and season did appear to have an impact on home-range area in this study.

Wild dog home-range area did vary with temperature and evapotranspiration in a delayed way, suggesting that either climate had a delayed effect directly or indirectly on the wild dogs. There was an inverse relationship between wild dog home-range area and temperature and evapotranspiration (with a time lag), so with an increase in temperature or evapotranspiration, there was a decrease in home-range size. Most of the work related to animals and climatic factors deals with relationships of species richness (e.g. Currie 1991), or animal production (e.g. Barnes and McNeill 1978). Other studies relate climatic factors with animal distribution. Although distribution is not synonymous with home range, home range is often treated as a delineation of an animal's utilization distribution of a landscape (Worton 1989), so relationships with distribution patterns are still relevant. Andrews and O'Brien (2000) found that the distribution of large terrestrial mammals is highly correlated with minimum monthly temperature and annual temperature, and in this study, strong correlation was found between home-range area and temperature lagged by one and two months. Evapotranspiration is related to temperature and precipitation, and as such, is important to plants and affects habitat structure (sensu Kimball and Bernacchi 2006). Andrews and O'Brien (2000) found only a weak correlation of carnivore distribution with variation in regional plant species richness and suggested this is due to an indirect relationship between carnivores and plants. If wild dog prey distribution is changing with respect to changes in vegetation, which in turn also takes time to change in response to climatic factors, this could explain why rainfall did not have a significant impact on wild dog home-range area in our study, and why the other climatic factors had a delayed effect. However, it is also possible that the wild dogs were responding to delayed changes in vegetation structure or had a delayed response directly to climatic variables. Wild dogs have a high energy-expenditure rate (3.04 kg meat/day for an adult male—Nagy 2001), and it is possible that higher temperatures and evapotranspiration were limiting movements and home-range area of the pack.

Wild dogs in MGR selected certain habitats differently than expected based on availability. Habitat selection in MGR varies seasonally as well, which could again be linked to climate and the to seasonality in prey distribution. In this study *Acacia nilotica* low closed woodland, characterized by short deciduous *Acacia* bush and tree species, and grassy understory (Van Rooyen 2004, see Appendix 1), was preferred by wild dogs. This level terrain with some openness is ideal for antelope species like impala and nyala, and though it has some cover, it is so dense as to prevent wild dog pack coordination and effective hunting. *Terminalia sericea* savanna, preferred in most seasons, is semi-open woodland (Van Rooyen 2004). Dense vegetation and closed areas impede the ability of hyaenas to locate and steal wild dog kills, as reported in Selous Game Reserve in Tanzania (found at only 18% of wild dog kills—Creel and Creel 1996). It could be the case that wild dogs are trying to avoid this hyaena kleptoparasitism in MGR and that that is why they selected a habitat with a good understory. Creel and Creel (2002) found wild dogs preferred deciduous and thorn woodlands and Andreka (1996) found that wild dogs prefer forest and open woodland. River floodplains and seasonal streams were avoided in most seasons, indicating perhaps that the openness of this habitat is not beneficial to the wild dogs. Riverine forest, also known as fig forest as for its fig tree species measuring up to 25 m tall (Van Rooyen 2004), was consistently avoided in MGR. These trees provide a dense canopy, resulting in a more tropical rainforest-type of habitat. The thicket can be dense in areas, and there is higher diversity of birds and animals, but it is not likely a good grazing area for antelope, and it is likely that habitat selection of wild dogs is dependent to a degree on prey distribution.

Where density of lions is low, wild dogs usually select habitats in relation to prey availability (Pole 1999). However, if competition and mortality due to hyaenas and lions is high, they will avoid prey-dense areas where these predators are also at high concentrations (Creel and Creel 1996; Mills and Gorman 1997). This brings up the probability that some habitats are not truly available to wild dogs. Johnson (1980) warns about assumptions of availability and their potentially drastic effects on results and interpretation of habitat selection studies. In MGR, there are no lions, but hyaenas are abundant. Unfortunately, there has not been quantification of hyaena or prey (impala, nyala, kudu) distribution in MGR to use for comparison. Because hyaenas limit wild dog distribution in other reserves, it is suspected to also the case in MGR. It is even possible that this competition was more important for the wild dogs here due to the lack of lions limiting and/or competing with the hyaenas as a keystone competitor (Roughgarden 1983; see also Tanner et al. 1994).

Keeping wild dogs within a reserve has some obvious advantages, such as monitoring and protection from outside threats including persecution by humans. Woodroffe et al. (2007) found that most wild dogs in protected areas died of natural causes, while those outside died mainly from human causes. Our study showed that wild dogs are frequently observed near roadways and are frequently caught and injured or killed in snares. Although it is possible that more observations were collected near roads due to the ease of sighting and methodology for finding dogs, it has been observed in the reserve that wild dogs travel along roads. Similar findings have been observed for other canids (e.g. red foxes—Silva et al. 2009). Though roadways can serve as corridors of movement, they are also dangerous and a noted cause of wild dog mortality in many wildlife reserves (Woodroffe and Ginsberg 1997). In comparison, there were a relatively low number of wild dog locations near tourist and ranger camps as well as near snare locations. Despite the low number of observed sightings in the vicinity of snares, these devices represent a very high risk for the wild dogs. In MGR, snares accounted for at least four deaths, and snaring individuals on at least three other occasions requiring anesthesia for removal. Local people often set these snares at the edges of reserves intending to catch antelope for food, not wild dogs or many of the other species often caught, including hyaenas. Wild dogs have a tendency to travel along and outside the fences of reserves and encounter roads, snares, and direct forms of human persecution (reviewed in Woodroffe and Ginsberg 1997). It is important that an increased effort be implemented to remove illegal snares to increase the likelihood of future reintroduction success in MGR. Anthropogenic factors such as these can create important implications for wild-dog habitat selection, and it would be expected that wild dogs would avoid habitats associated with negative consequences unless they offer some additional value that is worth the risk. Many of the current issues with wild-dog conservation stem from past direct persecution of the species in the forms of shooting, snaring, and poisoning by farmers and others who felt wild dogs were a threat to their livelihoods (Lindsey et al. 2004; Woodroffe and Ginsberg 1997). Lindsey (2003) found that wild dogs were the least-liked predatory species in South Africa and in Zimbabwe. In light of this, research has been done on the species' predatory habits and we now know much persecution was unfounded. Wild dogs have an extremely low rate of predation on livestock species, as shown by studies in which wild dogs tend to select wild prey species whenever available, even when livestock are present (e.g. Fuller and Kat 1990; Rasmussen 1999; Woodroffe et al. 2006). To illustrate this point, Woodroffe et al. (2005) showed that only one attack was reported per 1,000 km^2 per year in unprotected wild-dog habitat where livestock were more abundant than wild ungulates.

Because wild dogs are often found at vulnerable edges of protected areas, Woodroffe and Ginsberg (1998) suggest that only larger protected areas are going to be effective in conservation. This may indicate that many small reserves of suitable habitat are not viable areas for reintroduction; however there has been success with the meta-population project in South Africa (Lindsey et al. 2005). As of 2002, 10 packs were established in five isolated reserves, most of which are smaller in area than the home-range size observed in KNP (Hluhluwe-imfolozi, Madikwe, Marakele National Park, Shamwari Game Reserve, and Tswalu Kalahari Game Reserve), and are being monitored (Lindsey et al. 2005). The meta-population approach to wild-dog conservation aims to avoid catastrophic decline of subpopulations by minimizing typical one-pack problems, such as loss of animals, lack of new genetic material, susceptibility to environmental events, and population fluctuation due to emigration (Lindsey et al. 2005; Maddock 1999).

Gusset et al. (2008) give two main factors of wild dog-reintroduction success as fencing and social integration of individuals into a pack. Both of these criteria were met in MGR, yet the pack did not persist. Our goal was to determine some other potential factors affecting home range and habitat selection and thus the persistence of wild dogs in the area. A computer simulation study by Ginsberg and Woodroffe (1997) found that low population size followed by fragmentation were the most important factors influencing extinction risk in populations numbering fewer than 50 individuals. There were only 13 dogs re-introduced to MGR, and given the evidence of smaller home ranges elsewhere, a good next step would be to try introducing several smaller packs. It is suggested here that since the home-range size was larger than usual, single-pack dynamics (continuing dispersal) may have been a factor and that by introducing more packs, home-range size would be limited and there would be an increased chance of viability within MGR. There was a litter born before radio-tracking had begun but though mating occurred afterwards, there were no litters born, and there were then no wild dogs in MGR that were not related to the pups that were introduced and born shortly after reintroduction. This lack of reproduction certainly reduced the probability for this population to achieve viability within MGR. Reproductive challenges are not uncommon in reintroductions of animals. Reintroduced Florida panthers have had reproductive inhibition in areas of low prey density (Belden 1989) and reintroduced bobcats have reproduced initially but then inhibited it as population density increased (Diefenbach et al. 2006). The population density of wild dogs did not increase during the study, and local figures do not indicate a drop in prey species abundances within MGR over the study period. It is possible that the wild dogs were experiencing an Allee effect, where the growth rate is low at low densities (Armstrong and Seddon 2008; Caughley 1994; Courchamp et al. 2008). This can be due to social dysfunction in small groups, lack of suitable mates, or inbreeding (McCarthy 1997). This has important implications for conservation of endangered animals and often there is a critical size necessary for founding populations to establish successfully (Courchamp et al. 2008). Breitenmoser et al. (2001) found that for carnivores, and the release of more individuals significantly increases the success rates.

Though it is probable that one-pack dynamics are a major factor in home-range expansion in MGR and that this might be remediated by the introduction of multiple packs, it is also possible that there were not enough resources or space within the park and probable that competition with hyaenas is limiting the wild dogs in some way. It is recommended that more detailed surveys of the reserve be done to quantify distribution and density of prey and competitors in MGR to allow more detailed analysis of the wild dog distribution and determination of whether other reintroductions to this area would be successful. It is important to ensure that adequate resources and a niche exist for a species before reintroduction is done. This is especially important for specialist species, such as the wild dog, that do not appear to be able to adapt to restrictive conditions (such as a smaller area available). As an epilogue, two new wild dog packs have been introduced in recent months to MGR and will be monitored in a similar fashion to this study.

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4. HABITAT SELECTION AND MOVEMENT PATTERNS OF RED FOXES ON PRINCE EDWARD ISLAND, CANADA

4.1 ABSTRACT

Animal response to spatial heterogeneity (i.e. diversity and spatial spread of habitat types) in the environment can be reflected in fine-scale movement patterns and in habitat selection. Random walk models are often used to describe and predict animal movement and can characterize different strategies, such as optimal foraging. In this study, snow-trails of red foxes, *Vulpes vulpes*, on Prince Edward Island were used to determine habitat selection and movement path characteristics in comparison with expectations based on correlated random walk and as a Lévy walk models in an effort to understand the influence of spatial heterogeneity and human impact on movement. Turning angles, move directions, path length, tortuosity, and net displacement were examined. Human-use areas were only preferred by foxes at National-Park sites, and forest was only avoided at the more heterogeneous and patchy sites. However, fine-scale movements of foxes showed little response to differing degrees of heterogeneity, fragmentation, or human activity. Fox movement patterns did not appear to be consistent with a correlated random walk but were well described by a Lévy walk model. However, a Lévy walk model with

external directional bias may be an even better fit to red fox movement on PEI in a winter landscape.

4.2 INTRODUCTION

The natural environment may have resources distributed spatially in a patchy (or fragmented) and diverse (or heterogeneous), manner. The fragmentation and the heterogeneity of habitats within a landscape can influence movement patterns of animals (Johnson et al. 1992; Turchin 1998; With et al. 1999) and, thus, from these patterns we can begin to understand how animals perceive and use their environment to obtain resources (e.g. Ball et al. 2000; Mårell et al. 2002; With et al. 1999). An environment can have little diversity of habitat types and still be patchy but for the most part, landscapes that are patchy or fragmented are also more heterogeneous in nature. Animals make biological 'moves' from one point to another based on interactions with their environment. Each move can be characterized by a length, a direction, and a turning angle, the angle at which the direction has changed from that of the previous move (Turchin 1998). A movement path of an animal is composed of the total collection of such moves. There are a variety of measures to characterize a movement path including total length, net displacement, absolute direction, and tortuosity, or measure of its shape or twistiness (Turchin 1998). Since the movement of animals is largely based upon their interactions with the landscape, habitats of different structure or composition should result in different movement patterns. For example, in good foraging areas and in areas where animals are restricted, move lengths have been found to decrease and turning angles increase, resulting in a more tortuous or compact path (Bell 1990; Benhamou and Bovet 1989; Etzenhouser et al. 1998; Stapp and Van Horne 1997; Whittington et al. 2004).

Field methods are typically employed to obtain animal movement data, but theoretical models are useful for further describing and interpreting observed movement patterns. Computer simulations are valuable tools not only for testing basic theoretical models, but also for designing individual-based movement models that take into account more complexity in both walker (animal) and landscape. Simulations can be particularly useful when there is a limited amount of field data and it is desirable to model movement under specific conditions or when theoretical models do not have the complexity required to model realistic movement. For example, most theoretical models describe movement occurring in a homogenous landscape, which may not be representative of a natural landscape.

There are a number of theoretical models that are typically employed to describe animal movement patterns observed in field studies. The most basic model is the Brownian random walk (BRW) model, in which an animal (or other agent of movement) is equally likely to move in any direction, with no persistence or bias (Turchin 1998). However, this model is very simplistic and does not take into account the complexity of real animal behavior (Austin et al. 2004). The correlated random walk (CRW) model is often used to describe animal movement patterns where directional persistence is a dominating factor governing movement (Turchin 1998). This is a common model used in the study of insects (e.g. Kareiva and Shigesada 1983), but has also been used to explain the movement patterns of mammals, such as caribou, at larger spatial scales (Bergman et al. 2000). The Lévy walk (LW) model is another type of random walk model used to describe animal movement and is characterized by random movement with small moves in patches and fewer longer moves connecting patches of movement (Viswanathan et al. 2000). A LW has been used to model optimal foraging in a variety of animal species because movement paths have higher net displacement (and thus visitation of new foraging sites) than those of a BRW or a CRW model (Viswanathan et al. 1999; Weeks et al. 1995).

Computer simulations are a powerful means to test underlying assumptions in models typically used to describe animal movement and to probe movement in a variety of different landscapes. Simulations can be used to study the movement patterns of individual-based walker models in artificially generated landscapes with a variety of biases and conditions (e.g. Carter and Finn 1999; Gardner et al. 1989; Zollner and Lima 1999). Theoretical random walk models are often used in simulations, and CRW and LW models can provide realistic predictions (e.g. Bradshaw et al. 2007; Byers 2001; Schippers et al. 1996; Schumaker 1996; Zollner and Lima 1999).

Prince Edward Island (PEI) is found on the East coast of Canada. It is only about 5,767.2 km^2 (Fig. 1), with over a third of that area devoted to agriculture (PEI DAF 2000). As a result, PEI is composed of a patchwork of fields, forest, and human-use areas. PEI National Park (PEINP) is found along the North shore and is a popular destination for tourists and residents of PEI in the summer months. The red fox (*Vulpes vulpes*, also herein called 'fox') was the largest mammal on PEI until the arrival of the coyote in the early 1980's (Thomas and Dibblee 1986), and is now established in urban as well as rural areas. Many residents and tourists partake in the feeding of foxes in certain geographical areas of PEI, such as in PEINP. It is suggested that this feeding practice may have negatively affected the normal behavior and activities of the red fox. For example, red foxes are fed along some roadsides (personal communication P. McCabe PEINP Park Ecologist; personal observations), consequently habituating these animals to humans and vehicles and contributing to roadside mortality. In more isolated areas, where the feeding of foxes is not very common, foxes exhibit more "wild" characteristics, such as a fear of people. To gain a better understanding of the impact of human activities on red foxes on PEI, it is important to study populations in both natural and more human-impacted areas.

Human activities on PEI, such as agriculture and urban development, could directly impact fox behaviour through habitat loss and fragmentation. Climate change could also have effects on the movement patterns of the red fox by gradually changing resource and prey distribution. If critical habitats for foxes are removed, they may be forced to live in lower-quality habitats, upsetting the balance of the local ecosystem. As a result of habitat loss, foxes may be brought into closer proximity to urban or human-use areas, where there is increased risk of human-related mortality (e.g. road deaths, persecution). Because PEI is a sensitive fragmented coastal area subject to both climate change and disruptive human activities, it is important to monitor fox movement patterns and habitat selection. Fox distribution and movement patterns are also relevant to the potential effects that foxes could in turn have on human populations (e.g. zoonotic diseases).

There have been many studies on the home range and habitat selection of the red fox showing them to be very adaptable animals (Cavallini and Lovari 1991; Phillips and Catling 1991; Van Etten et al. 2007). The effect of resource patchiness on fox home range has also been studied (e.g. Lucherini and Lovari 1996; Macdonald et al. 1999). However, only one published study was found to examine the fine-scale movement patterns of red foxes using field data (Sargeant et al. 1965). No such studies have been done on PEI. In addition, there has been only one study done on PEI pertaining to fox distribution and habitat selection (Silva et al. 2009). The main objective of this study was to investigate the relationships of human activities, and landscape fragmentation and heterogeneity on the habitat selection and movement patterns of the red fox on PEI. It was hypothesized that foxes would select habitats and move differently within PEINP than at privately-owned sites. The rationale behind this idea is that PEINP sites, being public and visited intensely by tourists in the summer season, are theoretically more human-impacted and potentially more fragmented.

4.3 MATERIALS AND METHODS

In this study, I examined the habitat selection and movement patterns of the red fox at four study sites on PEI. The sites differed in the relative levels of human-impact and fragmentation. Live-trapping and snow-tracking were attempted at study sites to obtain movement data. In conjunction with GIS habitat information for the area, interactions of red foxes with their environment were assessed with resulting snow-tracking data. Computer simulations were performed to test some basic hypotheses of animal movement in fragmented landscapes, then to compare resulting movement paths to field observations for red foxes. Fox diet and parasite load were analyzed in a concurrent study in an attempt to further compare fox ecology among study sites and this work is found in Appendix 2.

Study Sites.—Brackley (46.41°, -063.18°), Stanhope (46.43°, -063.15°), and Cavendish (46.50°, -063.43°) are located in PEINP on the north shore of Prince Edward Island, and Alexandra (46.19°, -063.01°) and St. Catherines (46.19°, -063.31°) are located on private lands in southern PEI (Fig. 4.1). These study sites were known to have foxes, and St. Catherines and a portion of Brackley-Stanhope were used in a previous study (Silva et al. 2009). Study areas needed to be accessible in the winter, and sites were required along the North shore as part of funding source requirements. Within study areas, sites were selected based on preliminary surveys for signs of foxes such as scat and tracks. The Cavendish study site (1.54 km^2) is located along the Homestead

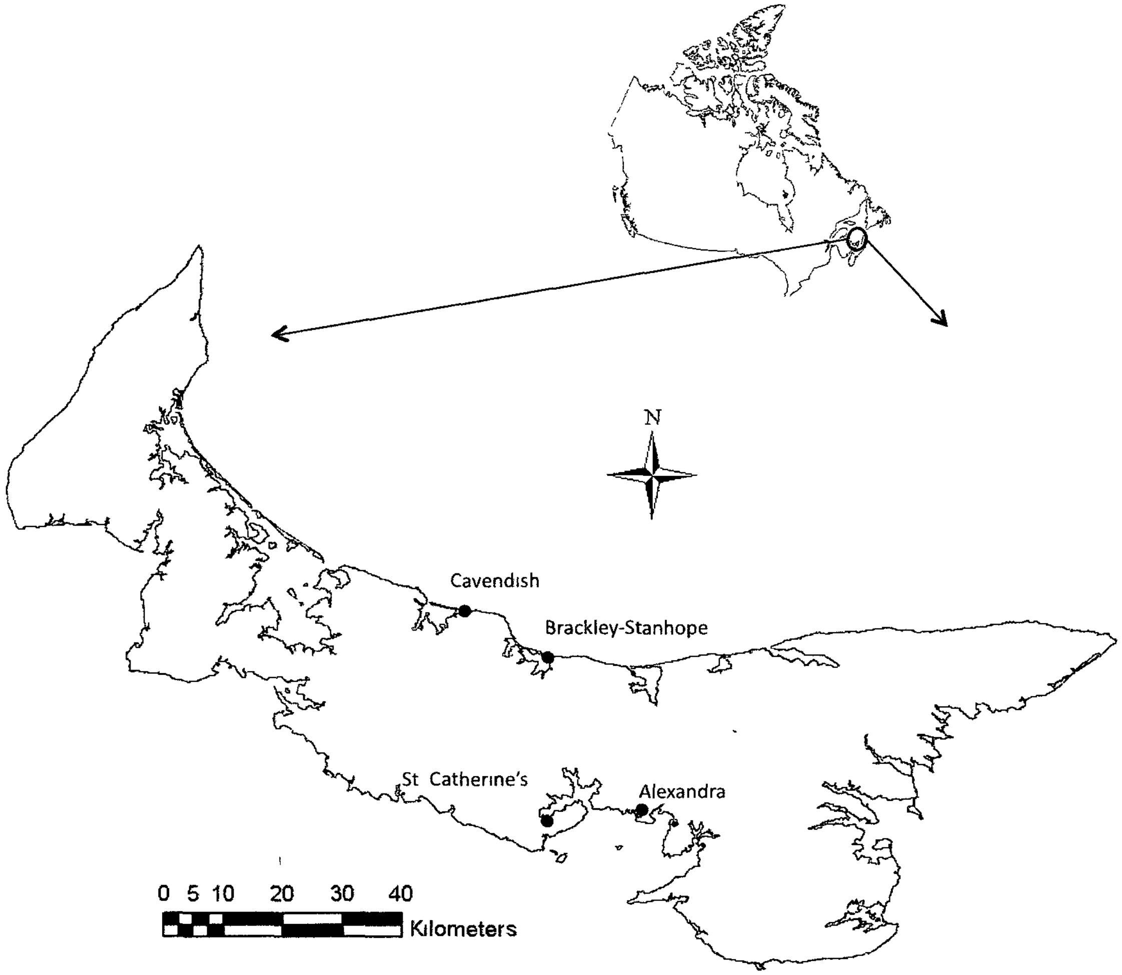

FIG. 4.1.—Map of Prince Edward Island drawn out from its location in Canada. Circles (●) indicate study sites.

trail, an 8 km stretch of biking and walking trail that intersects wooded areas, agricultural land, open fields, marshes, and picnic areas. The Brackley-Stanhope study site (1.14 km^2) is an amalgamation of two sites very close to each other in the PEINP. This combined site straddles a highway through the PEINP and includes picnic areas, playgrounds, public beaches, trails, parking lots, campgrounds, sand dunes, grassy areas, meadows, and forest. The Alexandra site (0.05 km^2) is mainly an agricultural area, with some residential areas and marsh. The St. Catherines site (2.49 km^2) is located on the West River, and includes agricultural land, forest with trails, and some residences. Study site areas were approximated by area contained within the outermost points of the recorded snow-tracking trails. Private lands were used with permission from landowners, and permission was obtained from PEINP authorities for research in that area.

Data Collection and Processing.—Live-trapping sessions were conducted from August 2009 to February 2010 at Stanhope and St. Catherines (Animal Care Protocol # 08-058- (1002873), Parks Canada Agency Research and Collections Permit # PEINP-2009-3372). Havahart 2-door box traps were used (Model #1050, 42"L x 10"W x 13"H, Woodstream Corporation, Lititz, PA), and each session was composed of a 3-6 day pre-baiting period during which the trap was wired open and bait was gradually placed closer to the trap. A variety of baits were used including bologna, bacon, duck, and chicken, and cover scent (Tink's Red Fox P, Tink's, Covington, GA, USA) was used. Traps were then set 1-2 times per day for a period of three days and were checked within 4-6 hours of setting. Traps were placed in areas where scat or tracks had been found, along animal trails, or in other areas where foxes had been observed by landowners or PEINP staff. A protocol was in place for subsequent handling, immobilization, and GPS-collaring of foxes (Appendix 3).

Snow-tracking was conducted at all study sites for the winter seasons of 2008 to 2009 and 2009 to 2010. Red fox tracks were initially located by surveying roads and habitat edges, as well as both walking and cross-country skiing trails. The trail was traversed from one end to the other. These 'ends' were located where it was uncertain where the trail continued on because of loss of visibility (melting or blowing snow) or mixing with other snowtrails (fox, snowshoe hare, etc). Locational fixes (latitude and longitude) and snow depth (centimeters) were recorded approximately every 5 m along each fox trail using a hand-held Garmin-GPS unit (Garmin eTrex Legend C, Garmin Ltd., Olathe, Kansas, USA). Only snow-trails longer than 25 m were included in this study. This limited the length of snowtrails collected but ensures that movement patterns of a trail resulted from one individual. Fixes in latitude and longitude were used for habitat selection analysis but were converted to XY coordinates (formulas from Barraquand and Benhamou 2008) for path analyses.

ArcView GIS (v. 9.3, Environmental Systems Research Institute, Inc., Redlands, California) was used to map the animal GPS locations from snow-tracking data onto a GIS layer of PEI (PEI DAF 2000). This GIS layer was used to classify land at the study sites into the following categories: forest, agriculture, human-use, roads, dunes, wetland, and abandoned land. Although this GIS is about 10 years old, the study sites used here have not had major changes in land use during that time period. Landscape types in the PEINP are preserved, and no major residential development or land clearing has occurred at either of the private study sites. The software package Fragstats (version 3.3; McGarigal and Marks 1995; www.umass.edu/landeco/research/fragstats/fragstats.html) was used to calculate landscape metrics, or mathematical calculations, characterizing the structure and diversity of each of the four study sites. The study sites were delineated by the 100% minimum convex polygons of datasets. The metrics chosen for this study were: (1) number of patches of habitat; (2) percentage of like adjacencies; (3) interspersion and juxtaposition index; (4) Simpson's diversity index; and (5) aggregation index (see Table 4.1 for more details). This combination of metrics was chosen for its ability to differentiate landscapes based on patchiness and heterogeneity.

Habitat Selection.—Habitat selection was examined at each study site with the Neu method; a straightforward application of the χ^2 goodness-of-fit test used to compare observed counts of animals in each habitat with the counts expected if habitats are used in proportion to their availability (Byers et al. 1984; Neu et al. 1974). The expected proportion of use (or availability) of a habitat type was defined as the ratio of the area of that habitat to the total area of the study site. The observed, or true, proportion of use of a habitat type was

TABLE 4.1.—Explanation of landscape metrics used in this study (adapted from McGarigal and Marks 1995).

Metric	Acronym	Units	Explanation
Number of patches	NP	None	Number of patches within the landscape
Percentage of like adjacencies	PLADJ	Percent	Measures degree of aggregation (dispersion) of patch types. Landscape with larger patches with simple shapes will have higher value.
Interspersion and juxtaposition index	IJI	Percent	Based on adjacent patches and isolates interspersion or intermixing of patch types. Approaches 0 when patch type adjacent to only one other patch type, Equal to 100 if a patch type is equally adjacent to all other types.

Continued

TABLE 4.1.—Continued.

Metric	Acronym	Units	Explanation
Simpson`s diversity index	SIDI	None	Measure of the diversity (heterogeneity) of landscape. Approaches 1 as the number of patch types increases and the distribution of area among types becomes more even.
Aggregation Index	AI	Percent	Approaches 100 when patch types are maximally aggregated into single, compact patches.

defined as the ratio of the number of animal locations in that habitat to the total number of locations recorded for the entire study site. The χ^2 test is first used to test whether the observed distribution of use differs from the expected distribution (based on expected proportions of use for habitat types). If there is a significant deviation, Bonferroni confidence intervals are calculated for each habitat type around the observed proportions of use to determine which habtiats specifically are preferred or avoided. If the expected proportion of use falls within the confidence interval, the habitat is used as expected (no significant difference), if it falls above the interval, the habitat is avoided, and if below, the habitat is preferred. 95% simultaneous Bonferroni confidence intervals were calculated for habitats based on the formula:

$$p_i - Z_{\alpha/2k}\, [\sqrt{(\, p_i(1- p_i)/n)}] \leq p_i \leq p_i + Z_{\alpha/2k}\, [\, \sqrt{(\, p_i\, (1- p_i)/n)}] \qquad (1)$$

where p_i = observed proportion of use, $Z_{\alpha/2k}$ is the upper standard normal table value with a probability of $\alpha/2k$, α is the critical level of significance (0.05), k = number of habitat types, and n = total number of observations (Neu et al. 1974).

Path Analyses and Model Comparison.—With the assistance of Dr. Sheldon Opps (Physics Department, University of Prince Edward Island), a movement analysis software tool was written in C programming language on a Macintosh (Mac OS X version10.5.8). For each snow-trail (herein ‘path’), this software was used to calculate the total length (L), net displacement (*R*), and straightness (ţ). Straightness was defined as the inverse of the typical tortuosity measure (ţ = net displacement/total path length). Turning angles and move directions were calculated from each step, and correlation in turning angles was calculated from successive steps away from the origin (or lags) using the Animal Movement Analysis Program (AMAP, created by Dr. Sheldon Opps in the Physics Department, UPEI in C++, Mac OS X version10.5.8). The lag at which the correlation in turning angles dropped to 0.368% of its original value (CorD, correlation decay) was measured graphically for each path as it could indicate the spatial scale at which movement pattern changes (direction). This value (equivalent to 1/e) was chosen as it represents the relaxation or life of an exponential decay (Pant and Levinger 1999; Sakurai 2006) and upon preliminary graphing of correlation of turning angles, exponential decay appeared to fit the data. The transition index (TrIn), or number of times an animal moved into a different type of habitat, was also calculated for each path to give a measure of habitat diversity within a path. Kruskal-Wallis tests were used to compare net displacement, length, average snow depth, TrIn, CorD, ţ, average turning angle, and average move direction of paths among sites, and were followed by Mann-Whitney U-tests for pair-wise comparisons where necessary. Two-tailed Spearman's rank correlation (Zar 1972) was used to examine relationships between snow depth and ţ and L, between L and ţ, and between TrIn and ţ and CorD within study sites. The goal of this analysis was to assess the influence of habitat characteristics on movement.

A basic assumption of a CRW is that neither the turning angles nor the move lengths are autocorrelated (Kareiva and Shigesada 1983; McCulloch and Cain 1989; Turchin 1998). It is understood that some autocorrelation of move lengths and turning angles is built into the sampling design since snow-trails were sampled at very frequent distance intervals, and not necessarily at the biologically distinct move intervals made by the animal. As a result, it is possible that sequential sampled points were actually part of the same move and therefore were dependent. Correlation in turning angles was examined graphically at different lags for each path. If the same general pattern was occurring at a study site, path autocorrelations were averaged to get a single correlation graph. This averaged autocorrelation data was then tested for significant autocorrelation (greater than two standard errors from zero) at different lags, or steps away from the origin. A CRW is typified by directional persistence or positive correlation in move directions, and turning angles concentrated around zero degrees (Turchin 1998). However, if angles are uniformly distributed around 360°, a Brownian random walk model is more likely to be appropriate (Cain 1985). Rayleigh z-tests were used to test the uniformity of turning angles at each study site and rose plots were generated to show this angle distribution graphically.

Comparison with a CRW was done at the step level and also at the overall path level (using AMAP) to see if movement differed at different spatial scales. For the step-level analysis, the observed net squared displacement (R_n^2) was calculated at each lag, n, for each path and then the mean net squared displacement was calculated as an average over all paths at each study site. The expected net squared displacement was calculated from the following equation (Kareiva and Shigesada 1983):

$$R_n^2 = nm_2 + 2m_1^2 \, [\{((c - c^2 - s^2)\, n - c)/((1 - c)^2 + s^2)\} + \{(2s^2 + (c^2 + s^2)^{(n+1)/2})/(((1 - c)^2 + s^2)^2)\}\, y] \tag{2}$$

where:

m_1 = mean move length (3)

m_2 = mean squared move length (4)

c = average cosine of the turning angle (5)

s = average sine of the turning angle (6)

$y = [(1 - c)^2 - s^2] \cos[(n + 1)\, \alpha] - 2s\, (1 - c) \sin[(n + 1)\, \alpha]$ (7)

$\alpha = \arctan(s/c)$ (8)

To compare the observed R_n^2 values with the expected ones, turning angles and move lengths were pooled over all paths for each site. Then bootstrapping was performed on pooled data in order to construct confidence intervals (at the 95% level) at each lag, n, about the expected R_n^2 values. A path-level analysis was done by log transforming the graph of net squared displacement against lag for each path. Regression analysis was then performed on each graph to obtain the slope (scaling exponent) of the line. The same procedure was used to determine the expected slopes based on the R^2 values predicted for a CRW. A two-tailed paired sample t-test was performed to compare the slopes obtained from field data to those expected for a CRW. A paired test was required because the R^2 predictions based on the CRW model are dependent on the observed movement data.

To determine if movement is characteristic of a Lévy walk (LW), the move length distribution is typically analyzed. A LW has scale-invariant properties that have a long-tail distribution as a result of a power-law relationship between path properties and successive steps (Shlesinger et al. 1993, Mårell et al. 2002, Ramos-Fernández et al. 2004). A power-law distribution typically takes the form:

$$X \sim x^a \qquad (9)$$

where variation in X is dependent on the exponent, a. The exponent for the move length distribution for a LW is between -2 and -3 (Ramos-Fernández et al. 2004) and -2 is the optimal value for efficient foraging (Viswanathan et al. 2000). The mean squared displacement of a LW also has a power-law relationship with successive steps, and the exponent should fall between 1 and 2 (Ramos-Fernández et al. 2004; Viswanathan et al 2000). Use of this scaling exponent is a way of looking at the 'waiting periods' associated with a LW (Ramos-Fernández et al. 2004). These exponents are obtained by graphing the log-log plot of either move length or mean squared displacement against step from the origin, or lag (Ramos-Fernández et al. 2004; Viswanathan et al. 2000). Since the data in this study had an artificially clumped move distribution around 5 m, the approximate interval at which measurements were taken, the slope (scaling exponent) was determined from the linear regression on the log-log plot of mean displacement squared as a function of lag. Although the AMAP program could be used to renormalize the movement paths to eliminate the artificial (serial) autocorrelation in move lengths, the number of measurements would become too small to provide for statistically meaningful path analysis.

Computer Simulations.—As a complementary approach to studying movement with field data, C language on a Macintosh (Mac OS X version10.5.8) was used to create simple agent-based Monte Carlo simulations of semi-random movement in a binary landscape. These simulations incorporated very simplified models designed to systematically explore the fundamental movement patterns of a random walker (with some inherent affinity) in different landscapes. They were not intended to mimic or predict the movement of foxes specifically, but to provide a baseline for comparison of movement patterns in a fragmented landscape. A landscape of 1,000 by 1,000 units was randomly decorated with 80:20, 50:50, and 20:80 percentages of 'good' and 'bad' habitats. The highest proportion of good habitat represented a more natural landscape, while a higher proportion of bad habitat represented a fragmented or patchy landscape. There were two types of walkers, a 'generalist' with an 80% affinity for both types of habitat, and a 'specialist' with an 80% affinity for good but only 20% for bad. The walker was set to the center of the landscape and allowed to make random steps in any direction, with a maximum length of 1 unit, up to 1,000,000 times. Boundaries reflected the animal back inward. The Monte Carlo simulation was run for 30 replicates were for each type of walker in each type of landscape (6 treatments). The landscape was randomly generated for each replicate in order to incorporate many possible variations in the configurations of the fragmented landscape.

The resulting movement paths were run through the same program used previously for path analysis. A one-way ANOVA was used to compare path straightness among landscape types for each generalist and specialist walkers. Two-sample t-tests were used to compare walker types in each type of landscape. The goal was to confirm hypotheses about generalist and specialist animal movements with respect to habitat fragmentation in order to draw further conclusions from field data. Generalist animals (with a high affinity for all habitat types) should move in a more random (tortuous) way even in fragmented habitats because they perceive habitat as almost homogeneous. Specialist animals (with a low affinity for some habitat types) should be restricted by their affinities and in fragmented habitats, should have more linear paths. Though the movement of foxes (and of wild dogs) is not likely as simplified as that of simulated walkers, some semblances may occur with movement of simulated generalists and specialists in fragmented landscapes that could allow us to make some general statements about the nature of these species.

All statistical analyses were done with Minitab v. 15.1.0.0, unless otherwise specified, with $P \leq 0.05$ considered significant, and $0.05 < P \leq 0.08$, marginally significant. All sample groups were first checked for normality with Kolmogorov-Smirnov tests.

4.4 RESULTS

Although considerable effort was invested in devising an effective live-trapping strategy, the trapping efforts were unsuccessful and no red foxes were caught. Discussions with local trappers have led to the modification of trap methodology for future studies. Snow-tracking yielded a total of 47 snow-trails over two winter seasons which were pooled over seasons to get a larger sample size. There were 11 paths in Alexandra, 17 in Brackley-Stanhope, 9 in Cavendish, and 10 in St. Catherines. Path lengths were not as long at Brackley-Stanhope and at St. Catherines as in another study (Silva et al. 2009) and this limits the amount of data on movement patterns that can be extracted. However, by ensuring that data collection was terminated where the direction of movement was uncertain, the likelihood of following a path that resulted from more than one individual or from the same individual at different times is decreased and the likelihood of obtaining movement patterns true to an individual is increased.

FragStats analyses showed that the study sites were very similar with respect to all metrics except for number of patches (Fig. 4.2), interspersion and juxtaposition index (Fig. 4.2), and Simpson's diversity index (Fig. 4.3). Based on higher numbers of patches, St. Catherines and Cavendish were more patchy or fragmented landscapes, and because they had higher interspersion and juxtaposition indices, the patch types were mixed in well amongst each other. Higher Simpson's diversity indices further indicate that these two sites are more heterogeneous than Alexandra and Brackley-Stanhope. Therefore, for the purpose of this study, it is assumed that St. Catherines and Cavendish were more fragmented (patchy) and heterogeneous.

Habitat Selection.—Despite the risk of spatially autocorrelated habitat data, all GPS fixes were used for the Neu method analysis of habitat selection.

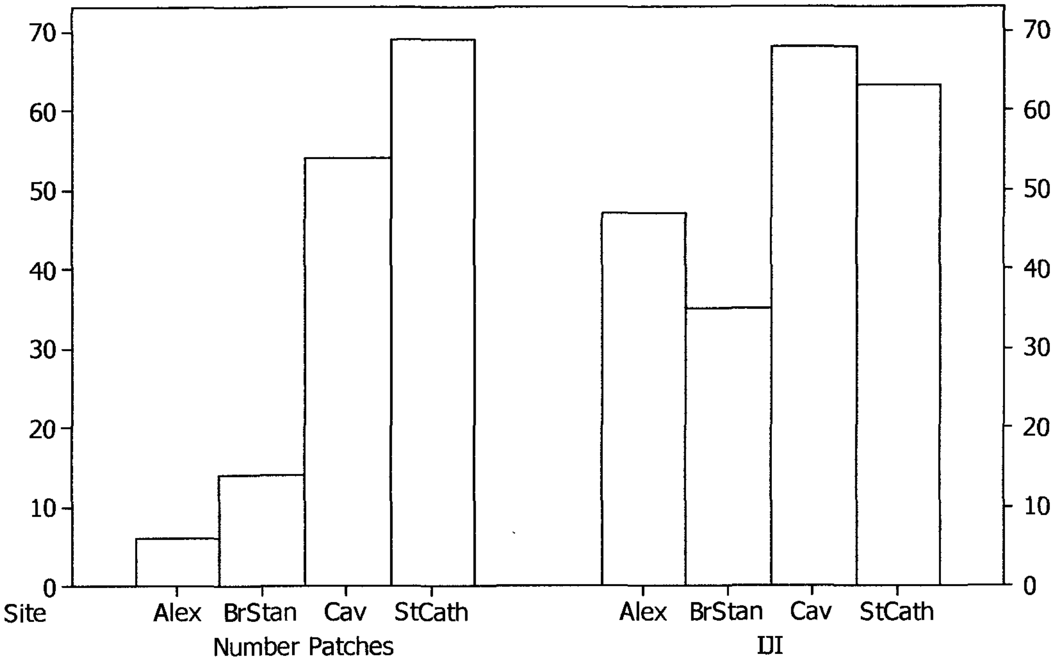

FIG. 4.2.—Site comparison for total number of patches (count) and interspersion and juxtaposition index (IJI-%). Alex is Alexandra, BrStan is Brackley-Stanhope, Cav is Cavendish, and StCath is St. Catherines.

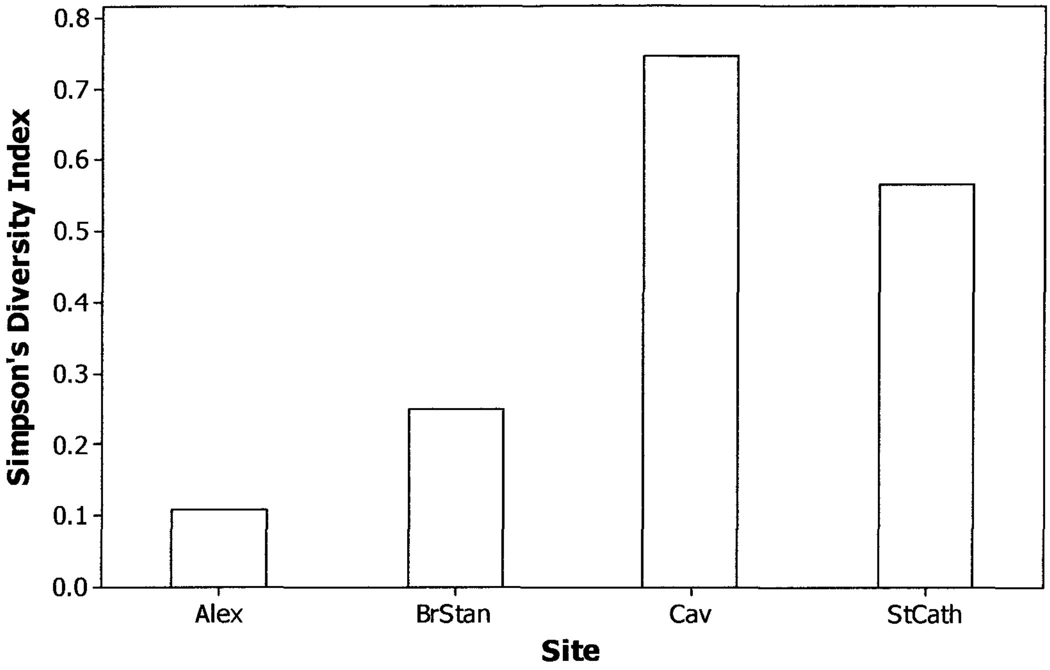

FIG. 4.3.—Site comparison with Simpson's diversity index (SIDI). Alex is Alexandra, BrStan is Brackley-Stanhope, Cav is Cavendish, and StCath is St. Catherines.

Because some trails were quite short (as short as 25 m), rarefying or renormalizing the data by re-sampling at larger intervals as suggested to remove autocorrelation (Boyce et al. 2002) could result in the loss of potentially important information on habitat selection. There were significant deviations from the expected distribution of use for each study site (χ^2 gooness-of-fit; $P < 0.001$), and Bonferroni intervals determined specific habitats that were preferred and avoided (Table 4.2). There was no consistent selection of habitat types across all study sites, but there were some interesting differences (Table 4.3). Human-use areas were preferred at PEINP sites (Brackley-Stanhope and Cavendish), while avoided or used as expected at private sites. Roads were used as expected at Cavendish and at Alexandra, while avoided at the other two sites. Wetland was avoided at all sites except for Alexandra, and dunes were used as expected. Abandoned land was used as expected at Cavendish but preferred at St. Catherines. Finally forest was avoided at Cavendish and at St. Catherines while used as expected at Alexandra and preferred at Brackley-Stanhope. At some study sites, there were fewer than 5 observations for human-use, road, and wetland habitat types. Although these results were still used because they relate to the research questions of this study, caution should be taken in interpretation and emphasis due to the limitations of the Chi-square test and Bonferroni confidence intervals with such small sample sizes.

Path Analyses and Model Comparisons.—There was a significant difference among study sites for average snow depth (Kruskal-Wallis test; $P < 0.001$,

TABLE 4.2.—Comparisons of use and availability of various habitat types used by red foxes based on snow-tracking data.

Habitat Type	Available Area (m^2)	Exp. Prop. Use	Obs. Counts	Obs. Prop. Use	Bonferroni CI	Use[1]
Alexandra (N = 166)						
Agriculture	51,541	0.944	142	0.855	$0.785 < p < 0.926$	--
Forest	2,542	0.047	15	0.090	$0.033 < p < 0.148$	0
Human-Use	181	0.003	1	0.006	$0 < p < 0.022$	0
Roads	86	0.002	2	0.012	$0 < p < 0.034$	0
Wetland	223	0.004	6	0.036	$0 < p < 0.074$	0
Brackley-Stanhope (N = 371)						
Dune	680,941	0.596	239	0.644	$0.580 < p < 0.708$	0
Forest	74,327	0.065	75	0.202	$0.148 < p < 0.256$	+
Human-Use	23,297	0.020	36	0.097	$0.057 < p < 0.137$	+
Roads	81,024	0.071	16	0.043	$0.016 < p < 0.070$	--
Wetland	283,703	0.248	5	0.013	$0 < p < 0.029$	--

Continued

TABLE 4.2.—Continued.

Habitat Type	Available Area (m^2)	Exp. Use	Obs. Counts	Obs. Use	Bonferroni CI	Use[1]
Cavendish (N = 310)						
Abandoned	400,296	0.259	94	0.303	$0.233 < p < 0.374$	0
Agriculture	564,248	0.366	128	0.345	$0.339 < p < 0.486$	0
Forest	337,715	0.219	35	0.113	$0.065 < p < 0.160$	--
Human-Use	119,164	0.077	41	0.132	$0.081 < p < 0.183$	+
Roads	30,532	0.020	10	0.032	$0.006 < p < 0.059$	0
Wetland	90,956	0.059	2	0.006	$0 < p < 0.018$	--
St. Catherines (N = 272)						
Abandoned	113,371	0.046	80	0.294	$0.221 < p < 0.367$	+
Agriculture	714,130	0.287	86	0.316	$0.242 < p < 0.391$	0
Forest	1,454,003	0.584	105	0.386	$0.308 < p < 0.464$	--
Human-Use	92,019	0.037	1	0.004	$0 < p < 0.014$	--
Roads	64,426	0.026	0	0	n/a	--*
Wetland	50,657	0.020	0	0	n/a	--*

[1] Use based on Bonferroni confidence intervals ($\alpha = 0.05$) around observed use. "+" indicates used more than expected; "--" indicates used less than expected; "0" indicates use according to availability or non-significant difference between expected and available. * indicates lack of use, 'n/a' indicates that a confidence interval could not be calculated due to lack of use.

TABLE 4.3.—Summary of habitat selection by red foxes on PEI[1,2].

	Study site			
Habitat Type	Alexandra (N = 166)	Brackley-Stanhope (N = 371)	Cavendish (N = 310)	St. Catherines (N = 272)
Abandoned			0	+
Agriculture	--		0	0
Dune		0		
Forest	0	+	--	--
Human-Use	0	+	+	--
Roads	0	--	0	--*
Wetland	0	--	--	--*

[1,2] Gray areas indicate a lack of that habitat type in the study site/area. "+" indicates used more than expected; "-" indicates used less than expected; "0" indicates use according to availability or non-significant difference between expected and available. * indicates lack of use.

Figure 4.4) and for net displacement (P = 0.047, Figure 4.5), and a marginally significant difference for total path length (P = 0.065, Figure 4.5). Although all pairs of sites were then compared, only some had significant differences. Brackley-Stanhope had significantly higher snow measurements than any other sites, followed by St. Catherines, then Alexandra, and then Cavendish (Table 4.4). Path net displacement was significantly higher at Cavendish than at Alexandra or at Brackley-Stanhope (Table 4.4), and total path length was higher at Cavendish than at Alexandra (Table 4.4). Within sites, snow depth varied in different habitat types (Fig. 4.6). There were no differences among study sites for path tortuosity, average turning angle, correlation decay, average move direction, or net displacement scaling factor (Kruskal-Wallis; P-values > 0.05). Although transition index did not differ significantly between sites, it did appear to have higher values for Brackley- Stanhope and Cavendish sites (PEINP) (Table 4.5). At Brackley-Stanhope, snow depth was negatively correlated with total path length, at Cavendish, snow depth was positively correlated with straightness (ţ) and ţ was negatively correlated with transition index, and at Alexandra and St. Catherines there were no significant within-path correlations (Table 4.6). Paths within study sites mainly showed a similar trend in correlation of turning angles for the most part (Fig. 4.7). There was no significant autocorrelation in turning angles of averaged paths at each site even at very short lags (P < 0.05), and this can be seen in the rapid drop in path autocorrelation (Fig. 4.8). Although it appears that there is fluctuation in autocorrelation around zero indicating changes in movement patterns of

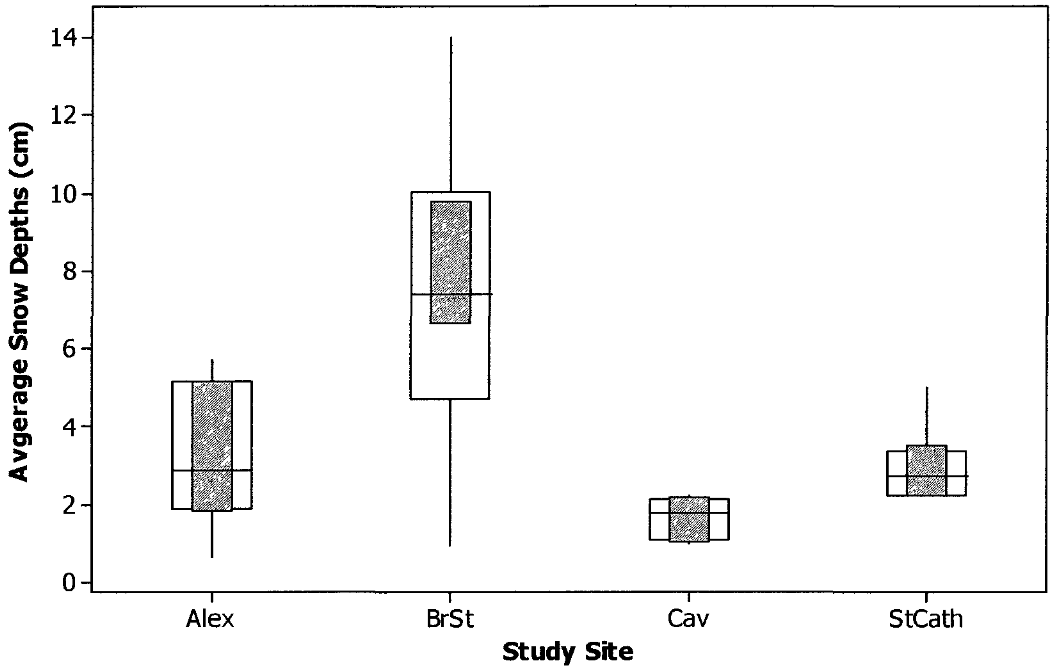

FIG. 4.4.—Site comparison by snow depth. Blank boxes outline the interquartile range, thatched boxes represent 95% CIs for the median. Alex is Alexandra, BrSt is Brackley-Stanhope, Cav is Cavendish, and StCath is St. Catherines.

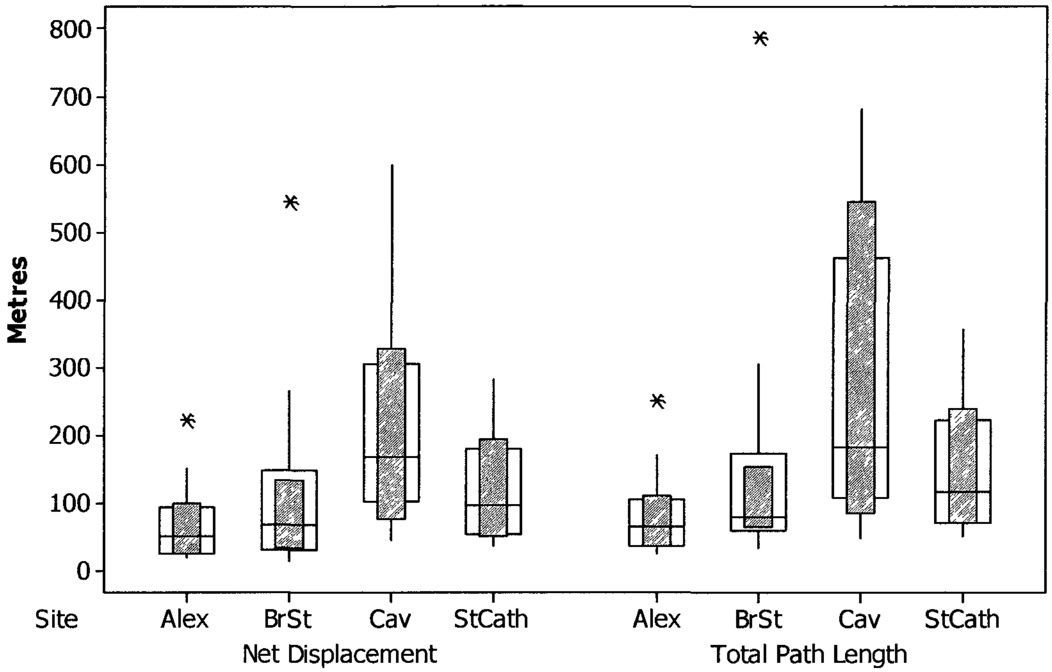

FIG. 4.5.—Site comparison by path net displacement and total path length[1]. [1] Blank boxes show the interquartile range, thatched boxes represent 95% CIs for the median. * represent outliers. Alex is Alexandra, BrSt is Brackley-Stanhope, Cav is Cavendish, and StCath is St. Catherines.

TABLE 4.4.—Summary of Mann-Whitney U-test comparisons between sites among which a KW test showed significant differences in snow depth, net displacement, and path length[1].

Study Site	Category		
Pair[2]	Snow Depth	Net Displacement	Path Length
A vs B	P = 0.002 (B)	NS	NS
A vs C	P = 0.056* (A)	P = 0.015 (C)	P = 0.019 (C)
A vs S	NS	NS	NS
B vs C	P = 0.001 (B)	P = 0.036 (C)	NS
B vs S	P = 0.006 (B)	NS	NS
C vs S	P = 0.001 (S)	NS	NS

[1] P-value, brackets indicate the study site that had higher values. [2] A means Alexandra, B means Brackley-Stanhope, C means Cavendish, S means St. Catherines. NS indicates no significant difference between sites. * indicates marginal significance.

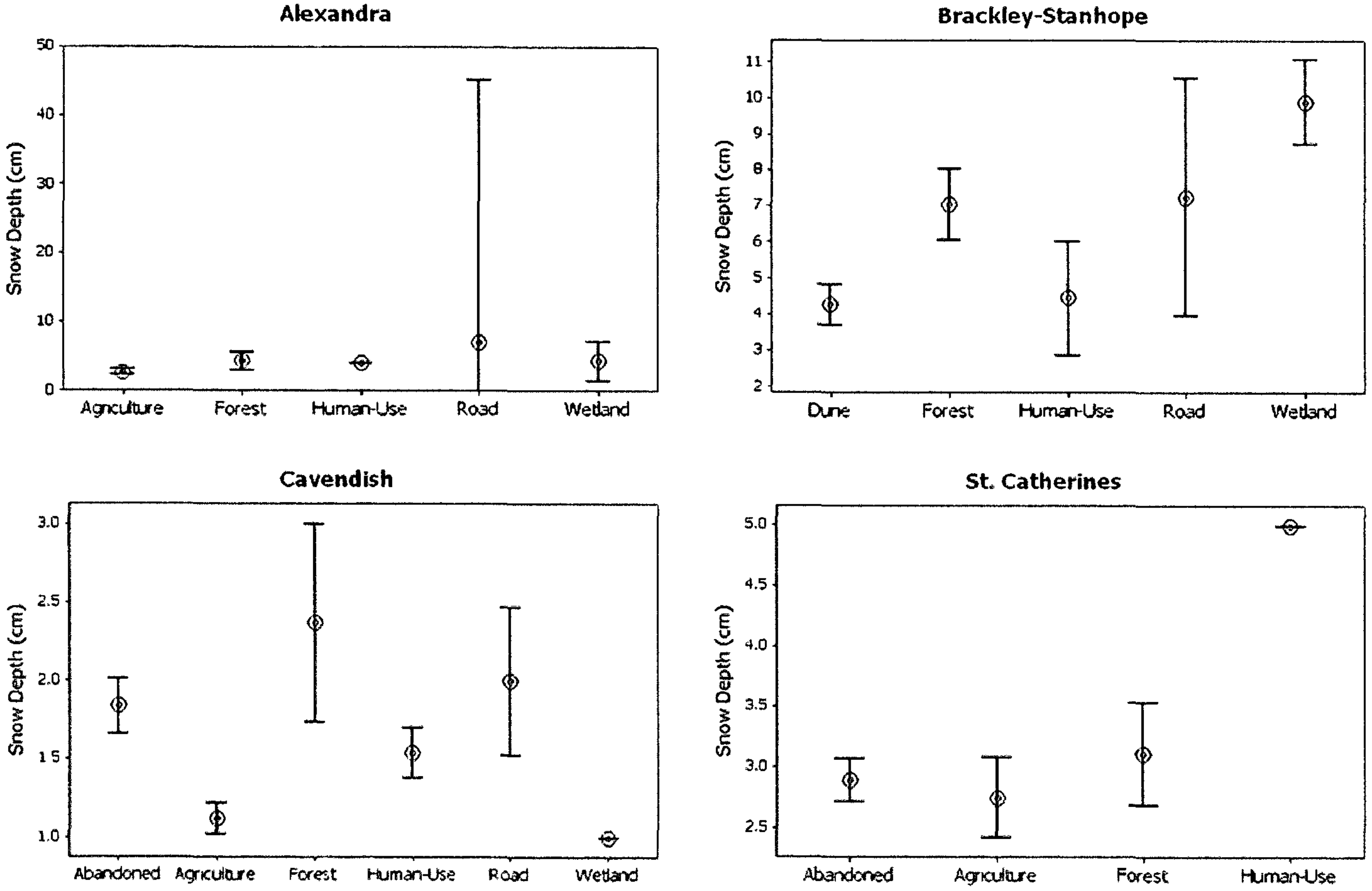

FIG. 4.6.—Snow depth variation in habitat types indicated by 95% intervals around the mean.

TABLE 4.5.—Study site comparison based on FragStats measures and basic path measurements.

Study Site	Variable[1]							
	NP	PLADJ	IJI	SIDI	AI	Snow (SE)	ţ (SE)	TrIn (SE)
Alexandra	6	95.671	47.154	0.109	98.439	3.065 (0.529)	0.826 (0.049)	0.636 (0.279)
Brackley-Stanhope	14	96.437	34.889	0.250	97.118	7.514 (0.905)	0.760 (0.056)	1.706 (0.498)
Cavendish	54	94.973	68.190	0.745	95.922	1.631 (0.168)	0.870 (0.041)	2.890 (1.410)
St. Catherines	69	96.527	63.222	0.566	97.166	3.012 (0.314)	0.790 (0.038)	1.600 (0.670)

[1] NP means number of patches, PLADJ is the percentage of like adjacencies, SIDI is the Simpson's diversity index, AI is the aggregation index, Snow is the average snow depth in centimetres, ţ is the average straightness (net displacement/total path length), and TrIn is the number of path transitions into different habitat types

TABLE 4.6.—Relationships of fox path characteristics tested with correlation analysis[1].

Study Site	**Pairs**[2]				
	Snow/ ţ	Snow/L	ţ /L	ţ /TrIn	CorD/TrIn
Alexandra	r_{sp} = 0.264	r_{sp} = -0.427	r_{sp} = -0.127	r_{sp} = -0.051	r_{sp} = 0.025
(df = 9, r_c = 0.700)					
Brackley-Stanhope	r_{sp} = -0.142	r_{sp} = -0.627*	r_{sp} = -0.123	r_{sp} = -0.201	r_{sp} = -0.259
(df = 15, r_c = 0.521)					
Cavendish	r_{sp} = 0.800*	r_{sp} = -0.367	r_{sp} = -0.583	r_{sp} = -0.881*	r_{sp} = 0.270
(df = 7, r_c = 0.786)					
St. Catherines	r_{sp} = -0.188	r_{sp} = 0.285	r_{sp} = 0.139	r_{sp} = 0.278	r_{sp} = 0.162
(df = 8, r_c = 0.738)					

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[1] df is the degrees of freedom, r_c is the critical value for a two-tailed test at the 95% significance level (Zar 1972), and r_{sp} is the Spearman's rank coefficient of correlation (* indicates significance). [2] Snow refers to snow depth, ţ means net displacement/total path length (straightness), L is total path length, TrIn is the transition index, CorD is the correlation decay (in turning angle). [3] NS indicates no significant relationship between pair values.

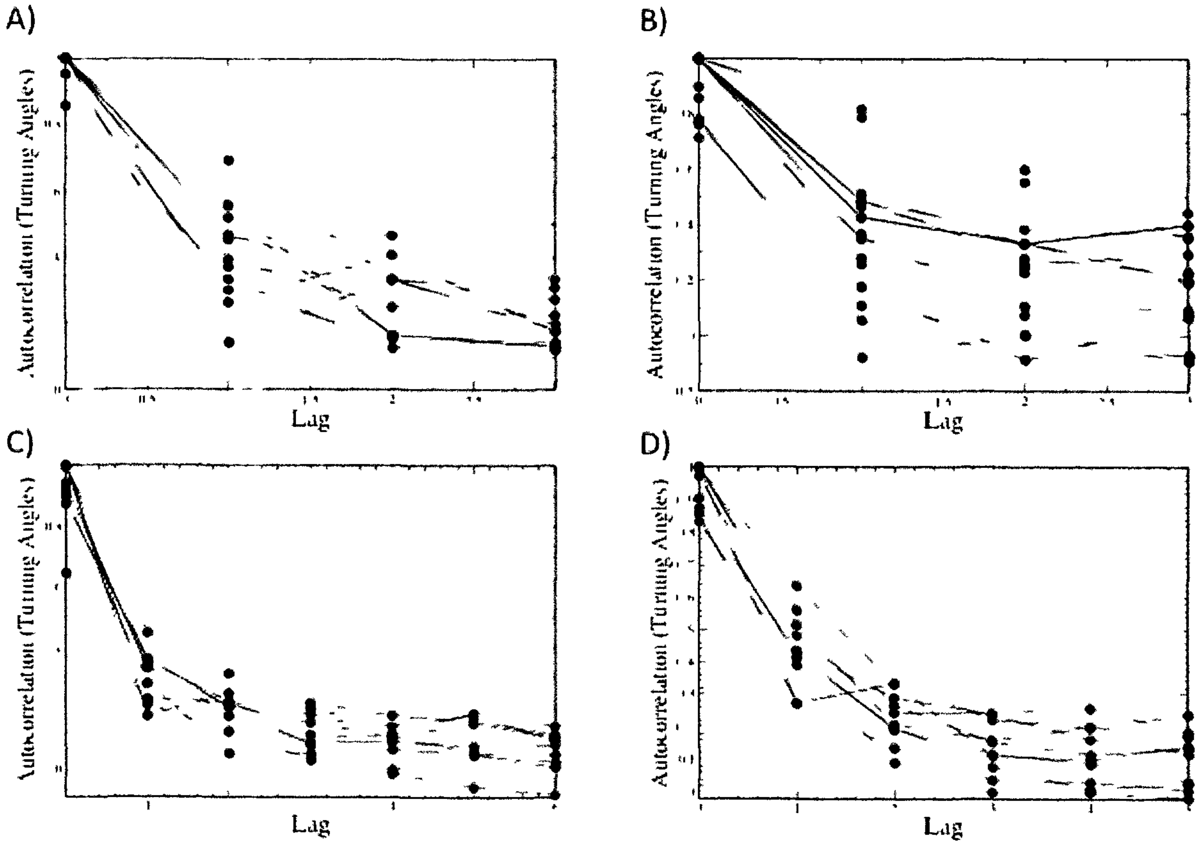

FIG. 4.7.—Correlation analysis of turning angles at A) Alexandra, B) Brackley-Stanhope, C) Cavendish, and D) St Catherines. Each line is a separate movement path.

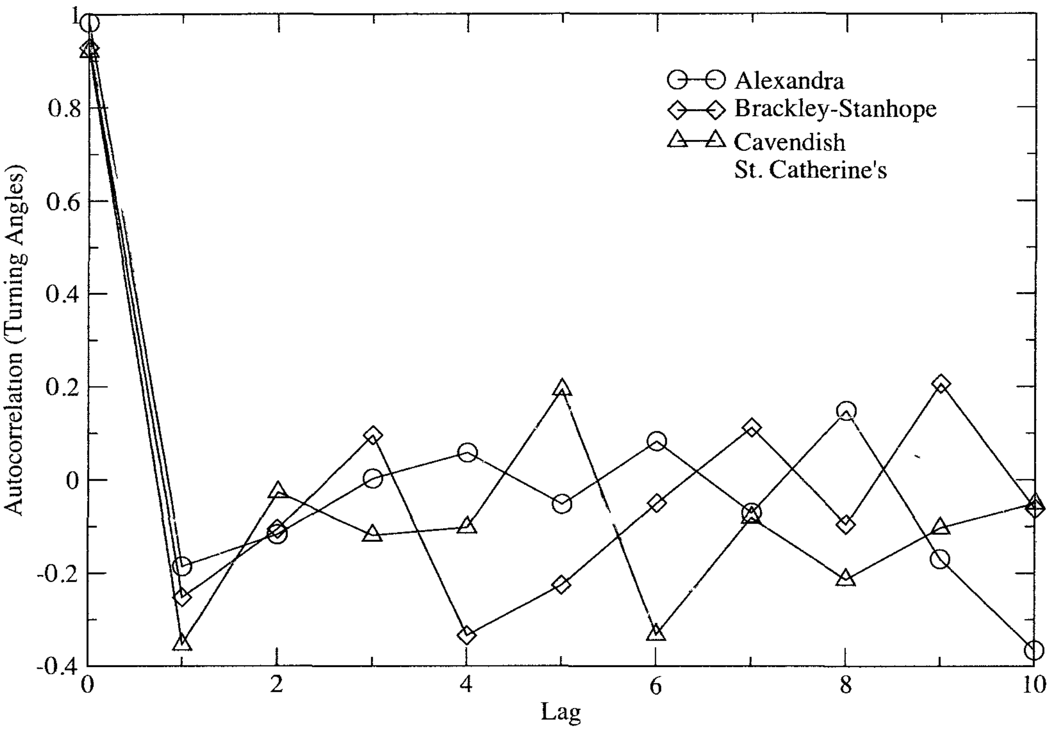

Fig. 4.8.—Correlation analysis of turning angles for study sites averaged over paths.

averaged paths, error bars showing the range of the original paths indicate this is likely the result of averaging (Fig. 4.9). Rayleigh z-tests showed that pooled turning angles were not uniformly distributed in Alexandra ($P < 0.001$), Brackley-Stanhope ($P < 0.001$), Cavendish ($P < 0.001$), or St. Catherines ($P < 0.001$) (Fig. 4.10).

Because turning angles were not autocorrelated and were clustered around zero, it appeared the data might fit a CRW model. However, the observed net displacement squared for all sites was higher than that predicted for a CRW for both the step-level analysis (Fig. 4.11) and the path-level analysis (Paired 2-sample t-tests; Alex: $P < 0.001$; Brackley-Stanhope: $P < 0.001$; Cavendish: $P < 0.001$; St. Catherines: $P < 0.001$). Therefore, foxes moved a longer distance, with a more direct path than would be expected from a CRW model at both scales of measurement. There was only one exception to this, at St. Catherines, where the mean net displacement squared fell within the bootstrapped 95% confidence intervals at lags higher than 50. Scaling exponents from log-transformed net displacement squared data plotted against lag fell between 1 and 2, with the exception of a single path (Fig. 4.12). These values are consistent with the expected mean squared displacement pattern of a super-diffusive Lévy walk (LW).

Simulations.—Simulated movement paths were obtained for generalist and specialist walkers in the three landscapes of differing fragmentation. Specialists and generalists appeared to react differently to fragmentation as shown by path

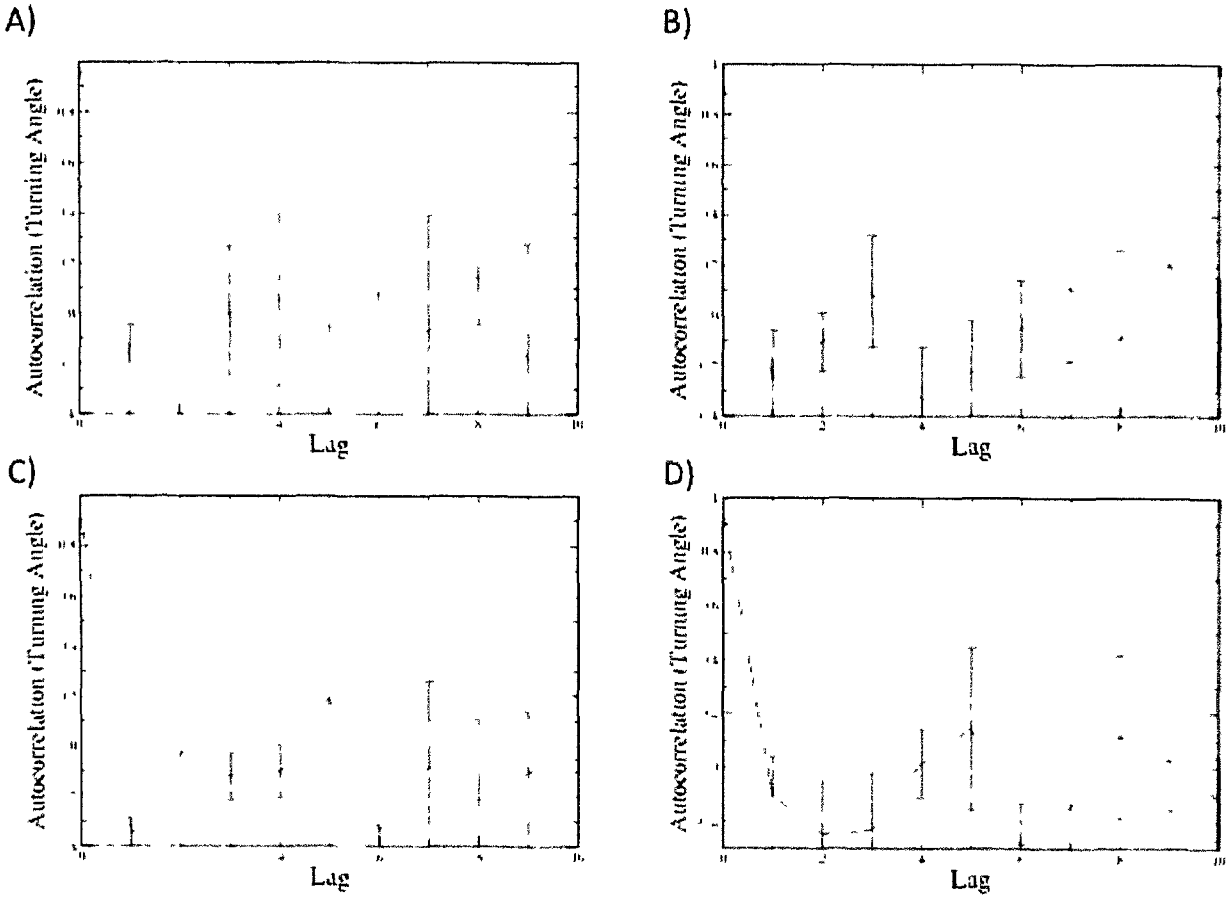

FIG. 4.9.—Correlation analysis for averaged paths for A) Alexandra, B) Brackley-Stanhope, C) Cavendish, and D) St. Catherines. Interval bars indicate the range of the original paths.

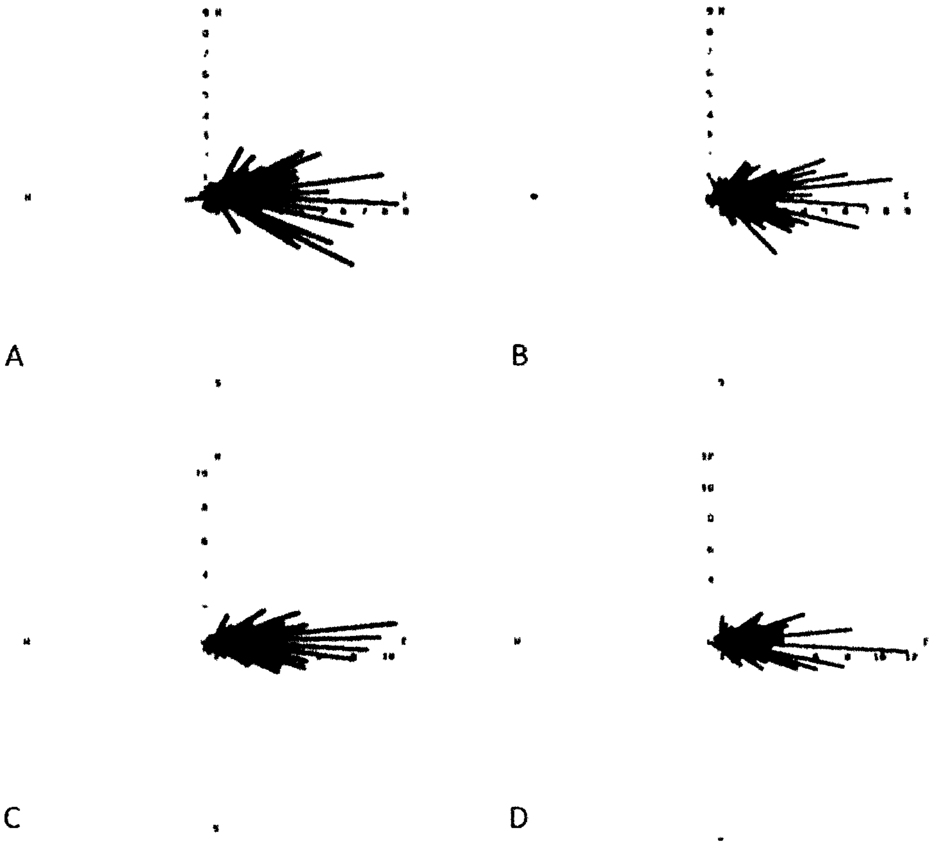

Fig. 4.10.—Roseplots showing turning angle distribution for A) Alexandra, B) Brackley-Stanhope, C) Cavendish, and D) St. Catherines.

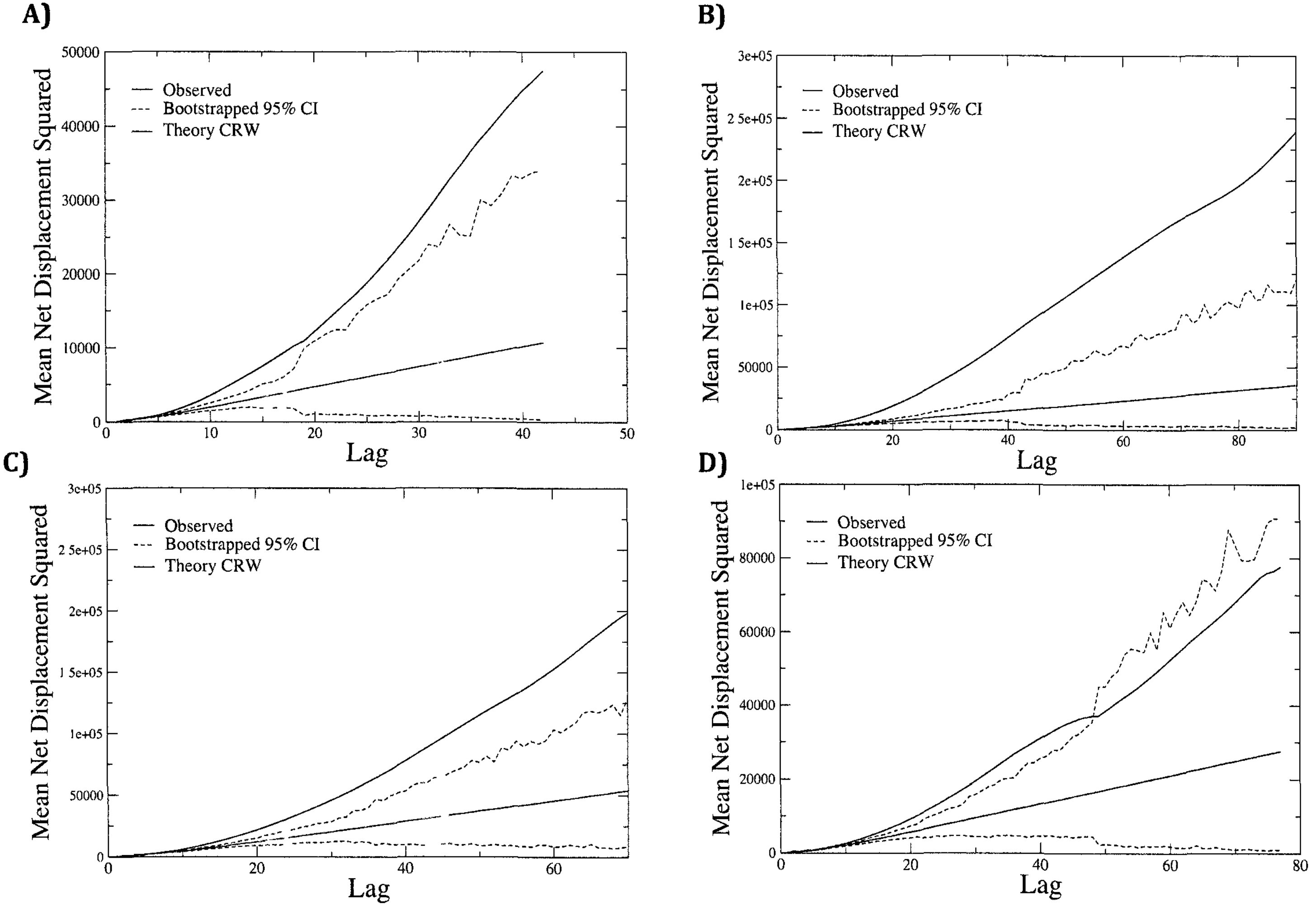

Fig. 4.11.—Comparison of observed mean net squared displacement to expected based on a CRW for paths in A) Alexandra, B) Brackley-Stanhope, C) Cavendish, and D) St. Catherines.

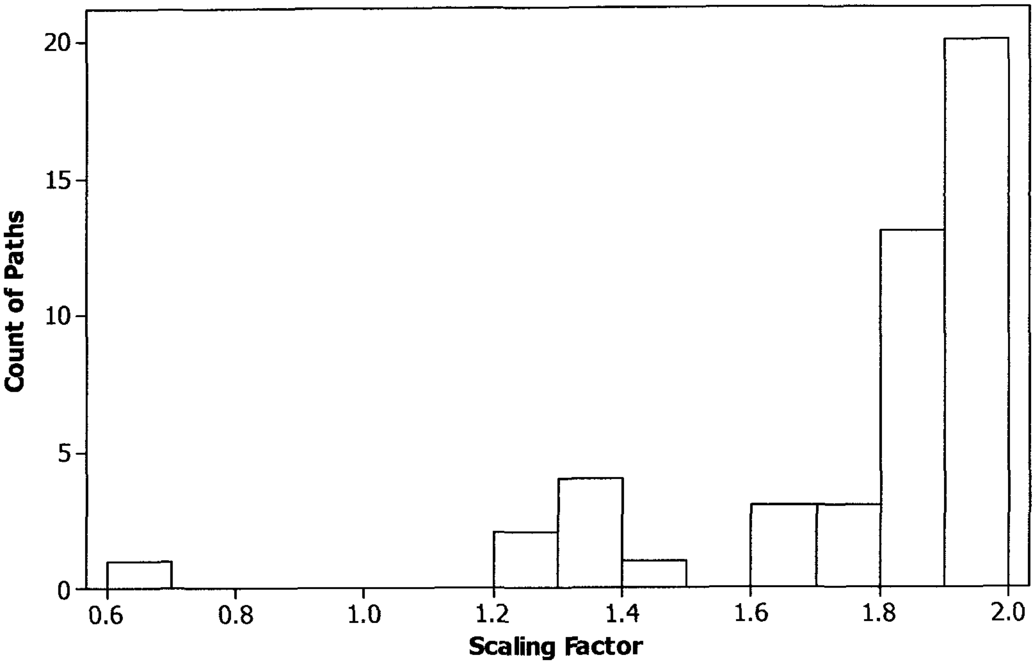

FIG. 4.12.—Distribution of mean net displacement squared scaling factors.

straightness (Fig. 4.13). Path straightness differed significantly between generalists and specialists for highly fragmented landscapes (Fragmentation level 3; 2-sample t-test; $P < 0.001$) and marginally for natural landscapes (Fragmentation level 1; $P = 0.052$). For specialists, paths became significantly straighter with each degree of fragmentation (ANOVA; $R^2 = 0.01762$; $P < 0.001$), but generalist paths did not differ significantly in straightness with differing degrees of fragmentation ($P > 0.05$) (see Fig. 4.14).

4.5 DISCUSSION

The snow-tracking method proved to be a successful means to obtain habitat selection information and fine-detail movement patterns of red foxes on Prince Edward Island. It was expected that there would be differences between sites located in the PEINP (Brackley-Stanhope and Cavendish) versus on private lands (Alexandra and St. Catherines) since recreational public land is used by more people of the general public, even in the winter (e.g. walking, skiing), and is therefore assumed to have a more consistent and direct human influence. There were some obvious differences in habitat selection between PEINP and private sites, but also interesting results for sites differing in heterogeneity and patchiness. Based on simulations, it was expected that generalist path straightness would not be affected by degree of patchiness but that specialists would have more direct paths with increasing patchiness. Because straightness was not significantly different among study sites, foxes appear to be generalists, and are moving through landscapes without much

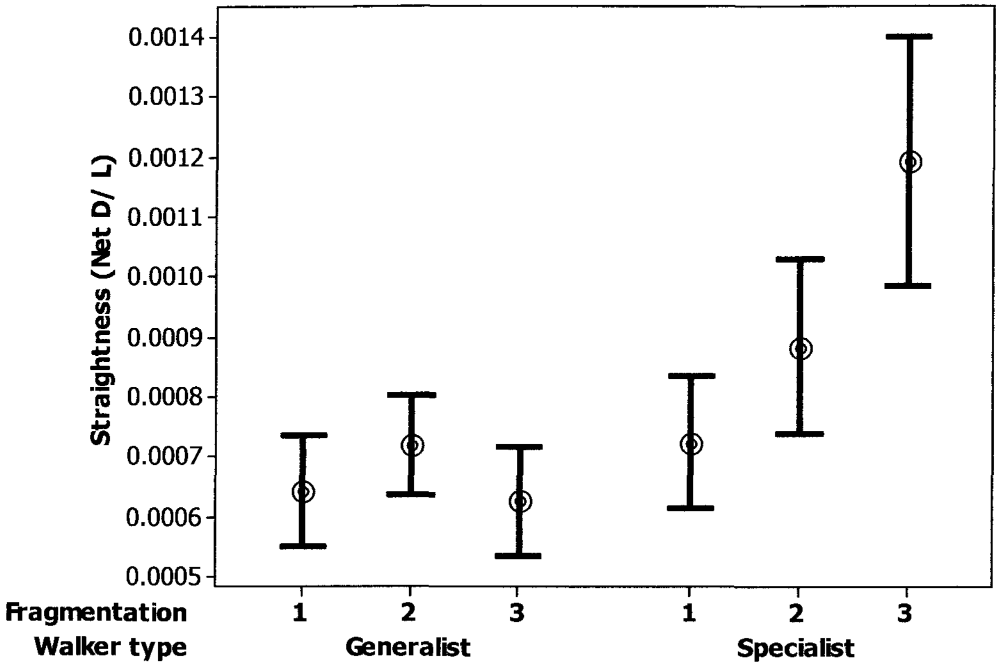

FIG. 4.13.—Interval plot for the mean tortuosity of simulated movement paths (95% confidence level). Fragmentation is listed in increasing order where 1 means least fragmentation (80% good habitat), 2 means intermediate (50% good), and 3 is patchy (20% good).

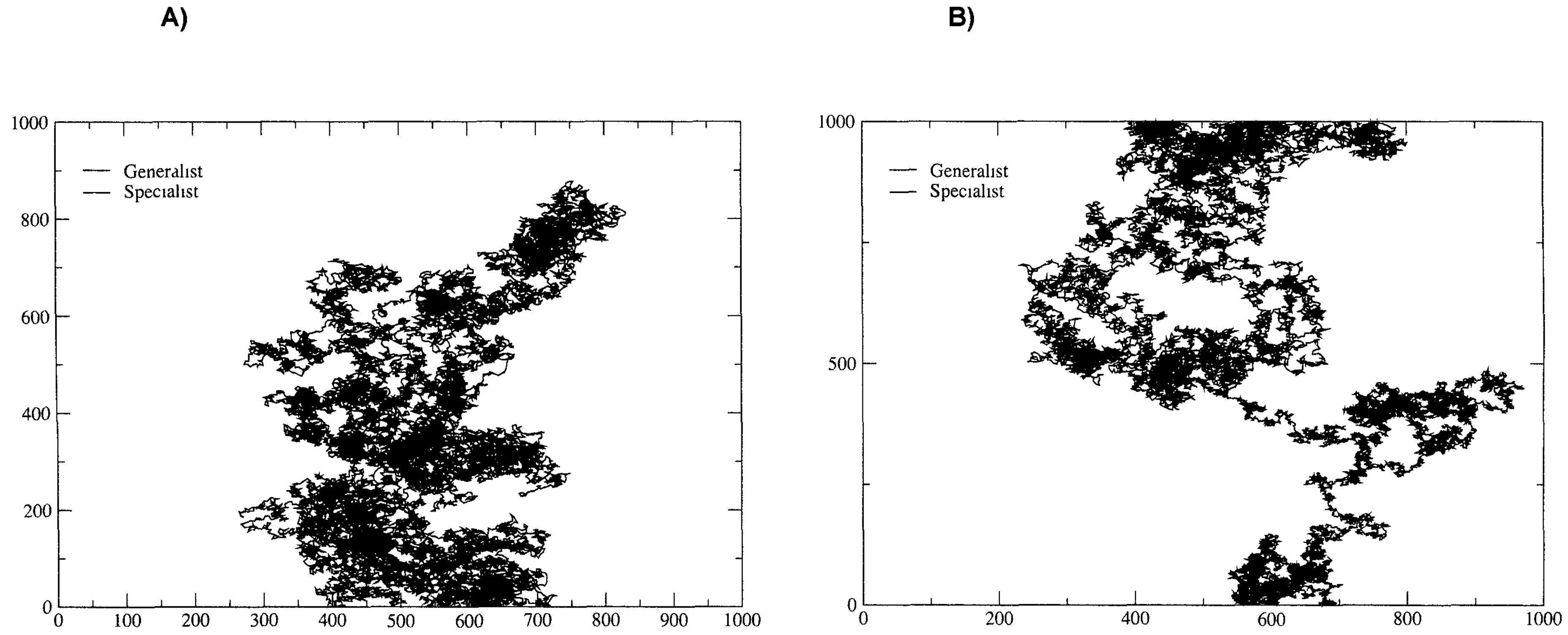

FIG. 4.14—Movement of a simulated generalist and specialist in A) a natural landscape (80% good habitat) and B) a patchy landscape (20% good habitat).

specificity. Only four counts of habitat preference were found over all study sites, and many habitats were used as expected. This further supports the apparent generalist trend observed in foxes on PEI. There were no significant relationships between move characteristics and snow depth at either Alexandra or St. Catherines (private sites). Animals at these sites are likely to be wilder in nature, and are perhaps more rigid in their movement patterns, while foxes at PEINP sites appeared to show more reaction to their local environment.

Habitat Selection.—It was expected that forest would be preferred at most sites due to its typical exploitation by foxes for denning and resting (e.g. Blanco 1986; Jones and Theberge 1982). Forest can also provide better foraging especially in periods of heavy snowfall (e.g. Cagnacci et al. 2004; Cavallini and Lovari 1991). However, Halpin and Bissonette (1988) and Theberge and Wedeles (1989) found that in the winter, brushy areas were preferred by red foxes, while hardwood stands were avoided, likely due to increased snow accumulation and softness (i.e. easier to sink in during movement) which makes travel more difficult. Forest at Alexandra and at Brackley-Stanhope was shorter and denser (i.e. less snow accumulation), so this could explain why forest was used more often at those sites. At Cavendish and St. Catherines, forests were more mature and open, and higher accumulation of snow in these areas may explain why forest was avoided at those sites. It is possible that with increasing fragmentation and landscape diversity, foxes do not prefer forest because other available habitats are more beneficial to them in some way. In the UK, foxes prefer a heterogeneous mix of scrub, woodland and farmland (Macdonald and Reynolds 2004). In addition, Kurki et al. (1998) found that red fox abundance increased in areas that had forest fragmentation and interspersion with agricultural fields, indicating that something is beneficial about this type of fragmented habitat. In areas characterized by a forest/agricultural mosaic as opposed to a large forested patch, there is an increase in successional stages of growth characterized by grass-dominated areas, which are preferred by various species of *Microtus* voles, a main prey of the red fox (Angelstam 1992; Henttonen 1989; Hansson 1994). Both St. Catherines and Cavendish study sites fit this mosaic description of forested area broken up by agricultural land. It is likely the case that foxes are using forest less as a result of the increase in open areas with suitable prey species, such as *Microtus pennsylvanicus*, a common small mammal species on PEI.

Although Silva et al. (2009) found that sand dunes were preferred by foxes on PEI, results from this study showed that they were only used as available. This was surprising since fox dens are often located on dunes in PEINP (personal observations) and the endangered piping plover also nests in these areas. The red fox is an important predator of the endangered piping plover (MaCivor et al. 1990), and in the PEINP, it is protected and monitored on a regular basis. However, the study did not take place during breeding season of foxes or plovers and this could be part of the reason. Foxes still used dunes as they were available and so it is important to continue to monitor them along with other species that use this sensitive habitat that is susceptible to changes in climate and continuing erosion. Foxes avoided other wetland habitats at all study sites, with the exception of Alexandra. It is probable that these habitats are not generally suitable for den construction and may have fewer prey species available than forested or agricultural areas. A possible reason for higher usage of marsh-type wetland at Alexandra than at other study sites is the close proximity of marsh to more suitable habitat, including agricultural fields. It is also possible that at Cavendish and St. Catherines, wetland preference was not exactly as defined here due to small sample sizes.

As predicted, human-use areas were preferred within PEINP (Brackley-Stanhope and Cavendish) more than at the private sites. Within PEINP, human-use areas included campgrounds, recreational areas, a wharf, residences, and institutional land. Human-use areas on private lands consisted solely of residences. It appears that foxes in PEINP are using human-use areas even in the winter months when there are far fewer people around. For this reason, it is probable that foxes have learned that areas frequented by people are abundant in food resources. Abundance of anthropogenic food sources is particularly obvious in the tourist season, when visitors feed foxes regularly. Our findings confirm the results of Silva et al. (2009) who found that foxes preferred human-use areas within the PEINP and spent significantly more time in them than in most other habitat types (except dunes and roads). In a National Park in Hokkaido (Japan), foxes sought anthropogenic food sources at great energetic cost outside of the tourist season when natural food sources were limited (Tsukada and Nonaka 1996). However, though snow limits natural food resources for foxes in PEINP in the winter, foxes have been observed feeding regularly on natural prey like vole and snowshoe hare (personal observations). Therefore, it is likely the case that foxes have chosen these areas for their increased foraging benefits in tourist season and remained there into non-tourist season because they provide sufficient natural food sources. Foxes at St. Catherines have the least amount of reported interaction with people and foxes are more timid and cautious of people, so it makes sense that human-use areas would be avoided at this site. Although Alexandra is located on private land, residents feed the foxes daily and thus the animals are accustomed to visiting human-use areas, so it is not surprising human-use areas were not avoided. Because sample size was small at both private study sites, caution should be taken in interpreting the difference between PEINP and private sites as solid fact. Further studies with greater sample sizes would be required to confirm these results.

Agricultural land, though not as regularly disturbed as residences and other human-use are, was created by and still is influenced by people. This type of habitat was used as expected in Cavendish and St. Catherines but avoided in Alexandra. Agricultural areas have a documented abundance of small mammals, so it was surprising that foxes did not prefer this habitat. However, because data were collected in winter, and no information on specific crops or small mammal abundance or richness were collected, there is little to comment on. Even if prey were abundant enough to support foxes, it is possible that prey were more easily found elsewhere in the winter. Agricultural land is open, and thus more exposed to weather conditions that may be unfavorable in the winter. It appears that, at Alexandra, it was not beneficial for foxes to use agricultural land when others habitats were available.

Roads are a man-made habitat type and are the "unnatural habitat" that tends to have the greatest adverse effects on natural areas (Trombulak and Frissell 2000). Studies on the fine-scale movement of animals in proximity to roads have found that they can be barriers to movement and cause important changes in movement patterns (e.g. Rondinini and Doncaster 2002; Whittington et al. 2004). In the current study, roads were used as expected at Alexandra and at Cavendish and avoided at Brackley-Stanhope and at St. Catherines. These results give no consistent conclusions based on access type (i.e. PEINP or private areas) or heterogeneity of study site. Roads have historically had a significant negative impact on foxes in PEINP; a conservative estimate of 12 foxes were killed on the main road through the Park in the 2003 summer season alone, mainly in the Brackley-Stanhope region (P. McCabe, PEINP Park Ecologist, personal communication). This road traversing Brackley-Stanhope bisects the park and foxes are observed crossing it regularly to get from one habitat to another (Silva et al. 2009; personal observations). Animals typically do not use roads as corridors of movement (Forman 1995), but sometimes foragers will move short distances along them (Bellis and Graves 1971; Romin and Bissonette 1996) and large predators will use quiet roads at night (Bennett 1991; Forman 1995). Foxes at this study site are also often observed sitting along the roadside where it is surmised that such learned behaviour is the result of feeding by tourists. Silva et al. (2009) found that roads were used as expected inside PEINP (Stanhope study site) in breeding (winter) season but preferred during the kit-rearing season. This finding could be the result of the proximity of den sites to the road due to the physical layout of the park, but it is also probable that this is where food sources are most easily accessible for feeding a litter (Silva et al. 2009). In the current study, roads were avoided at Brackley-Stanhope in winter, which may indicate a change in habitat use or simply failure to detect snow-trails along roadways. The latter could be the result of a low amount of snow accumulation along roads or frequent disturbance. The avoidance of roads at St. Catherines was not surprising since there are large tracts of land on each side of the road that bisects it, and foxes are not accustomed to proximity to people or traffic. Again, sample sizes was small at private study sites and further research would be required to make definitive statements on preference.

Coyotes are a common competitor of the fox and are known to exclude and even kill foxes (e.g. Harrison et al. 1989). In Yellowstone National Park, coyotes displaced foxes feeding on elk carcasses two thirds of the time (Gese et al. 1996), showing the importance that coyotes can have in limiting food resources. Risk of interaction with coyotes impacts the choices foxes make, including that of habitat selection (Van Etten et al. 2007). Due to these risks associated with direct competition it would be beneficial for foxes to avoid preferred habitats and home ranges of coyotes. This partial exclusion in certain habitats has been reported by Van Etten et al. (2007) who found that foxes preferred some wooded and sagebrush areas in Yellowstone National Park, while coyotes exploited more open areas. Coyotes on PEI have been found to use habitat types as available (Field 2003). Although it is known that coyotes are present in the vicinity of the study sites examined here, it is difficult to hypothesize about the effect of coyote presence on foxes on PEI without further distribution and habitat-use information on the coyote at these specific study sites.

Since locational fixes were taken at short intervals along paths, serial autocorrelation in location may be occurring, however most habitat data has spatial and temporal autocorrelation (Otis and White 1999). The issue is that although gathering more data gives better individual information, speculation across individuals when this autocorrelation occurs is not always valid (Otis and White 1999). Because the number of different animals tracked in this study was unknown and the dataset was limited (i.e. short and relatively few paths), it was important to keep all of the data in order to maximize the likelihood of representative results for both habitat and movement analyses.

Path Analyses.—Many of the fox movement path attributes, such as path shape (as measured by straightness, ţ), average turning angle, average move direction, transition index, and correlation decay, were similar across study sites. However, there were some path characteristics that varied, possibly in response to small-scale site differences. Brackley-Stanhope had the greatest snow depth of all sites and Cavendish, the smallest snow depth. The majority of trails from Cavendish were observed in more open areas, such as agricultural land and walking paths, while more of the trails at Brackley-Stanhope were found in wooded areas. At Cavendish, the greatest snow depth was found in forest, which was avoided by foxes, while a relatively moderate snow depth was found in forest in Brackley-Stanhope where foxes preferred this habitat type (see Fig. 4.6). The relationships between snow depth and other path characteristics were examined because of the hypothesized constraints snow imposes on animal movement, and as our results suggest, possibly habitat selection. Increased costs of locomotion through snow have been shown in a number of studies (e.g. Crete and Lariviere 2003; Dumont et al. 2000; Parker et al. 1984), and this is especially important for carnivores hunting for prey in snowy landscapes (Crete and Lariviere 2003). At Brackley-Stanhope, where there was the highest snow depth, path length decreased with an increase in depth, showing that snow does limit fox movement at this site. Ables (1969) found that snow depth had a significant negative association with distance travelled in radio-collared foxes. He specifies that this association occurred during deep snows when an ice crust formed and cut the paws of foxes. Crete and Lariviere (2003) found coyotes had adapted to travelling in snow by selecting shallower areas and areas where snow was hardened by human or animal activity, suggesting that sinking in snow increases energy expense of movement. As a result of this physical limitation, as well as the decreased likelihood of foraging opportunities in deeper snow, it was expected that foxes would move more linearly through areas of greater accumulation. Paths in Cavendish did indeed become straighter with increasing snow depth, suggesting that snow may have been limiting to foxes at this study site as well. Alternatively, foxes may have been adapting to local conditions and optimizing their foraging in different ways, such as scanning intermittently for better habitat and heading directly that way. Although the relationships of snow depth with path characteristics were different at Brackley-Stanhope and at Cavendish, imposed limitations were observed at both. With climate change, ice formation is decreasing in major bodies of water, resulting in lower-speed winter winds. In coastal areas, this will allow for increased snow accumulation and also increase its moisture content, making animal travel through it more difficult. Therefore, it is likely that with climate change, snow and local habitat conditions will have a more profound impact on animal movement than observed here.

Total path length was greater at Cavendish than at Alexandra. Longer paths at Cavendish could be resulting because the site is more isolated from roads that act as barriers to movement. It could also be the case that the strong Southerly coastal winds may have reduced the visibility of longer paths at Alexandra. Paths at Cavendish also had greater net displacement than at two of the three other sites, showing that foxes were moving more directly, perhaps due to a higher level of competition (coyote tracks were also observed frequently at this site), a higher degree of patchiness, or a different distribution of resources. It is interesting that the paths observed in Cavendish did not differ significantly in net displacement from those of St. Catherines, which was also patchier. At Cavendish, paths became more tortuous (less straight) with an increase in transitions between different habitat types. This indicates that foxes there altered their movement in response to a change in habitat. Departure from one habitat type for another likely occurs if foxes are not satisfied with the conditions or resources found. At Cavendish, habitats may not have been as favorable, or it may have been an optimal strategy to explore multiple habitats for some reason other than resource distribution, such as competition from coyotes.

Transitions into different habitat types did not appear to affect the path tortuosity at the three other sites or correlation decay of paths at any sites, showing that a) the habitat delineations may not have been biologically significant to foxes or b) that crossing over into different habitats does not affect the movement behaviour of foxes significantly. In a good habitat, a long correlation decay was expected, whereas when resources are scarce, it was expected there would be a shorter decay, as animals would need to change search strategies and therefore turning angles. Mukherjee et al. (2009) found that patch use of wild foxes did not differ between habitat types, likely due to their inability to determine patch quality accurately. Alternatively, foxes may perceive habitats differently, but still manage to optimize foraging using similar movement, acting as generalists. Although the number of transitions into different habitats was not significantly different among sites, the highest values were found at sites within the PEINP, which seems to indicate that foxes are exploring a higher number of habitats in those locations. This could be an adaptive approach of foxes in these more disturbed and human-impacted sites, whereby they may forage more effectively by exploring many habitats. Exploratory movements are of high value in young or inexperienced animals that are not familiar with their surroundings (Etienne et al. 1996). Deviations from set movement paths have also been documented in ants to result from external biases acting dominantly over internal persistence (Wehner 1981 in Etienne et al. 1996). Red foxes use olfactory cues when caching food and for social behaviours (Henry 1977; Macdonald 1979), and rely heavily on auditory cues when hunting (Osterholm 1964). It would appear that in the PEINP foxes are using external cues such as these more often to guide movement, in addition to internal persistence and memory. Since this study took place in the winter season, the distribution of resources like prey may not have been as obvious as during other seasons, forcing more exploration.

Doncaster and Macdonald (1997) provide evidence that red foxes can follow regular, predictable paths. They showed that a fox's movements on one night were loosely dependent on those of previous nights, indicating memory. Therefore, it was hypothesized that foxes in this study would move based on some internal memory and organization, and not with a simple BRW. CRW and LW models were thus chosen to compare with field data. Although turning angles were clustered around zero and there appeared to be some directional persistence in fox movement, the mean net squared displacement consistently exceeded the predictions based on a CRW, demonstrating superdiffusive, power-law behaviour. When a CRW under-predicts displacement, the animal is likely moving directly through unfavorable habitat (Hooge and Eichenlaub 1998 in Bergman et al. 2000), though this conclusion is unlikely to be the case for fox movement in general in this study. It is more likely that averaging paths at study sites might mask a fit with a CRW model. For example, one single long linear path averaged with many others could cause the average net displacement squared to appear much larger than it truly is within the site. At St. Catherines, the net displacement squared fell within the bootstrapped confidence intervals at higher lags, which was likely the result of many paths of length shorter than the lag distance, but could indicate that patterns consistent with a CRW model are found at such high spatial scales.

Although move lengths were autocorrelated, partly as a result of sampling frequency, turning angles were not. The use of small step measurements as the unit of analysis can be problematic (Turchin 1998). Nams (unpublished data) shows that even CRW movement paths will not appear to fit a CRW model if they are discretized, or sampled at a regular time or distance interval that is not equivalent with the natural step of the moving animal. This discretization can lead to falsely rejecting CRW as the appropriate walk model by increasing the correlation between turning angles and overestimating the distance travelled (Nams unpublished). Turchin et al. (1991) and Wiens et al. (1993) have suggested that elimination of autocorrelations among moves could allow a better fit with the CRW model. Data can be resampled (i.e. by only using every second or third data point) to minimize discretization (Boyce et al. 2002) but in this case, would have resulted in the loss of data from a dataset that was small to begin with. This would result in the loss of potentially important information at small spatial scales and result in poor statistics due to even smaller sample size. The sampling interval chosen was approximately 5 times the biological stride of a fox and was chosen to collect data at the smallest spatial scale at which foxes might make decisions that result in movement changes. Selection of scale is an arbitrary process, but because the turning angles were not autocorrelated, it is likely that sampling was not an issue in model failure. The CRW model also assumes a homogenous environment and homogeneity along the path (Nams 2005; Turchin 1998) and it is possible that paths were collected from potentially different habitat patches. However based on the lack of response of tortuosity (at most sites) or turning angle correlation to patch transitions, it is unlikely that the environment is perceived as heterogeneous or patchy by the foxes in this study.

Movement patterns described by a Lévy walk (LW) demonstrate higher expected mean squared displacement than predicted by a BRW or a CRW (Weeks et al. 1995). Scaling exponents obtained from regression analysis of the log-transformed data of this study supported predictions based on a Lévy walker model. There was only one movement path that did not comply with this model. A LW has superdiffusive movement that promotes efficient foraging on sparsely distributed resources because more new sites are visited than revisited (Berkolaiko et al. 1996, Larralde et al. 1992; Viswanathan et al. 2008; Viswanathan et al. 1999). As discussed in the introduction, Lévy walks are considered to model optimal foraging movement. Optimal foraging is defined by

Viswanathan et al. (2002) as a maximization of encounters with prey, food, and mates. A LW maximizes these encounters for predators that are larger and faster than their targets (Viswanathan et al. 2002), as are foxes. A CRW results largely from local scanning processes (Bartumeus et al. 2005). However, higher searching strategies such as spatial memory are often used by animals to locate resources (e.g. Gillingham and Bunnell 1989), and olfactory (Benhamou 1989) and visual (Laca and Ortega 1996) cues can allow animals to search more effectively. Foxes are known to use memory to relocate food stores (Macdonald 1976, 1977) and auditory cues when hunting (Osterholm 1964), and therefore likely use higher foraging strategy than simply reacting to their immediate surroundings.

Composite Brownian walk (CBW) models, formed by superimposing different Brownian mechanisms of movement at different spatial scales, can imitate LW patterns. CBW models are characterized by intermittent search processes punctuated by linear movement, and result in minimized search times and efficient foraging strategies (Benichou et al. 2006). Benhamou (2007) found that a CBW composed of one model with a large mean move length and one with a short mean move length mimicked the LW patterns of a predator randomly seeking prey in a patchy environment. Simulated composite Brownian walkers can even exceed Lévy walkers in efficiency of movement between good patches (Fig. 4.15, S. Opps unpublished data). Foxes may be using a LW at certain spatial scales, but overall a composite Brownian walk may better explain their movement. Although a LW was a

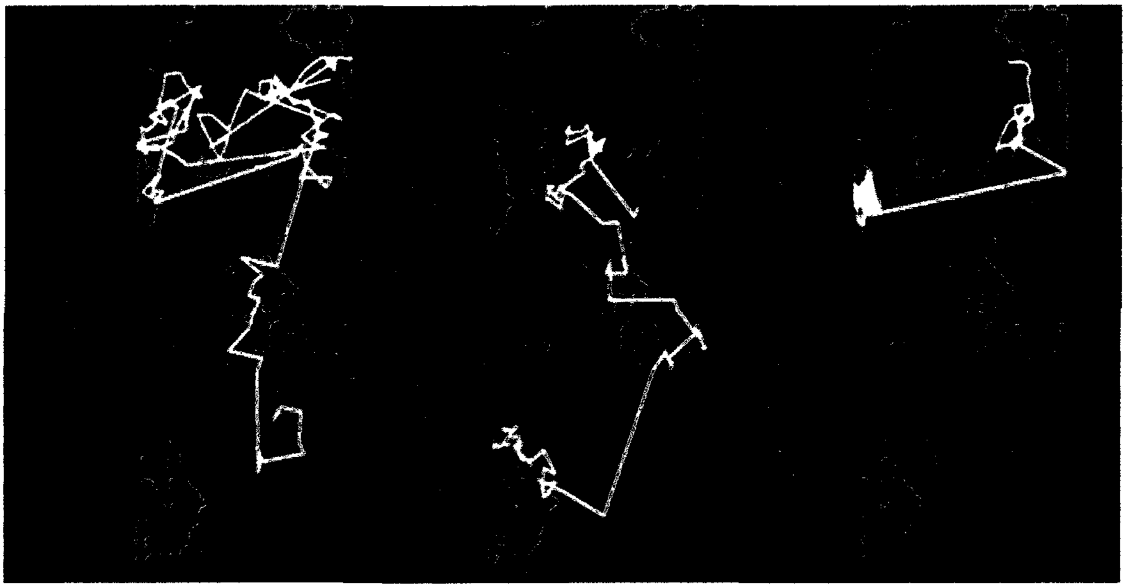

FIG. 4.15.—Comparison of simulated Levy, Brownian, and composite Brownian walkers (white is the movement path) on a landscape of good patches (red) amongst bad habitat (blue). S. Opps unpublished data.

probable model for fox movement, turning angles were clustered around zero implying some level of directional persistence. As a LW is a non-oriented form of movement (Benhamou 2007), there appears to be an additional bias affecting the overall direction of fox movement on PEI that is not accounted for by the LW model.

Snow-tracking is a highly weather-dependent field technique. Weather conditions can lead to deterioration of snow-trails at differing rates in different habitat types, potentially leading to observation bias. For example, tracks in open areas will be more prone to rapid infill by wind. It can also be difficult to identify fox tracks and to follow a specific trail through dense areas where trails are interspersed. For these reasons, there were a limited number of snow-trails that were long enough to consider for analysis in this study and differential conditions at study sites may lead to biases in observed habitat selection. Future studies on fine-scale movement patterns of foxes on PEI should use GPS-collars to obtain longer stretches of movement and measures of home range that were not possible to obtain with snow-tracking. GPS-tracking would also minimize observation bias. Although GPS- tracking of red foxes was unsuccessful in this study due to ineffective trapping methods, revision of the trapping protocol to employ modified leg-hold traps is underway with the help of local hunters and trappers.

CONCLUSIONS

Each habitat type (except dune) was used differently from expected at at least one study site, and there were no consistencies in selection over all study sites. This seems to indicate that foxes use resources differently based on their geographic location or have behavioural adaptations to the local site conditions. Human-use areas were used more than expected within the PEINP (Brackley-Stanhope and Cavendish), which was predicted to occur due to the close contact of people with wildlife in this area. Based on the heterogeneous natures of Cavendish and St. Catherines, it was expected that foxes in these areas would move differently (if foxes perceived habitats as very different in quality) and select habitat differently. Only forest was consistently used differently in the two more heterogeneous sites compared to the other sites, showing that habitat use of foxes does not appear to be affected by habitat patchiness. Assuming fragmentation affects landscape heterogeneity, the results here suggest that foxes are not overly affected by fragmentation and are able to adapt to habitats affected by human activites. There is some evidence to suggest that snow depth limits foxes on PEI as shown by a decrease in path tortuosity at Cavendish and in path length at Brackley-Stanhope. Although foxes exhibited habitat selection on PEI, movement patterns within different habitat types remained largely the same as shown by little change in tortuosity or turning-angle correlation with patch transition. This may indicate that foxes on PEI are not very affected by patchiness or fragmentation. Fox movement was not consistent with a CRW, but was consistent with a LW based on scaling exponents and super-diffusive behaviour. However, the movement was directed, so although a LW could represent an optimal search strategy for foxes on PEI in the winter, the application of more detailed models incorporating external biases in future research into fox movement in this area is recommended.

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5. OVERALL DISCUSSION

5.1 CONCLUSIONS ON ANIMAL MOVEMENT AND HUMAN INFLUENCE

The primary goal of this study was to look at animal distribution and movement patterns and the influence of spatial heterogeneity and human activities on them. As people develop land, they often fragment and destroy natural habitat. The effects of this fragmentation on animal populations can be measured through direct observations of aberrations, but also with some quantifiable scientific measures. Proximity to human settlements and access to anthropogenic resources, such as shelter and food, can benefit animals, but there are also potential adverse effects due to habitat loss, human persecution, and roadways. Some anthropogenic effects on animals may be more difficult to measure and monitor as they occur slowly over long periods of time; for example, some gradual effects of climate change.

Habitat alteration is the most drastic widespread impact on animal populations. Whether it is the development of land for agriculture, for urban centres, or for recreational purposes, more natural habitat is fragmented every year as human populations continue to expand. As this development occurs, animals are affected differentially as certain species are more prone to extinction due to their physiological needs or behaviour. If animals can adapt to changing conditions, or disperse out of the area, they will less likely become isolated in areas of non-suitable habitat and thus, less likely to decline. Species reliant on very specific conditions are typically termed 'specialists,' while animals more flexible in their ecological needs are called 'generalists' (sensu Levins 1968). By looking at animal movement path characteristics, spatial distribution, habitat selection, and diet, we can gain an understanding of their ecological needs and how they interact with the landscape.

The two species studied here are influenced by human activities in different ways, and in very different parts of the world. The study of movement patterns at both small and large spatial scales is important, although the scale of study will determine the type of ecological question that can be answered. Large-scale patterns give an overview of animal distribution and movement, while small-scale patterns can show detailed interactions with, and response to, the local environment. African wild dogs were studied using larger-scale measurements, with the use of radio-tracking data collected twice daily, in the interest of maintaining a record of where the pack was located. Red foxes were studied at a fine-scale with snow-tracking data, collected at 5 metre intervals, in order to look at mechanisms of movement through patchy landscapes. Though these species are different and were studied at different spatial scales, they are both mammalian carnivores that have important roles in their biological communities and are both under the influence of human activites in some way.

African wild dogs are specialists, preying mainly on small and medium sized antelope species (Kruger et al. 1999), and have an innate ranging behaviour that requires large tracts of suitable land (Woodroffe and Ginsberg

1998). As a result of this high level of dispersal, they are found at low densities and are naturally at risk of extinction but, with habitat fragmentation, such as fencing off of reserves, ranching practices, and road construction, their risks are even greater today (Ginsberg and Woodroffe 1997). Using radio-telemetry data, it was found that reintroduced wild dogs in a small game reserve (Mkhuze, South Africa) had a home range that extended to and beyond the reserve boundaries. Wild dogs selected habitat differently by season and their home-range size was correlated with temperature and evapotranspiration, indicating some response to climate and potentially adaptation to local conditions. Despite monitoring, wild dogs did not persist in the reserve, as slowly the pack size decreased due to snaring, disease, and hunting injuries. It is apparent that wild dog requirements were not met in entirety in Mkhuze game reserve and that direct human influence played a role in their decline there.

The red fox is usually considered a generalist and is known to inhabit a diversity of habitat types (e.g. Phillips and Catling 1991; Van Etten et al. 2007; Cavallini and Lovari 1991). Snow-tracking data from this study showed that movement patterns are generally similar across study sites with some adaptations to local conditions. This flexibility was also apparent in habitat selection, which was not consistent across study sites for any particular habitat type. Foxes also appeared to demonstrate movement attributes characteristic of a Lévy walk (LW), which is standard model used to describe optimal foraging of resources. A LW is considered optimal because it results in visitation of more new foraging sites (and thus not depleted sites) than do other common walk models (Viswanathan et al. 1999; Weeks et al. 1995). It is not surprising that foxes were foraging optimally since they are known to use spatial memory and a variety of external cues (e.g. Doncaster and Macdonald 1997; Macdonald 1979). To summarize, foxes appear to interact with their local environment, showing flexibility in movment and distribution.

To examine some fundamental movement patterns of random walkers, computer simulations were performed in very simple fragmented landscapes. The results showed that generalist and specialist random walkers had different search strategies in landscapes with different levels of fragmentation. Specialists were significantly affected by patchiness in the landscpe and they moved directly (i.e. with straighter paths) in areas with little suitable habitat. Generalists, however, showed a similar path shape (straightness) regardless of fragmentation due to the equal weighting of the quality of both types of landscape. Although the simulations used a simple random walk model and very basic landscapes, some parallels can be drawn between the movement patterns observed in the simulations and those from the field studies of wild dogs and red foxes (even though the observed patterns may not necessarily be the result of a simple random walk mechanism).

Wild dogs had a high level of dispersal within the reserve. Since they continued moving beyond reserve boundaries, it could be speculated that as a result of fragmentation, their movement tended to be more directed through unsuitable habitat that did not satisfy all of their requirements. Such movement patterns are consistent with the specialist simulations. Although the measure of fragmentation in this study has been defined with respect to the landscape, the population of wild dogs itself is also fragmented. The wild dogs in Mkhuze were part of one pack, which was a subpopulation in the metapopulation of wild dogs managed in many smaller reserves in South Africa. As discussed in Chapter 3, it is likely that the need for unrelated individuals for breeding was not satisfied and led to movement out of the area. This would be a biologically-driven mechanism for movement that is independent of resource distribution and landscape fragmentation.

Fox movement path shape (straightness) was not different at sites identified as having higher patchiness and heterogeneity as compared to the others. Thus, foxes seem to fit the trend observed for a generalist walker. At some sites, foxes showed response to habitat transitions and snow depth showing that some limits are imposed on foxes, but also that foxes adapt to these local conditions. It has been argued that it is the generalist characteristic of fox populations that has led to its widespread establishment and success around the globe (Macdonald and Reynolds 2004). Inversely, it could be that it is due to the specialist requirements of the wild dog that that species is in decline.

Direct human effects, including persecution, are a documented risk for wild dogs, and as habitat, and thus populations are fragmented, risk increases for low-density, wide-ranging species such as the wild dog (Woodroffe and Ginsberg 1997). Direct anthropogenic effects also occur on foxes on PEI, and include trapping and accidental road kills. Another type of direct anthropogenic effect on foxes on PEI is feeding. Diet was slightly different at study sites, but no consistent results were shown regarding anthropogenic food sources in PEINP. Indirect anthropogenic effects such as climate change are likely important to both species as local habitat characteristics such as vegetation structure and snow depth will be affected. These effects are more difficult to predict, but continued monitoring can reveal trends over time.

Both wild dogs and red foxes are social species, and thus interactions with conspecifics will have important effects on movement patterns and spatial distribution. Foxes can be territorial (e.g. Woollard and Harris 1990; Poulle et al. 1994), and formation of territories limits the distribution of other foxes. Wild dogs, on the other hand, are not territorial and are rarely aggressive even with unrelated packs (Estes and Goddard 1967), but resource limitations likely still delineate available areas. Wild dogs were radio-tracked as a pack, which is considered the basic social unit, in an area with no other packs, and thus social observations of intraspecific interactions could not be made. Foxes were snow-tracked, which does not allow identification of specific individuals. Unfortunately, there was no information available on competitors of wild dogs (spotted hyaena) or of foxes (coyote) that were present in the study areas, and that likely limited their distributions. Examining the spatial use of these study sites by competitors would be the next logical step in obtaining more complete information regarding decisions made by wild dogs and by foxes in selecting habitat and moving within it. Distributions of prey species would also be valuable information since both study species are predators and their movements are driven by the need to forage.

The study of animal movement patterns can give us insight into how animals are interacting with their environment. Understanding the link of individual to environment can help us minimize the negative effects of habitat fragmentation on animals. This understanding is thus vital to the development of successful conservation or management strategies.

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6. APPENDICES

APPENDIX 1. **Mkhuze Game Reserve Habitat Details** (adapted from VanRooyen 2004)

Habitat Type	Location	Characteristic Species	Other
Riverine forest	Lower MGR, along Mkhuze River and tributaries	*Ficus sycomorus, Acacia xanthophloea, Rauvolfia caffra, Syzygium guineense, Cordyla africana, Trichilia emetica, Trichilia dregeana Ekebergia capensis, Acacia schweinfurthii, Azima tetracantha Grewia caffra, Ficus capreifolia, Phoenix reclinata*	Stabilizes river banks and prevents erosion
Acacia nigrescens tall open woodland	On red, loamy soil at the base of the Lebombo mountains	*Acacia nigrescens, Sclerocarya birrea, Dichrostachys cinerea, Ozoroa paniculosa, Acacia tortilis, Dombeya rotundifolia Gymnosporia buxifolia, Themeda triandra, Heteropogon contortus, Panicum coloratum, Panicum maximum, Urochloa mosambicensis, Eragrostis spp. and Bothriochloa insculpta*	
Low Thicket	On flat, poorly drained lowlands with clay soil	*Euclea divinorum, Acacia luederitzii Acacia grandicornuta, Acacia nilotica, Spirostachys africana, Ziziphus mucronata, Acacia nigrescens Euclea undulate, Panicum maximum* and *Eragrostis* spp.	Dense thicket with poor grass structure

Continued.

Continued.

Habitat Type	Location	Characteristic Species	Other
Dry Closed Woodland	Low-lying areas, drainage areas, clay soil South of Hluhluwe river North to False Bay Park, and North to Mkhuze river in MGR	*Spirostachys africana, Berchemia zeyheri, Mystroxylon aethiopicum, Apodytes dimidiata, Ziziphus mucronata, Sideroxylon inerme, Schotia brachypetala, Acacia grandicornuta, Acacia luederitzii, Strychnos decussa, Euclea divinorum, Carissa bispinosa, Capparis tomentosa, Asparagus natalensis, Maytenus undata, Dovyalis caffra, Scolopia zeyheri te, Dalbergia obovata, Acacia schweinfurthii, Grewia caffra, Strophanthus spp.*, *Sarcostemma viminale, Asparagus falcatus*, *Asparagus natalensis* and *Scutia myrtina, Kalanchoe natalensis, Senecio fulgens, Peristrophe natalensis, Panicum proliferum, Stenotaphrum glabrum* and *Setaria sagittifolia.*	Sparse, herbaceous undergrowth
Lebombo open woodland	On rocky hills of Lebombo mountains	*Acacia nigrescens, Combretum apiculatum, Acacia burkei, Acacia caffra, Combretum molle, Combretum zeyheri, Lannea discolor* and *Pterocarpus rotundifolius, Themeda triandra, Digitaria eriantha, Panicum maximum, Heteropogon contort, Eragrostis spp., Aristida* spp., *Aloe marlothii, Aloe sessiliflora, Euphorbia cooperi, Euphorbia tirucalli, Ficus abutilifolia, Ficus glumosa, Olea europaea* subsp. *africana, Ptaeroxylon obliquum, Olax dissitiflora, Cussonia natalensis, Ficus* spp., *Chrysophyllum viridifolium, Combretum kraussii, Celtis africana, Homalium dentatum,* and *Heywoodia lucens.*	Wooded grassland, woodland, and forest patches, herbaceous layer developed or not

Continued

Continued.

Habitat Type	Location	Characteristic Species	Other
Terminalia sericea savanna	False Bay Park, Mkuze Game Reserve up to the Palm Savanna in the Mozi area.	*Terminalia sericea, Sclerocarya birrea, Acacia burkei, Acacia robusta, Strychnos madagascariensis, Strychnos spinosa, Combretum molle, Combretum zeyheri, Garcinia livingstonei, Peltophorum africanum, Afzelia quanzensis, Albizia versicolor, Antidesma venosum, Dichrostachys cinerea, Tabernaemontana elegans, Vangueria infausta, Canthium inerme, Ozoroa engleri, Ozoroa obovata, Xylotheca kraussiana, Panicum maximum, Diheteropogon amplectens, Hyperthelia dissoluta, Andropogon gayanus, Pogonarthria squarrosa, Perotis patens, Digitaria eriantha, Corchorus junodii, Indigofera vicioides* and *Asystasia gangetica.*	Open to closed deciduous woodland, grey to reddish sandy soils, canopy ranging from 5 to 12 m in height. Related to the Sand Forest and Woodland communities
Acacia tortilis low open woodland	MGR plains East of Lebombo mountains	*Spirostachys africana*, *Schotia brachypetala*, *Acacia nilotica, Themeda triandra, Bothriochloa insculpta, Dactyloctenium australe, Chloris virgata, Aristida congesta* subsp. *barbicollis, Heteropogon contortus* and *Eragrostis rigidior*	Poor herbaceous layer
Acacia nilotica low closed woodland	On plains with sandy loam to clay soil	*Acacia nilotica*, *Acacia grandicornuta, Acacia tortilis*, *Acacia nigrescens, Ziziphus mucronata, Sclerocarya birrea, Dichrostachys cinerea*, *Themeda triandra, Heteropogon contortus, Digitaria eriantha, Cenchrus ciliaris, Bothriochloa insculpta*, and *Eragrostis heteromera*	

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Continued.

Habitat Type	Location	Characteristic Species	Other
Palm savanna	On sandy soil West of Mbazwane river and North of Mkhuze swamp (Mozi area)	*Hyphaene coriacea, Phoenix reclinata, Syzygium cordatum, Sclerocarya birrea, Albizia adianthifolia, Strelitzia nicolai, Strychnos madagascariensis, Strychnos spinosa, Ekebergia capensis, Acacia robusta*, *Combretum molle, Chaetacme aristata, Garcinia livingstonei,* and *Trichilia emetic, Dichrostachys cinerea, Vangueria infausta, Gymnosporia buxifolia, Euclea natalensis, Antidesma venosum, Sapium integerrimum*, *Parinari capensis* subsp. *Incohata, Helichrysum kraussii, Themeda triandra, Andropogon gayanus, Trachypogon spicatus, Digitaria eriantha, Dactyloctenium geminatum, Eragrostis gummiflua,* and *Cymbopogon plurinodis*	Variety of trees, well developed grass layer, two prominent palm species
Lebombo wooded grassland	On shallow and sandy soils on Lebombo mountains	*Elionurus muticus, Andropogon gayanus, Tristachya sanguineum, Tristachya biseriata, Brachiaria serrata, Hyperthelia dissolute, Heteropogon contortus, Themeda triandra, Hyparrhenia fillipendula, Terminalia phanerophlebia, Combretum apiculatum, Acacia nigrescens,* and *Lannea discolor.*	

Continued.

Continued.

Habitat Type	Location	Characteristic Species	Other
River floodplains and seasonal streams	Lower Mkhuze floodplains, along Mozi drainage line in Eastern MGR	*Acacia xanthophloea, Ficus sycomorus, Echinochloa pyramidalis, Hemarthria altissima, Cynodon dactylon, Phragmites australis, Echinochloa pyramidalis, Hemarthria altissima, Eriochloa , meyeriana, Cynodon dactylon, Cyperus fastigiatus, Persicaria attenuate, Centella asiatica, and Phragmites australis.*	Dense grass cover
Freshwater lakes and pans	Flat, low-lying area with permanent to seasonal pans	*Brachylaena discolor, Strelitzia nicolai, Albizia adianthifolia* and *Apodytes dimidiate, Schoenoplectus scirpoides, Typha capensis* and *Phragmites australis, Echinochloa pyramidalis, Schoenoplectus scirpoides* and *Phragmites australis*, *Nymphaea nouchali* var. *caerulea, Nymphioides thunbergiana, Aponogeton* spp., *Utricularia* spp., and *Potamogeton schweinfurthii.*	Variation in salinity
Human habitation	Towns, forestry stations, holiday resorts		

APPENDIX 2:

A COMPARATIVE ANALYSIS OF RED FOX DIET AND PARASITE LOAD AT FOUR STUDY SITES ON PRINCE EDWARD ISLAND, CANADA

ABSTRACT

The red fox is increasingly found established in urban areas and proximity to human populations may be affecting its natural foraging strategies. This proximity is also of concern for human populations as the red fox is a vector for many different diseases including some parasites that are transmissible to humans and domesticated animals. In this study, parasitic and macroscopic analyses were conducted on samples of red fox scats from four study sites on Prince Edward Island (Canada) that differed in degree of human impact (public versus private) and in spatial heterogeneity (i.e. diversity of habitats) in order to examine the impact of human activities on fox diet and health. The most commonly found parasite was *Crenosoma vulpis*, a lungworm that is also transmissible to domesticated dogs. Some other parasites of interest were *Uncinaria stenocephala* and *Toxocara canis*, both of which can cause disease in humans. Foxes appear to include many different types of food in their diet, strengthening the argument that they are ecological generalists. The two main categories of food items (vertebrates and vegetation) were found with similar frequency at all study sites, indicating that the foxes had the same basic diet. There was some local variation in other categories like fruit, which seems to indicate that the foxes adopted slightly different foraging strategies at different geographic locations. Within scats, vertebrates were the most important, or

abundant, food category. Anthropogenic food items were rarely found, even within the Prince Edward National Park where it was hypothesized foxes would have a less natural diet. Despite these reported differences among study sites, based on the relative percent bulk of food categories, samples at the different study sites were not significantly different and, thus, fox diet, as a whole, was similar for all study sites. Foxes on PEI appear to have a largely natural diet despite their interactions with people. However, they do carry parasites of concern, and precautions should be taken to avoid direct contact with the animals and their fecal remains.

INTRODUCTION

The red fox (*Vulpes vulpes*, herein also referred to as 'the fox') is the most widely distributed carnivore in the world and is very adaptable with respect to habitats it can occupy (Jedrzejewski and Jedrzejewska 1992). The fox is considered a generalist predator due to its varied diet (e.g. Englund 1965; Jedrzejewski and Jedrzejewska 1992; O'Mahoney et al. 1999, Sidorovich et al. 2006). The most frequently consumed natural food items are rodents (particularly *Microtus* vole species), followed by carrion, birds, lagomorphs, fruit and invertebrates in varying orders of importance (Dell'Arte et al. 2007; Jedrzejewski and Jedrzejewska 1992; Lockie 1959; Macdonald 1977; O'Mahoney et al. 1999; Reynolds and Aebischer 1991; Sidorovich et al. 2006; Webbon et al. 2006).

The red fox is established in many urban areas and, as shown by the higher density of urban foxes, these areas appear to have some attributes that are attractive to the species (Gloor 2002; Harris 1981; Macdonald and Newdick 1982). Foxes are characteristically shy of humans and so a behavioural adaptation has also had to occur to allow migration to urban areas. It has been hypothesized that foxes occur in urban areas because they have learned to exploit anthropogenic food sources (Contesse et al. 2004). Since foxes frequently revisit food sources such compost heaps, gardens, and vineyards, it would appear that they find it efficient to forage in human-use areas (Contesse et al. 2004; Lovari et al. 1996). For example, although foxes tend to eat available prey in Shiretoko National park (Hokkaido, Japan), they spend a lot of extra energy to find anthropogenic food sources when natural food sources are low (Tsukada and Nonaka 1996). Furthermore, Tsukada (1997) also showed that foxes under the age of one year demonstrated “begging” behaviour if their den was within 20 m of road edge. Because of increased proximity with human populations, management of foxes is a priority in areas where they are vectors of disease and infection and where they prey on livestock and threatened species (Webbon et al. 2006).

Prince Edward Island (PEI, also referred to as ‘the island’) is located in the Gulf of St. Lawrence on the east coast of Canada. The fox was the largest mammal on PEI until the arrival of the coyote in the 1980’s (Thomas and Dibblee 1986). Foxes are now established in urban areas as well as rural, having lost some of their instinctual fear of humans. The fox is perceived as a charismatic species on PEI and tourists and residents often feed them. Especially close contact of foxes with people has been observed in the PEI National Park (PEINP) (personal observations). A recent study showed low quality refuse in the stomachs of foxes on PEI, suggesting that foxes are gaining access to household waste or are being directly fed (Kelly-Clark and Silva unpublished data). PEINP officials observe road deaths of foxes in the Park each year (P. McCabe, PEINP Park Ecologist, personal communication). This is likely due to animals foraging along roadways (especially in the summer) or crossing to other habitats (Silva et al. 2005). Despite fox abundance and its wide distribution on PEI, there has been little research conducted on foxes there. Research into red fox diet on PEI is warranted since the close proximity to, and interaction with, human populations on PEI is likely altering the natural foraging patterns, food intake, and possibly the parasitic infection of foxes since transmission of many parasite species occurs between domesticated and wild animals.

Scat analysis is a relatively easy and non-invasive way to investigate an animal's diet and the types of parasites infecting it (sensu Lockie 1959; Zajac and Conboy 2006). Scats have been used in this type of research of the red fox in many areas of the world (e.g. Dell'Arte et al. 2007; Jedrzejewski and Jedrzejewska 1992; Sidorovich et al. 2006), but to date there has been only one published study on PEI on this subject (Wapenaar et al. 2006). In that study, fox scats were tested for the presence of *Neospora caninum* in the interest of prevention of transmission to bovine hosts (Wapenaar et al. 2006). Diet information for foxes in different areas could be useful for determining the influence of anthropogenic food sources on PEI. Some general conclusions may be made on the health of foxes, as estimated by the type and number of parasites found in scats. A decline in health may make animals more susceptible to parasitic infection and disease (sensu Doums and Schmid-Hempel 2000). However, some parasites are consumed in prey (e.g. Bjork et al. 2000; Pfieffer al. 1997), and these species, termed spurious parasites since they are not truly parasites of the host, could be indicators of a natural diet. Comparison of parasite load at different study sites could allow an analysis of disease risk, and educational measures could then be employed to aid in prevention of disease spread to other animals and human populations in the area.

Very little is known about parasitic infection of foxes on PEI in particular. One known fox parasite on the island is lungworm (*Crenosoma vulpis*), which is commonly found in red foxes and domestic dogs (Levine 1980; Zajak and Conboy 2006). On PEI, lungworm is an important causal agent of upper respiratory disease in domestic dogs (Bihr and Conboy 1999). Not only can parasites carried by wildlife be transmissible and harmful to domesticated animals, but also to people. *Echinococcus multilocularis,* commonly found in foxes (Zajac and Conboy 2006), is a small tapeworm that can cause potentially fatal alveolar echinococcus in humans upon exposure (Craig et al. 1996; WHO/OIE 2001). A study in Great Britain by Smith et al. (2003) found that *Toxocara canis* and *Uncinaria stenocephala* were among the three most frequently found parasites in foxes. Both species are easily transmitted in the environment and, if contracted by people, can result in toxocariasis (Richards et al. 1993, Mizgajska 2001, Richards and Lewis 2001). Some other common parasites found in fox feces are *Strongyloides stercoralis,* and *Eucoleus* spp. (Zajac and Conboy 2006).

The objectives of this study were to examine scat samples for presence of various parasites of interest, to determine diet composition, and to explore the use of ultra-high-performance liquid chromatography-tandem mass spectrometry (UHPLC-MS) in a novel way to assess biochemical signatures and the importance of certain organic compounds in the diet. Four study sites were sampled, two located in public areas with higher human density and two located in more private, rural areas. It was hypothesized that unidentified or obviously anthropogenic items would occur more frequently and with a higher importance in scats found in areas of higher human impact. If human activities decrease the natural content in fox diet and that is detrimental to their health, parasite load (with the exception of spurious parasites) should increase in areas with more human activity.

METHODS

Study Sites.—In this study, four study sites were used: Alexandra, Brackley-Stanhope-Dalvay (BSD), Cavendish, and St. Catherines. Most of these study sites were outlined in Chapter 4 of this thesis (page 127; see Fig.

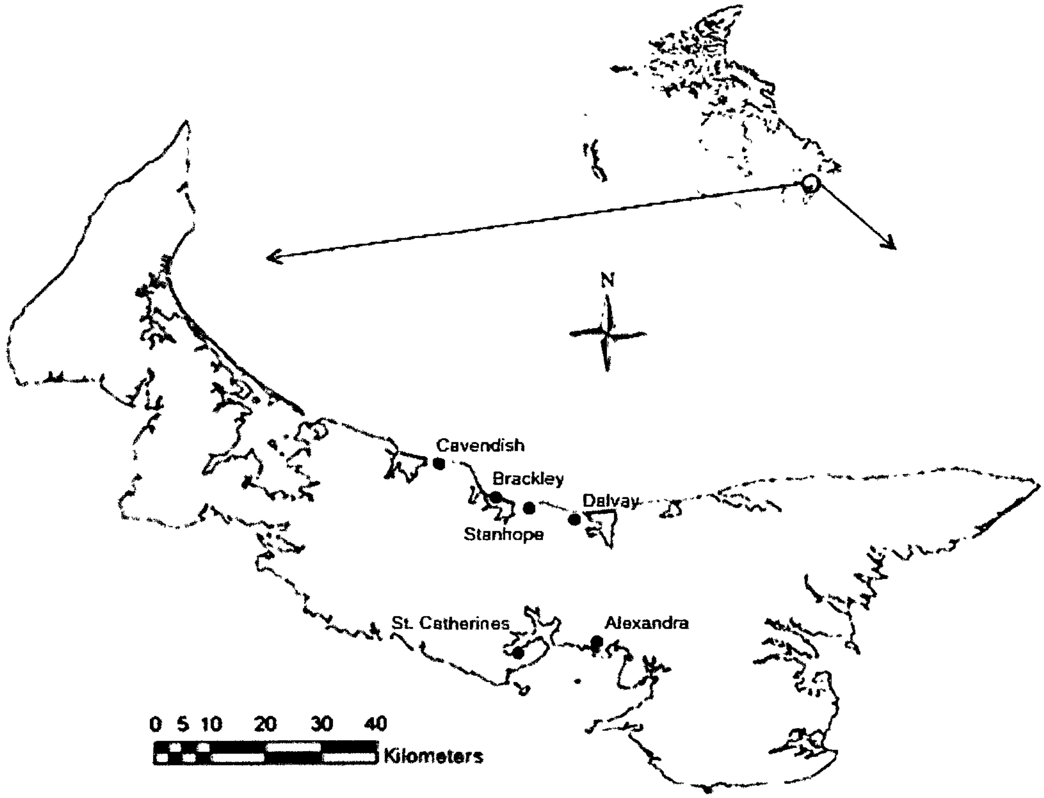


FIG. 1.—Map of Prince Edward Island, drawn out from Canada, showing the individual study sites (●).

1). Brackley-Stanhope was used in Chapter 4 and BSD used here is an extension of that study site to include Dalvay (about 5 km from Stanhope) because these sites had the same public access and basic geographical location. BSD and Cavendish are found in the PEINP and are thus open to the public, while Alexandra and St. Catherines are privately-owned sites. FragStats software (v. 3.3; McGarigal and Marks 1995) was used in Chapter 4 (page 131) to determine the heterogeneity and the fragmentation of these study sites. Cavendish and St. Catherines were patchier based on the number of patches and the interspersion of patch types, and more heterogeneous based on Simpson's diversity index for habitat type (pages 142-143). As such, they are considered here to be sites that are more fragmented and more heterogeneous.

Collection.—Scats were collected from study sites between November 2008 and January 2010. First, sites were visited 2-3 times to identify areas used by foxes (i.e. where foxes or their signs were seen most often). Opportunistic searches were then conducted in identified areas to collect scats. Sites were traversed slowly while scanning a path approximately 5 m wide for scat. This search procedure is more time efficient for gathering large samples of scats than are searches along rigid transects. Once a scat was found, it was measured quantitatively (length and diameter) and qualitatively (shape and odour) and, if judged to fit the description of fox scat (Elbroch 2003; Halfpenny 1998; Schmitt and Juell 1994), was collected into a re-sealable plastic bag. The Scats collected had to be judged to be relatively fresh based on texture, odor, and moisture for parasite analysis; however, older scats were also collected for macroscopic analysis (i.e. physical sorting). Samples were then placed in a cooler with an ice pack to maintain low temperatures to preserve them for parasite analysis. Study sites were surveyed monthly at a minimum, and bi-weekly at a maximum, as weather conditions and site rotation allowed. The scats collected were assumed to be a representative sample from foxes in the area, though it is recongnized that a limited number of individuals may be represented.

Laboratory Analyses.—Parasite analysis needs to be performed within a short period of time in order to detect live larvae and to preserve integrity of eggs (Zajac and Conboy 2006). For this reason, only fresh scats could be used and the analysis had to be completed within 3 days of collection. A small sample of each fresh scat was analyzed for known parasites with zinc sulfate flotation and Baermann technique (modified from Zajac and Conboy 2006 with recommendations from G. Conboy, AVC, PEI; see Appendix 4). The remaining portion of scat was frozen along with older scats until diet analysis could be performed. Spurious parasites, those that are found in prey species of a predator (Zajac and Conboy 2006), were also noted, as they can tell us about consumed material (G. Conboy personal communication; Bjork et al. 2000).

Each scat was thawed for diet analysis and was washed with water in a 0.5 mm sieve until the water ran clear (Reynolds and Aebischer 1991; Webbon et al. 2006). The scat was then separated into material that fit into different categories. The categories were selected as general classes of ingested items (adapted from Van Dijk et al. 2007; Zabala and Zuberogoitia 2003): vertebrate (including fur, bone, feather, eggshell), invertebrate (including shellfish and insects), vegetation, fruit (including fleshy fruit and seeds), inorganic (rock), unidentified, and anthropogenic. It is important to note that food items of little or no nutritional value (e.g. rock, unidentified) were still included in analyses as they can offer information about foraging activities and adaptations in addition to diet itself (Moreno-Black 1978; Rose and Polis 1998). Only items that were obviously not made of natural materials (e.g. plastic, rubber) were classified as anthropogenic, as it is difficult to discern scavenged meat and bones from natural food sources (Schmitt and Juell 1994). The washed and sorted material from each scat was air-dried in Petri dishes. Once dried, each food category of a scat was placed in a Petri dish with a grid (32 cm^2), to a maximum thickness of 1 cm. The number of grids covered by each category was recorded as well as the total number of grids covered by the entire scat sample.

In addition, eleven fresh scat samples were also used to investigate biochemical signatures of important metabolic compounds in fox diet. This was done using ultra-high-performance liquid chromatography-tandem mass spectrometry and a protocol developed for chemical separation and identification (Dr. Russ Kerr, Patricia Boland, Fabrice Berrue, National Research Council, UPEI; see Appendix 5). High-performance liquid chromatography involves forcing a solvent through a separation column at high pressure in order to separate the compounds within it, after which they can be identified based on their retention in the column (Lindsay 1992). In mass spectrometry, ionized substances are accelerated then deflected by a magnetic field (Gross 2004). The amount of deflection allows the identification of the mass of each component (Gross 2004). This technique can be coupled to mass spectrometry to fragment the compound and compare with databases of compounds to determine the identity by the amount of time it takes to pass through the column (Lindsey 1992). More recently the use of smaller particles in the separation column has increased speed and peak capacity, termed ultra-high-performance liquid chromatography (Swartz 2005). Some important applications of high-performance liquid chromatography-tandem mass spectrometry (HPLC-MS) include protein profiling and identification of protein biomarkers for disease treatment (Radulovic et al. 2004), drug metabolite identification (Bruce et al. 2008; Wang et al. 2007; Walles et al. 2007), food analysis (Lu et al. 2008), and forensic examination of evidence (Bendroth et al. 2008). Unfortunately, the stable masses of molecular components of interest were not in a database for comparison and compiling them would be beyond the scope of this project. Despite the limitations encountered here, this technique has the potential to tell us more about species ecology from scat given a greater expertise.

Data Analysis.—The frequency of occurrence (F_o) of each parasite species was calculated for each site as the percentage of scats in which the species was found. F_o was calculated in this same way for food categories. Frequencies of occurrence of parasite species and of food categories were then compared graphically by study site. The number of categories found in each scat (diversity of diet) was also recorded for all samples, and was compared among sites using one-way ANOVA followed by Tukey multiple comparison tests (95% CI).

The relative percentage bulk (RPB; a measure of importance or abundance) of each food category within a scat was calculated as follows (adapted from Birks and Dunstone 1985; Remonti et al. 2007; Jenkins et al. 1979):

$$\text{RPB} = 100\ [(\text{\# grids of a category}/\ \text{\# of grids of sample})] \qquad (1)$$

Though not all food categories were laid to the exact same thickness in the Petri dish, effort was made to ensure that they were as similar as possible.

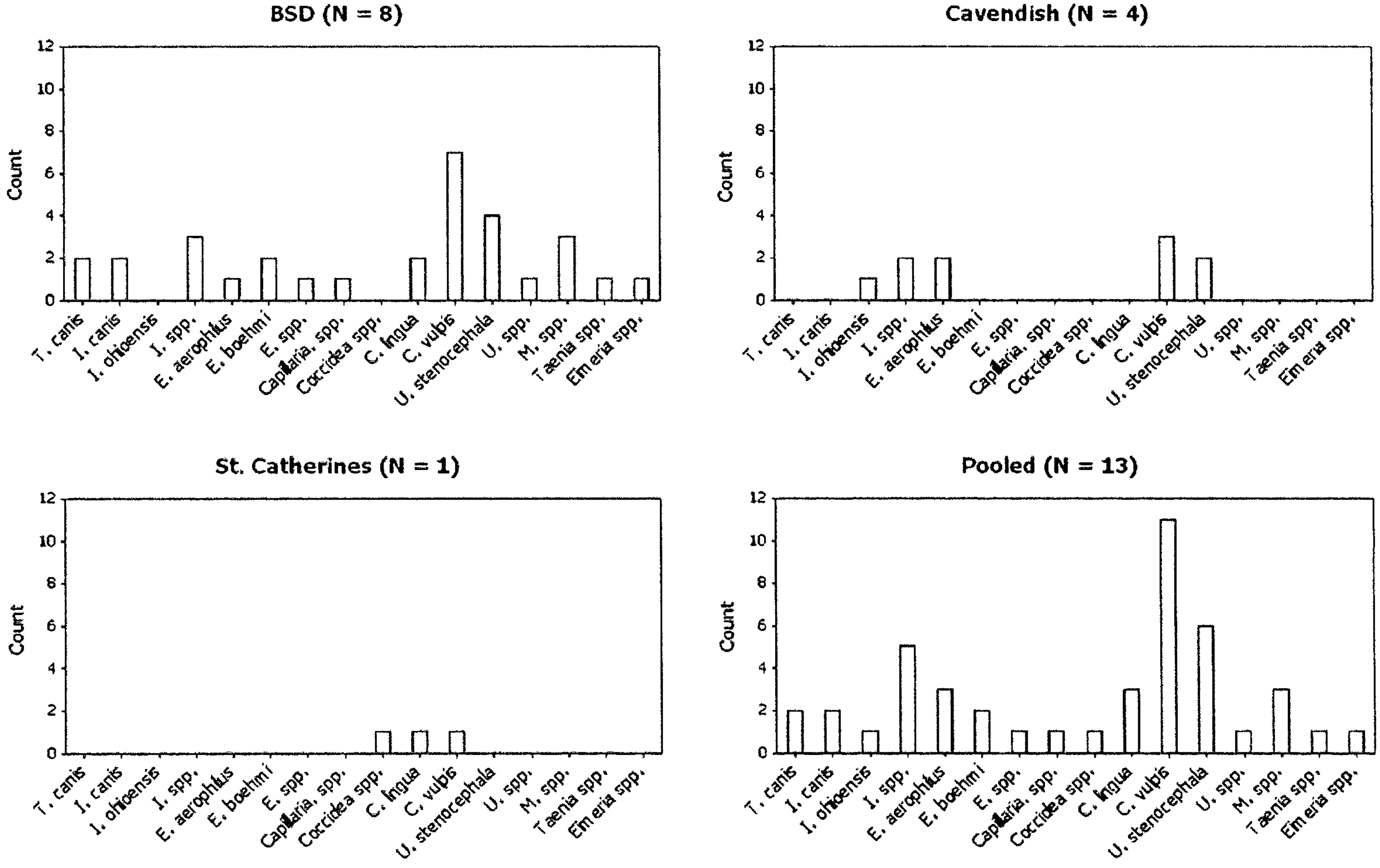
Similarity of study sites based on RPB was assessed using Primer software (v. 5.0, PRIMER-E Ltd, Ivybridge, United Kingdom). A multidimensional scaling (MDS) plot was created based on Bray-Curtis similarities of RPB data for study sites. MDS plots show similarity based on many factors (or dimensions) as clustering on a 2-dimensional plane. The reliability of the MDS plot was verified (a stress value of < 0.1 indicates the plot is very reliable, Kruskal and Wish 1978) and significance of the plot was evaluated using a one-way ANOSIM. Global R indicates the degree of similarity between the tested groups and varies between –1 and 1. If all replicates within sites are more similar to each other than any replicate from different sites, the value of R is 1 and values close to zero indicate that the similarity among sites is very high (Clarke and Warwick 1994). The significance level (or P-value) indicates whether the study sites are significantly different. A Kruskal-Wallis test was done for the RPB of each food category to compare among sites, and was followed by Mann-Whitney U-tests for post-hoc pair-wise testing where necessary. RPB data were also pooled together over sites in order to assess the general importance of food categories to fox diet on PEI. Most natural food items like small mammals and insects are available at all sites, although this pooling may mask the importance of some other categories such as fruit at individual sites.

Unless otherwise indicated, all statistical analyses were done using Minitab v.15. Marginal significance was interpreted as $0.05 < P \leq 0.08$.

RESULTS

A total of 54 scats were collected in this study. Out of those 54 scats, 17 were collected at Alexandra, 16 at BSD, 11 at Cavendish, and 10 at St. Catherines. Of these scats, only a small number could be used for parasite analysis due freshness constraints (1-3 days old was considered fresh). Eight samples from BSD, 5 from Cavendish (4 in which parasites were found), and one from St. Catherines were used for parasite analysis.

Parasite Analysis.—There were differences among study sites in the parasite species present and in the F_o of these species (Fig. 2), with a higher F_o of most parasite species at BSD and at Cavendish. *Crenosoma vulpis* occurred in 11 of the 13 parasite-containing scat samples, *Uncinaria stenocephala* was


BSD (N = 8)

Cavendish (N = 4)

St. Catherines (N = 1)

Pooled (N = 13)

FIG. 2.—Bar graphs of total counts of infected fox scats by study site and parasite species.

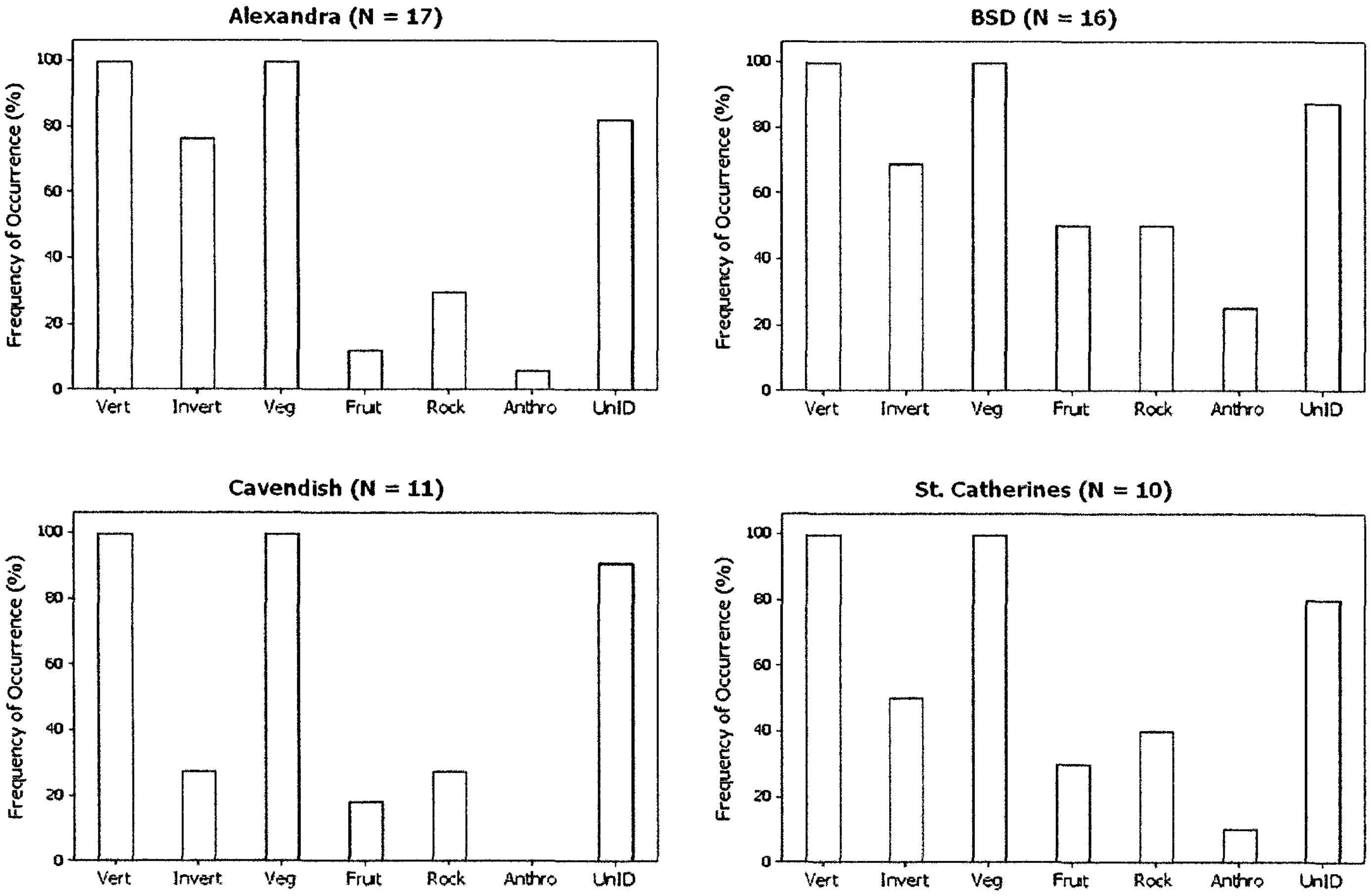
found in 6 samples, *Isospora* spp was found in 5, and *Eucoleus aerophilus*, *Crypotcotyl lingua*, and *Monocystis* spp. were each found in 3 samples (Fig. 2). Other parasite species found in this study only occurred in one or two samples.

Macroscopic Analysis.—All 54 scats were used in macroscopic analysis. F_o and RPB of categories appeared to differ among sites (Table 1). Although statistical analysis could not be conducted for F_o data, there were some trends found among study sites (Fig. 3). Vertebrates and vegetation were found in all scats. Unidentified items and invertebrates were the next most frequently found items. Anthropogenic items were found most often at BSD and were never found at Cavendish. All scats had at least two different food categories present. Alexandra averaged 4.1 ± 0.218 categories per scat, BSD, 4.9 ± 0.301, Cavendish, 3.6 ± 0.244, and St. Catherines, 4.1 ± 0.379. Scats at BSD were significantly more diverse than those at Cavendish (ANOVA and Tukey's Test; P = 0.023; R^2 = 0.1714), but the other comparisons were nonsignificant.

The MDS plot based on RPB values (Fig. 4) had a stress of 0.09, so was a reliable measure of similarity. Although the MDS plot had a lot of scatter, it appeared as though site B (BSD) was dissimilar from the others. However, one-way ANOSIM showed sites were very similar (Global R = 0.023, P = 0.201), and looking at pair-wise comparisons, only Alexandra and BSD were significantly different (R = 0.11, P = 0.022). RPB varied over sites (Fig. 5), but there were no significant differences among sites for vegetation, rock, or anthropogenic food

TABLE 1.—Summary of frequency of occurrence (F_o) data and relative percent bulk (RPB ± SE) data for study sites by food category.

Category	**Study Site** Alexandra (N = 17)		BSD (N = 16)		Cavendish (N = 11)		St. Catherines (N = 10)	
	F_o	RPB	F_o	RPB	F_o	RPB	F_o	RPB
Anthropogenic	5.88	0.02 ±0.02	25.00	0.78 ±0.70	0.00	0.00 ±0.00	10.00	0.02 ±0.02
Fruit	11.76	0.68 ±0.65	50.00	6.53 ±3.61	18.18	1.68 ±1.13	30.00	1.89 ±1.24
Invertebrate	76.47	14.88 ±3.87	68.75	4.60 ±1.91	27.27	6.44 ±3.97	50.00	1.82 ±0.82
Inorganic	29.41	0.10 ±0.04	50.00	0.31 ±0.13	27.27	0.05 ±0.03	40.00	0.12 ±0.06
Unidentified	82.35	8.38 ±2.54	87.50	19.78 ±5.25	90.91	2.58 ±1.29	80.00	3.78 ±1.17
Vegetation	100.00	9.33 ±2.47	100.0	22.57 ±5.95	100.00	10.92 ±2.76	100.00	10.49 ±1.86
Vertebrate	100.00	66.62 ±6.42	100.00	45.41 ±8.12	100.00	78.33 ±5.66	100.00	81.88 ±3.55


Alexandra (N = 17)

BSD (N = 16)

Cavendish (N = 11)

St. Catherines (N = 10)

FIG. 3.—Site differences in frequency of occurrence of food categories[1]. [1] Vert means vertebrate, Invert means invertebrate, Veg means vegetation, UnID means unidentified, and Anthro means anthropogenic.

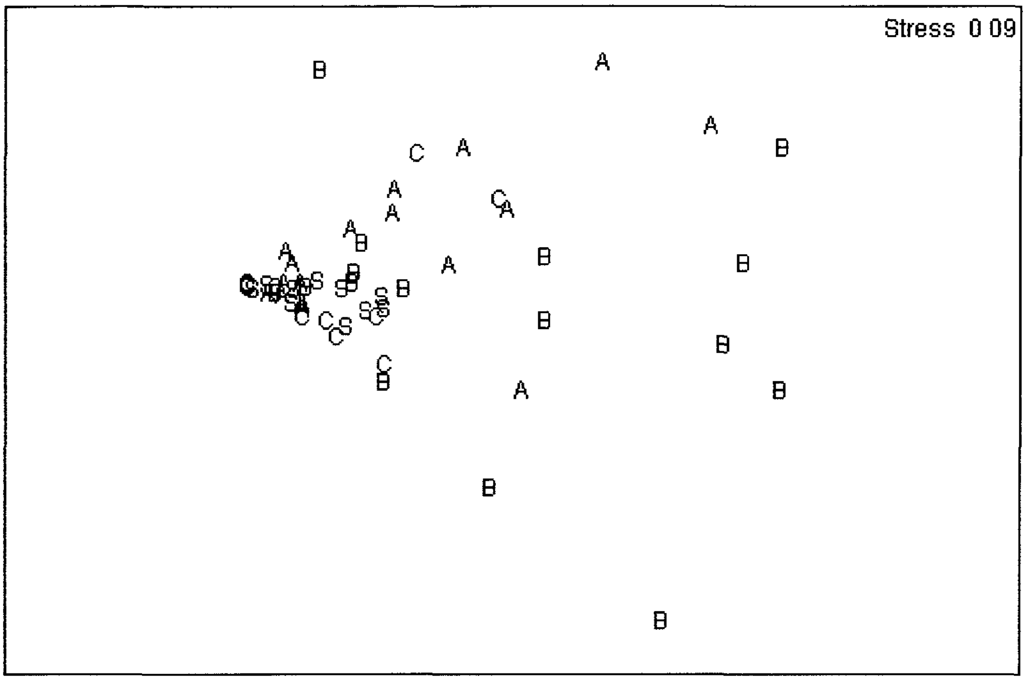


FIG. 4.—MDS plot showing site similarity based on RPB of food categories. A means Alexandra, B means BSD, C means Cavendish, S means St. Catherine's).

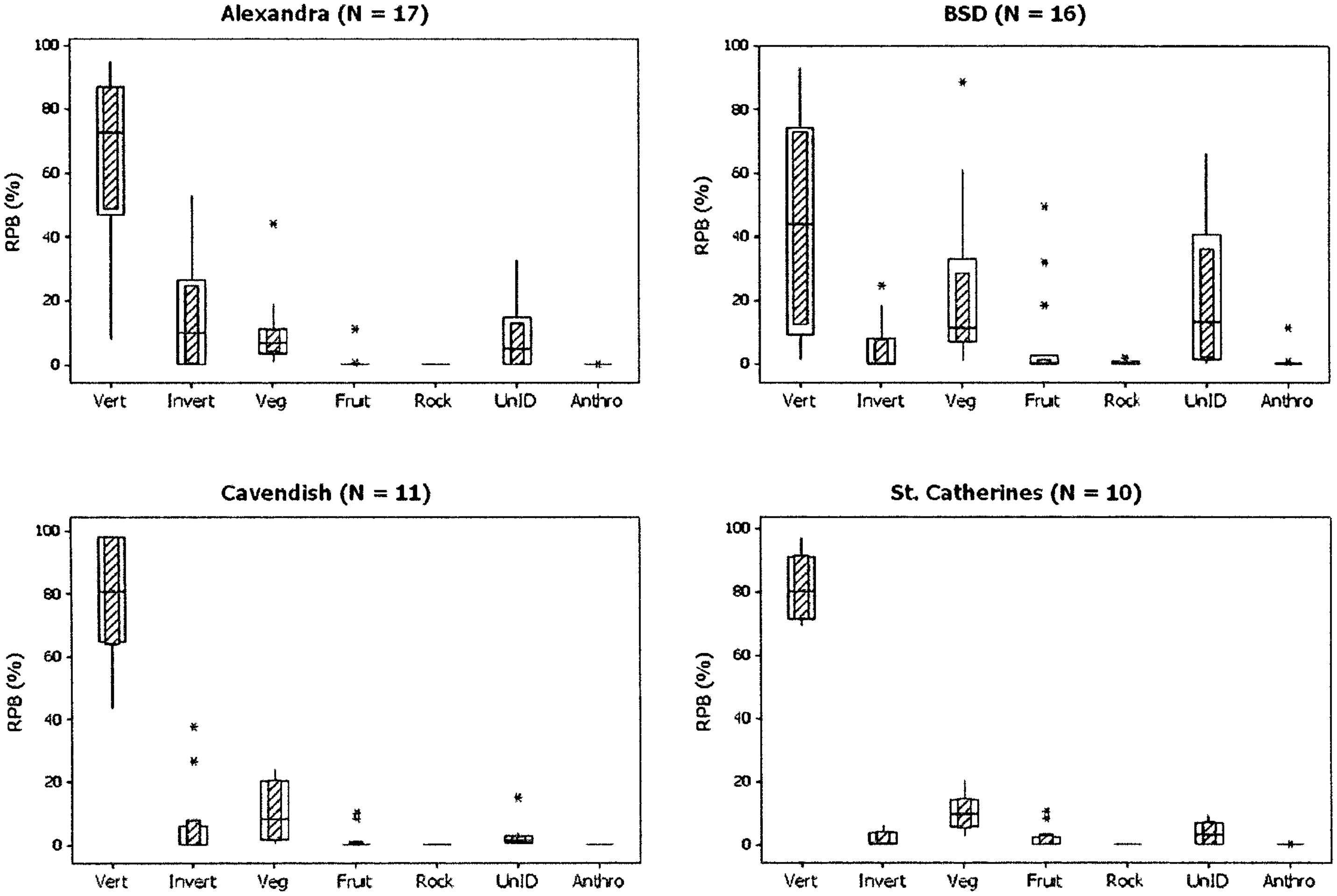


FIG. 5.—Boxplots of relative percent bulk of food categories[1] by study site. [1] Vert means vertebrate, Invert means invertebrate, Veg means vegetation, UnID means unidentified, and Anthro means anthropogenic.

categories (Kruskal-Wallis: $P > 0.05$). Study sites did differ significantly in terms of RPB of vertebrates (Kruskal-Wallis; $P = 0.007$) and invertebrates ($P = 0.044$), and marginally in terms of fruit ($P = 0.058$) and unidentified material ($P = 0.062$). Mann-Whitney U-tests determined pair-wise differences among sites for those categories (Table 2). When all data was pooled together to compare overall importance of categories, there were significant differences of RPB between food categories (Fig. 6, Kruskal-Wallis; $P < 0.001$). Vertebrates were more important than all other categories, followed by vegetation, unidentified material, and invertebrates (Table 3).

DISCUSSION

Some variation in fox diet and in parasite infection was found among study sites on PEI. Some parasites capable of causing mild to serious disease conditions were found in fox scats. *Crenosoma vulpis*, a nematode lungworm, was found in 84.6% of sampled scats and was present at all three sites assessed, indicating that foxes across PEI are frequent carriers of this parasite. This is a rare parasite in North America, except for the Atlantic provinces where it frequently causes a non-fatal chronic cough in canid definitive hosts (Zajac and Conboy 2006). *Eucoleus aerophilus* (and the less frequently found and less serious *E. boehmi*) is also a lungworm and causes bronchopneumonia in foxes (Zajac and Conboy 2006). These latter two lungworm species were found at BSD and at Cavendish. Lungworm is transmissible to domestic dogs, but the symptoms are less severe, usually a chronic cough or sneezing with nasal

TABLE 2.—Summary of Mann-Whitney U-test comparisons between sites among which a KW test showed significant differences in vertebrate, invertebrate, fruit, and unidentified food categories.

Study Site	Category			
Pair[2]	Vertebrate	Invertebrate	Fruit	Unidentified
A vs B	P = 0.050 (A)	P = 0.061* (A)	P = 0.011 (B)	NS
A vs C	NS	P = 0.045 (A)	NS	NS
A vs S	NS	P = 0.026 (A)	NS	NS
B vs C	P = 0.007 (C)	NS	NS	P = 0.022 (B)
B vs S	P = 0.003 (S)	NS	NS	P = 0.054* (B)
C vs S	NS	NS	NS	NS

[1] P-values shown (* indicates marginal significance). Brackets show the study site with a higher value. [2] A means Alexandra, B means BSD, C means Cavendish, S means St. Catherines.

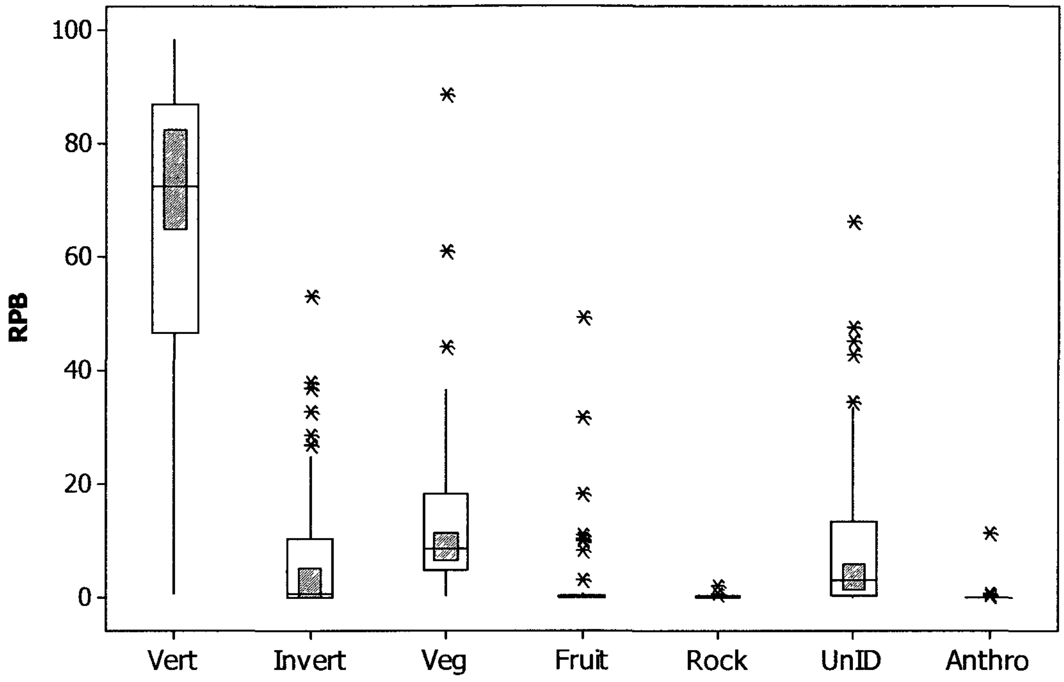


FIG. 6.—Boxplot[1] of all data pooled together to compare relative percent bulk between categories[2]. [1] Inner boxes represent the 95% confidence interval for the median. * represents outliers. [2] Vert means vertebrate, Invert means invertebrate, Veg means vegetation, UnID means unidentified, and Anthro means anthropogenic.

TABLE 3.—Pairwise comparisons of food categories in pooled data using Mann-Whitney U-tests as post hoc tests[1].

Category[2]	Vert	Invert	Veg	Fruit	Rock	UnID	Anthro
Vert		$P < 0.001$ (Vert)	$P < 0.001$ (Vert)	$P < 0.001$ (Vert)	$P < 0.001$ (Vert)	$P < 0.001$ (Vert)	$P < 0.001$ (Vert)
Invert			$P < 0.001$ (Veg)	$P = 0.001$ (Invert)	$P < 0.001$ (Invert)	$P < 0.001$ (UnID)	$P < 0.001$ (Invert)
Veg				$P < 0.001$ (Veg)	$P < 0.001$ (Veg)	$P = 0.002$ (Veg)	$P < 0.001$ (Veg)
Fruit					NS	$P < 0.001$ (UnID)	$P = 0.011$ (Fruit)
Rock						$P < 0.001$ (UnID)	$P = 0.003$ (Rock)
UnID							$P < 0.001$ (unID)

[1] P-values (significant if < 0.05). Brackets show the category with higher values.
[2] Vert means vertebrate, Invert means invertebrate, Veg means vegetation, UnID means unidentified, and Anthro means anthropogenic.

discharge (Zajac and Conboy 2006). *Isospora* species were found at both BSD and Cavendish and are often found in young and otherwise healthy dogs, causing diarrhea, abdominal pain, and weight loss (Zajac and Conboy 2006). The potential for transmission of these species from foxes to dogs and vice versa is something important to consider given the close proximity of foxes to human populations and their domesticated animals on PEI.

Uncinaria stenocephala (hookworm) was found at BSD and at Cavendish at the second highest frequency. Hookworm is frequently found in dogs and foxes andc can cause chronic diarrhea and deterioration in health (Zajac and Conboy 2006). It can be contracted from ingesting larvae from the environment or from prey species (Zajac and Conboy 2006). It is not surprising that hookworm was found in fox scats, though its presence in wildlife could also mean higher prevalence in domesticated dogs in the area. Hookworm is also transmissible to people, and can cause potentially fatal toxocariasis (Mizgajska 2001; Richards et al. 1993; Richards and Lewis 2001). *Toxocara canis* (dog roundworm), found in two samples from BSD, can also cause toxocariasis in people, as well as neonatal death in canids (Zajac and Conboy 2006). *Isospora* species, found at BSD and Cavendish, are sometimes transmissible to humans, and can cause serious disease, particularly in immune-suppressed individuals (Lindsay et al. 1997). *I. canis* and *I. ohioensis* (dog coccidea), which are often found in young canids causing diarrhea, abdominal pain and weight loss (Zajac and Conboy 2006) were identified in some samples, but remaining *Isospora* found could not be identified to species and could well be those infecting human hosts. Parasites such as *U. stenocephala, T. canis*, and *Isospora* spp. are of zoonotic importance as they can be spread to people, especially children playing outside, and precautions should be taken to prevent infection in areas where these parasites are present in animals.

Some of the other parasite species found in this study do not really infect foxes but are instead found in their prey species, often called spurious or "false" parasites. *Crypocotyl lingua* is typically found in fish-eating birds and mammals (Stunkard 1930). This parasite was found at BSD and at St. Catherines, where there is a water supply close by, and so it is likely that foxes there are consuming fish hosts. *Monocystis* is an earthworm parasite that is very host specific and has all its life stages in one organism, thus is non-pathogenic to people (Sheridan 1986). Foxes often consume large quantities of earthworms, though they can be difficult to detect and quantify in scat even with microscopic techniques (Reynolds and Aebischer 1991). Though microscopic analysis was not done, the presence of *Monocystis* parasites indicated that foxes at BSD are including earthworms in their diet. *Taenia*, *Eimeria*, and *Capillaria* were each found in one sample at BSD and were likely the result of consumption of infected prey as well. *Taenia*, a cestode, is typically contracted by dogs by ingestion of other host species, though the infection is usually not serious (Zajac and Conboy 2006). *Eimeria,* a protozoan, is found in many different types of animals (e.g. ruminants, birds, rodents, etc.) and causes diarrhea and gastrointestinal problems in hosts (Zajac and Conboy 2006). Finally, *Capillaria,* a nematode, is found in birds and sometimes has an earthworm intermediate host (Zajac and Conboy 2006).

Although sample sizes were small and prevalence of parasites could not be compared among sites in a quantitative way, various parasites of disease interest were found, as well as some that gave additional information on fox diet. This was the first effort to document a range of parasites occurring in red foxes on PEI and, based on the results and on the disease vector role of foxes elsewhere in the world, it is an important work. Only one sample was found at St. Catherines, so although it would appear that foxes in PEINP have a greater diversity and frequency of parasitic infections, more samples are required for the private sites in order to have representative results. There was also evidence that zoonotic diseases are found in foxes on PEI and for this reason, the public should be cautious in its proximity to such wildlife.

In order to investigate fox diet, the frequency of occurrence (F_o) and relative percent bulk (RPB) of food categories were assessed in scats. Though study sites were not different overall based on RPB of food categories in an MDS plot, there were some important differences observed between study sites. All scats contained at least 2 different categories of food items out of 7 possible. The only significant difference for scat diversity was that between BSD and Cavendish (BSD > Cavendish). This could indicate that foxes at BSD have a greater variety of resources available than at Cavendish, and have learned to exploit them, or that they are simply have a more general diet and will consume a greater variety of items. Animals that learn about and take advantage of the quality of their environment more closely fit an "ideal free distribution," in which individuals are foraging optimally by maximizing encounters with prey or food items (Bernstein et al. 1988). From this it appears that foxes at BSD are more generalist foragers compared to those at Cavendish.

Vegetation was found in every scat and had the second highest RPB overall. One explanation for this finding is that foxes directly seek vegetation as a food source. Another possible explanation is that vegetation is ingested accidentally as a result of foraging or ingestion of herbivorous prey species. As an example, vegetation could be ingested during the capture and consumption of a mouse in a grassy field or while foraging on insects. In other scat studies, vegetation is sometimes considered to have little nutritional value for carnivores and is categorized as a non-food item or is simply omitted from any analyses (see Reynolds and Aebischer 1991). In this study, vegetation was kept in analyses because no behavioral observations or tests were done to determine if it was actively searched out as a food item or if it was accidentally ingested. Kelly-Clark and Silva (unpublished data) found that in foxes on PEI in the breeding (winter) season, vegetation was second only to small mammals in frequency of occurrence in stomach contents. This seems to indicate that vegetation is consumed on a regular basis, whether accidentally or on purpose. Rocks were also observed in many samples in the current study, but in low quantities, and this could also be the accidental consequence of foraging activities (see Faurot et al. 1986). It is also possible that despite precautions taken by the research team, some small amounts of rock or vegetation may have been incorporated into a sample from the ground on which it rested. This means that little can be inferred from rock occurrence.

Vertebrates were also found in every scat sample, indicating that small mammals are a frequently used food source for foxes on PEI. Similar results were found in other studies (e.g. Jedrzejewski and Jedrzejewska 1992; Macdonald 1977; Sidorovich et al. 2006), including a stomach content analysis study conducted on PEI (Kelly-Clark and Silva unpublished data). Foxes were frequently observed hunting for small mammals and on some occasions remains were found at study sites. Alexandra, Cavendish, and St. Catherines all had higher amounts of vertebrate per scat than BSD, suggesting that small mammals are a relatively less important food category at BSD than at the other sites. A possible explanation for this is that BSD is the most public and human-influenced of the study sites, with a greater availability of other food sources, and therefore foxes are eating a higher diversity of foods. This is partially supported by the comparison of diversity of components in scats, where BSD samples were more diverse in diet than Cavendish samples, although they were not more diverse than at Alexandra or at St. Catherines.

Invertebrates and fruit were found in varying frequencies of occurrence among study sites and with different relative percentages of bulk. Importance of these food categories was only significantly different among study sites for a couple of instances. Alexandra scats had more invertebrate content than all other sites and BSD had a higher content of fruit than Alexandra. Variation in diet categories like these are likely due to differences in local availability, which was not assessed in this study.

Anthropogenic food items were found at a relatively low frequency of occurrence at all study sites at which they occurred. This category had the lowest RPB overall and RPB did not differ among sites. Kelly-Clark and Silva (unpublished data) also found that anthropogenic food items formed only a minor part of red fox diet even during the winter. However, other studies have found a much more obvious impact of anthropogenic food sources on fox diet. Contesse et al. (2004) found that anthropogenic food was used more frequently in a city centre than in the surrounding area and that more than 50% of the mean fox stomach content was anthropogenically-sourced (scavenged meat, compost, pet/wildlife feeding, garden material, domesticated animals, etc.). It was predicted in the current study that both BSD and Cavendish sites would be more impacted by people due to their extensive use by tourists and residents in the summer and thus would have a higher frequency of occurrence and proportion of anthropogenic items in fox diet. However, although anthropogenic items were present in more BSD samples than those of other sites, they were absent from Cavendish samples. Although both BSD and Cavendish sites are located within PEINP, there are some differences between the two sites that may affect the availability of anthropogenic food items. BSD is more central and is frequented more often by tourists and residents all year round. It has multiple campgrounds, a hotel, public beaches and recreational areas in addition to a network of trails. By comparison, Cavendish has a single campground and a walking/biking trail with picnic areas. There is also a main road bisecting BSD—while the Cavendish site is more isolated from roads and residential areas. It is important to note that anthropogenic food was considered in this study as anything that was obviously not natural in composition and that, with this classification, it is possible that some scavenged food may have been classified into other categories such as vertebrate or fruit.

Not all items in scats could be identified, and unidentified remains were left in samples from all study sites. Degradation of some main food items into unidentified remains was expected. It was hypothesized that unidentified material would be indicative of anthropogenic-sourced foods that were digested. Reynolds and Aebischer (1991) recognize that scavenged human garbage is often much more digestible and therefore hard to obtain in any quantity in the scat. Unfortunately, due to limited experience, unidentified remains could not be classified as anthropogenic in source. This is where the use of UHPLC-MS would have been useful, and future studies should consider this technique for molecular identification of well-digested remains. The importance of this unidentified material in fox scats varied over study sites, and BSD had significantly higher amounts than Cavendish or St. Catherines. Since BSD is likely a site most highly impacted by human activities, it is possible that an increase in anthropogenic food consumption could be translating to the observed higher amount of unidentified material in this area. BSD was not significantly different from Alexandra in RPB of unidentified material, which is interesting since foxes in the area of Alexandra studied are fed anthropogenic food directly on a regular basis (personal observations).

In all data pooled, the most frequently found categories were vertebrates and vegetation, and the most important were vertebrates, vegetation, unidentified material, and invertebrates. This is indicative of a diet largely composed of small mammals, plants, and insects. Foxes are often viewed solely as predators of small mammals, despite being ecological generalists. However, other studies also support the important role of fruit and insects in fox diet (Lanszki et al. 1999; Murdoch et al. 2009). Though not all categories of food items varied significantly in RPB or importance, vertebrates did, which shows that variation can occur in fox diet even for the most important and frequently occurring food categories.

CONCLUSIONS

Red foxes on PEI are generalists, consuming many different food items. There were some differences among sites however, the same basic types of food were consumed at all study sites with the exception of anthropogenic items. This is not surprising considering foxes at all study sites are capable of digesting the same things. Since many of the categories of food differed in importance (RPB) among sites, it is likely there is differing resource availability or flexibility in foraging strategy. Sidorovich et al. (2006) also found that despite a much higher importance of rodents in the diet, there was a regional specificity in diet of red foxes.

It was hypothesized that there would be a higher frequency of occurrence of parasites (except for spurious species) in PEINP. Conclusive statements could not be made comparing parasite infection among study sites due to low sample sizes; however, some parasites of clinical importance, and also some of zoonotic importance, were found, stressing the importance of safety precautions around red foxes. In addition to the highly documented role of foxes as vectors of rabies (e.g. Chomel 1993), foxes are prone to transmission of sarcoptic mange, canine distemper, parvovirus, and toxoplasmosis (Macdonald and Reynolds 2004). It was also hypothesized that diet of foxes in PEINP, theoretically an area of higher human impact, would be different than that at private sites, with unidentified and anthropogenic food items being more common and more important in scats. It turned out that there was a very low frequency of occurrence of anthropogenic food items in scats, even within PEINP. However, there was a higher RPB of unidentified (and potentially anthropogenically-sourced) material at BSD, a site of high human impact, compared to two more natural and rural sites (St. Catherines and Cavendish).

This study stresses that foxes are capable of foraging for a largely natural diet and that even on PEI where foxes are considered 'safe' wildlife, they carry parasites that can have some serious health implications for people and domesticated animals. Some areas for future study could include the species identification of vertebrates, invertebrates, and fruit in scat to further classify food preferences of foxes. Collection of a larger sample of fresh scats would allow for statistical comparison of parasite prevalence between areas of differing human use. Finally, food items or classes of compounds in fox diet and scat that cannot be visually identified might be molecularly identified with the use of UHPLC-MS.

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APPENDIX 3: LIVE-TRAPPING AND HANDLING PROTOCOL

This live-trapping and handling procedure was accepted as UPEI Animal Care Protocol # 08-058- (1002873). Permission for live-trapping was obtained from land authorities, from Parks Canada in the form of a Research and Collections Permit (# PEINP-2009-3372), and verbally from individual landowners. Live-trapping was conducted from August 2009-February 2010.

Live-Trapping

The live-traps used in this study were Havahart live box traps intended for large raccoons (Model #1050, 2-door, 42"L x 10"W x 13"H, Woodstream Corporation, Lititz, PA). Leg-hold traps are known to have higher success rates in capturing animals (Field 2003), however the risks of injury may also be greater with this trapping method (Olsen et al. 1986). Box-traps were weathered in a wooded area for three weeks prior to the first trapping session. As often as possible a more natural bait in the form of duck carcasses from a local taxidermist were used, but supplementing that was chicken, bacon, wieners, bologna, apples, and pork. A cover scent was used for lure (Tinks 69 Red FoxP, Tink's, Covington, GA, USA). For all trapping sessions the traps were pre-baited (wired open) for 3-6 days before the actual live-trapping was conducted. Traps were equipped with a small blanket for animal comfort and to hide the trap plate and bait was placed at the very back of the trap with one door set during trapping. Up to six traps were set in a study area before dusk and before dawn and were checked within 4-6 hours. Further into the study, this was modified to two night checks after an evening set.

Handling and Immobilization

If non-target captures were in good health and not aggressive, the trap was covered with a dark blanket, moved to an open area, and wired open so the animal could move out. If the animal did not appear healthy or was very aggressive in the trap, the university veterinarian (Dr. Jonathan Spears) was to be contacted. NB. Non-target captures (3 raccoons, 2 skunks, and 3 cats) did not have any obvious injuries from the trap and were safely released.

In the event of a red fox capture, the following plan was to be put in action:

1) The main researcher briefly assesses health and aggression before returning with a helper to weight the fox and cage together with a 20-kg Pesola scale. The mass of the cage (pre-recorded) is then deducted so that dosages of anaesthetizing and tranquilizing drugs could be measured. The dosage is ketamine (8 mg/kg) and xylazine (0.5 mg/kg) (adapted from Kreeger 1999 with consultation from Dr. Mark Johnson DVM). The research team will wear gloves and protective clothing at all times when handling animals

2) The fox is squeezed in the cage with rebar so that injection can be safely done IM by syringe into the lumbar muscle or the rear flank.

3) Once the animal is down, an initial physical exam is done to assess the animal including rectal temperature, pulse, and respiration. These vitals are monitored repeatedly during the immobilization before the beginning of any procedure.

4) The GPS-collar is then prepared. Sirtrack GPS/VHF collars with internal timed release (Model GWC171, 25 mm wide, 120 g, Sirtrack, Hastings, New Zealand) were to be used. These collars record a GPS position every 15 seconds for 21 days and are is equipped with a VHF-radio component so that the animal can be tracked manually. This collar also has a drop-off mechanism programmed for one month after application. A magnet is applied to activate the VHF- and GPS-components. The radio-tracking component is tested with a receiver and then the collar is fitted snugly to the animal. Only a small finger should fit between the collar and the animal's skin.

5) Two millilitres of blood are drawn from the cephalic vein into a purple top tube for analysis of animal health and parasite load.

6) Both ears of the fox are then ear tagged with a unique combination of coloured and numbered tags.

7) The animal is then replaced back into the trap (wired open) and the research team waits until the animal wakes up. If the animal's head is not up 45 minutes from the last ketamine injection or 20 minutes after the first leg movement, the antagonist, atipamezole will be injected IM at a dosage of 1mg per 10 mg xylazine administered.

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APPENDIX 4: SCAT PARASITE ANALYSIS PROTOCOLS

Zinc Sulfate Flotation (modified from Zajac and Conboy (2006))

[Used to detect protozoans and eggs]

1) Place a thumbnail size sample (2-3 g) of scat in a paper cup and add enough water to dissolve the sample.
2) Use a wooden stick to crush and dissolve the sample in the water.
3) Filter the mixture through a double layer of cheesecloth and pour the resulting solution into a 15 ml centrifuge tube, topping up with more water.
4) Spin the tubes in a centrifuge set to speed six for 10 minutes (I used a Beckman Model TJ-6, USA).
5) Pour off most of the liquid in one quick motion, and then fill the tube halfway with a 33% $ZnSO_4$ solution. Use a wooden applicator to break up the pellet, and then top up with more $ZnSO_4$.
6) Spin the tubes for another 10 minutes, and then again pour off the liquid. Top up with $ZnSO_4$ to the point that a convex meniscus is formed.
7) Place a cover slip on top of this meniscus and allow it to sit for 10-15 minutes.
8) Lift the cover slip straight up and onto a glass slide for examination with a light microscope (I used a Zeiss West Germany 46 40 42-9903).

Baermann Technique (modified from Zajac and Conboy (2006))

[Used to isolate larvae, especially lungworm, from fresh samples]

1) Set up a glass funnel with rubber tubing for each sample. Close the ends of the tubes with metal clamps and fill the funnels halfway with very hot water.
2) Lay a double layer of cheesecloth over each funnel, and put a portion of the scat sample within it, ensuring it is completely covered with water. Leave this to sit (preferably under a fume hood to limit odour) between 8 and 24 hours.
3) Draw off the first 15 ml from each funnel into a 15 ml centrifuge tube and spin the tube in a centrifuge on speed six for eight minutes (I used Beckman Model TJ-6, USA).
4) Pour off most of the fluid in one quick motion, and then use a pipette to mix up the remains. Pipette two separate drops onto a glass slide, and add a drop of iodine to kill the larvae. Cover the drops with cover slips for viewing with a light microscope (I used a Zeiss West Germany 46 40 42-9903). Examine drops until the species of interest are found or the entire sample has been exhausted.

APPENDIX 5: ULTRA-HIGH-PERFORMANCE LIQUID CHROMATOGRAPHY- TANDEM MASS SPECTROMETRY (UHPLC-MS)

Protocol (Modified from Drug Discovery Process (Tricia Boland, Fabrice Berrue, and Dr. Russ Kerr, National Research Council, UPEI)):

1) Freeze-dry falcon tubes containing samples overnight (poke holes in plastic covers and use a doubled Kim Wipe under cap to prevent leakage).
2) Weigh all dry samples on weigh boats and record masses.
3) Break up samples by hand into separate pre-labeled 50 mL scintillation vials.
4) Cover each sample with a mixture of DCM: MeOH (1:1, to dissolve both soluble and insoluble compounds) and sonicate in a beaker containing water for 20 minutes.
5) Let particles settle, then pipette off the top liquid (excluding the bottom ~2 mm which may contain salts and/or insoluble particles which could cause potential problems in the fractionation step) and filter it liquid through a cotton pipette plug into a pre-weighed 20 mL scintillation vial labeled crude extract.
6) Let this first extraction dry under airflow while a second identical extraction is done. A 1mL sample of this is filtered into a 20 mL vial labeled Fraction Zero (not fractionated but kept for

reference/comparison). The remainder of this extraction is filtered into the crude extract vial.

7) Once the Crude Extract is dried and weighed, samples weighing 100 mg or can be fractionated, but those weighing more must be dissolved in DCM: MeOH (1:1) until there is about 100mg/ml. Transfer 1 mL of this diluted sample to a new 20 mL vial and allow to dry under airflow.

8) Add a wide-mouth spatula of Bulk C-18 is to each of the vials of 100 mg or less along with ~1 mL of DCM: MeOH (1:1), sonicate, and allow to dry under airflow.

9) Label a separate C-18 sep pack for each sample, and attach to a vacuum manifold. Label 20 ml culture tubes for each sample and each fraction (1-6).

10) Prepare 10 mL of each eluent for each sample and fraction: Water: MeOH (9:1), Water: MeOH (5:5), Water: MeOH (2:8), AcN (100%), Acetone (100%), and MeOH: DCM (1:1).

11) To load each sample onto the column (sep pack), add ~1-2 mL of the first eluent to the sample vial, sonicate, and mix with a pipette to dissolve. Add 1 mL at a time to the column turning the stopcock and allowing the vacuum to draw the liquid into the culture tube in between additions. Once the ~5 mL is loaded, add the remaining ~10 mL of pure eluent 1 mL at a time to the column, allowing the vacuum to draw the liquid into the culture tube in between additions.

12) After the first fraction is completed, remove the tubes with the first fraction and replace with those for the second. Extract fractions 2-6 using the same process is followed as for fraction 1.

13) Dry the tubes and weigh them. Fractions 1-4 will not easily dry under air flow and thus can be dried on the GeneVac at 'HPLC Fractions' setting at 30 ° Celsius overnight. Fractions 5-6 can be dried under airflow overnight. If Fraction 3 is not drying, put it under airflow or on GeneVac 'Aqueous' setting at 30 ° Celsius overnight.

14) Label 96-well plates with a column for each sample and a row for each fraction: Row A- Crude Fraction 0, Row B- Fraction 1, Row C- Fraction 2, Row D- Fraction 3, Row D- Fraction 4, Row E- Fraction 5, Row F- Fraction 6, and Row H- Excess Crude (not fractionated).

15) Wash each tube with 1 mL of MeOH: DCM (1:1) and transfer to corresponding wells in the 96-well plate. Dry the plates under a funnel with airflow.

16) Use an ACCELA autosampler to draw and pump each sample through a Sedex 80 TELSD (UHPLC) adding different eluent combinations, then through a Finnigan LXQ Mass Spectrometer to determine molecular weights of compounds in the sample solutions.

Results:

I present here some examples of spectra obtained using this protocol on red fox scats collected on PEI. NH02 is a sample obtained from Brackley, and C02, from Cavendish. I show fractions 1-4 for comparison. Though I could not identify which compounds might be of interest in the scat, there are some similarities in the peaks that likely indicate some molecular consistency in scat content regardless of study site.

The graphs shown in Fig. 1 are mass spectrometry graphs, and represent the most abundant compounds in the scat. The molecular weight is that of the most stable ion on a molecule in the fraction and the height of the bar indicates how abundant the compound is.

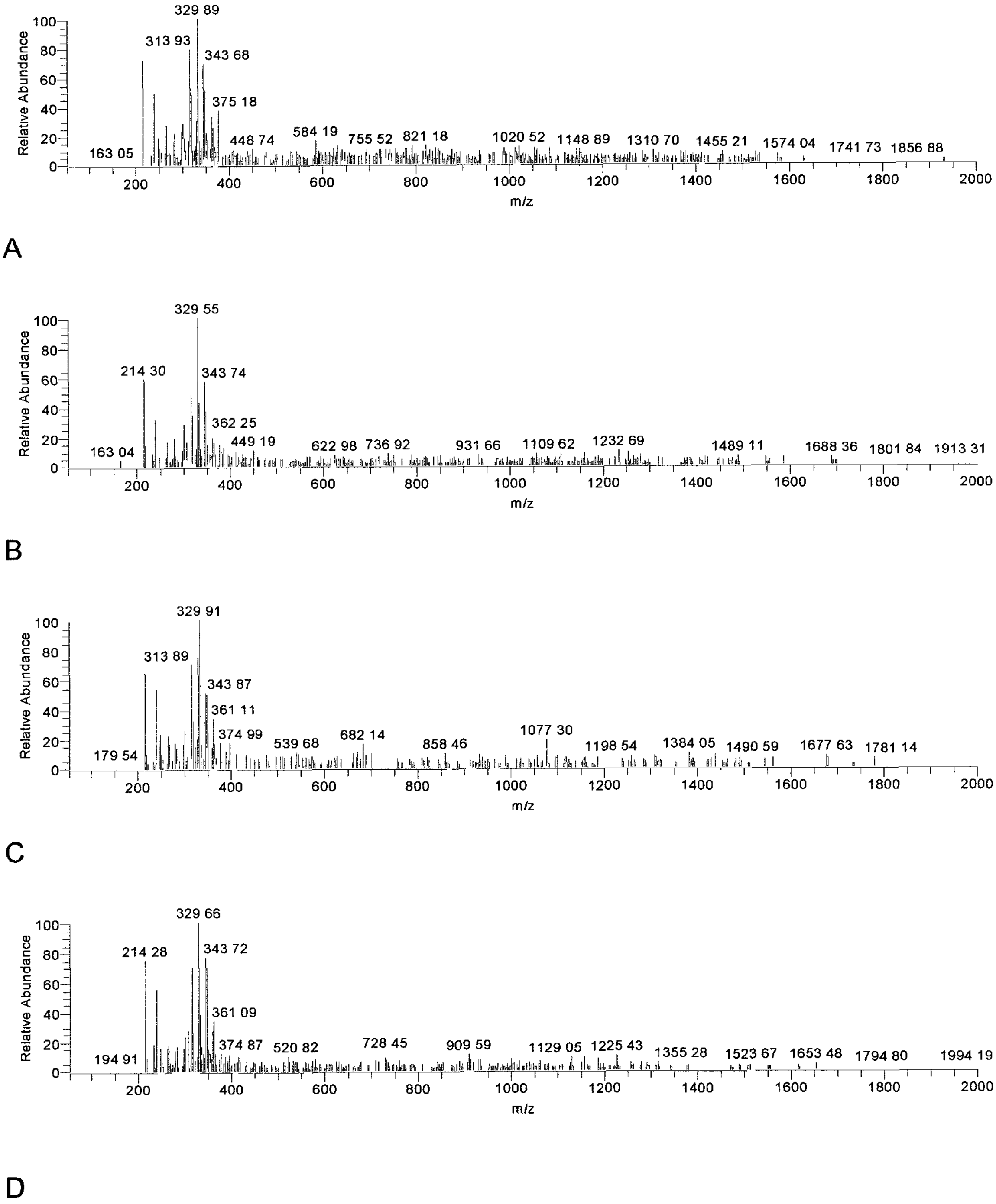

Fig. 1. UHPLC-MS output for A) sample NH02 (Brackley), fraction 1, B) sample C02 (Cavendish), fraction 1, C) sample NH02 (Brackley), fraction 2, D) sample C02 (Cavendish), fraction 2.

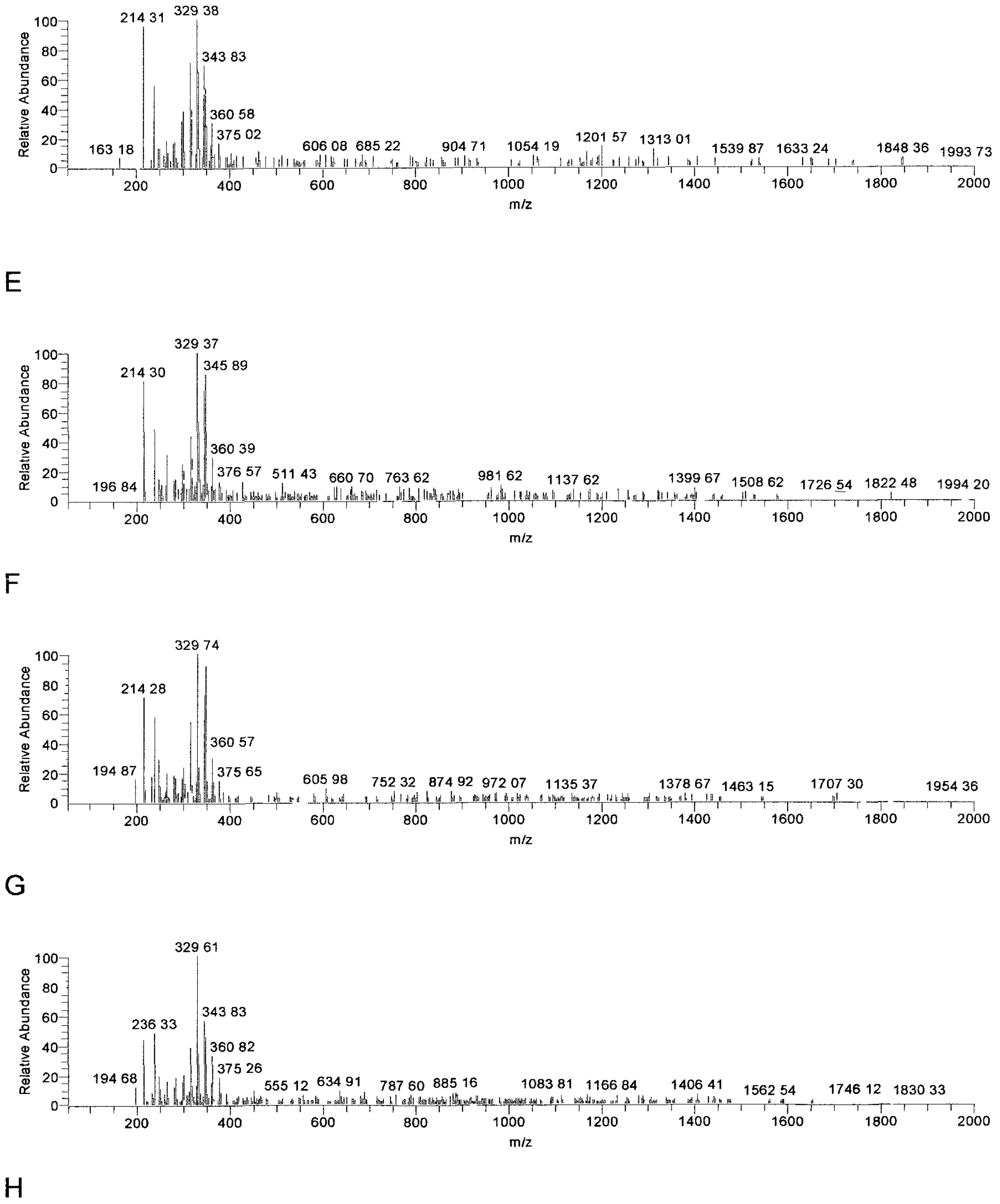

Fig. 1. UHPLC-MS output for E) sample NH02 (Brackley), fraction 3, F) sample C02 (Cavendish), fraction 3, G) sample NH02 (Brackley), fraction 4, H) sample C02 (Cavendish), fraction 4.