THE EFFECTS OF LANDSCAPE STRUCTURE AND BODY SIZE ON THE SPECIES RICHNESS AND OCCURRENCE OF BREEDING BIRDS ON PRINCE EDWARD ISLAND

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ABSTRACT

The primary goal of this thesis was to examine the effects of landscape structure, body size, latitude and longitude on the species richness and occurrence of avian species breeding on Prince Edward Island. Variation of species richness and occurrence within functional groups (landbird, seabird, shorebird, waterfowl) and species occurrence within trophic groups (carnivore, omnivore, herbivore, insectivore) is examined. Spatial data on species counts were obtained from Erskine (1992) and avian body size data were obtained from Dunning (1993). Information on land-cover types (agriculture, forest, wetland, roads, human-used areas) were obtained from the provincial government. ArcView GIS and Fragstats were used to calculate several metrics that characterized the structure and complexity of the different land-cover types (area, shape, and aggregation).

Habitat metrics, latitude and longitude, and body size information were related to avian species richness in seventy-six 10 km x 10 km sampling cells. Explanatory variables were related to avian species richness using multiple regression analysis, and models were chosen using Akaike's Information Criterion. In total, 156 species were found to breed in Prince Edward Island. Species assemblages varied between 9 and 98 species. Land-cover types, longitude, latitude and body size explained up to 49% of the variation in avian species richness on Prince Edward Island, though each functional group responded differently to particular variables. These findings suggest that avian species richness on Prince Edward Island is strongly influenced by human activities such as alteration of forest habitat and expansion of agriculture.

At the species level, habitat metrics were related to the occurrence of 102 avian species (species where occurrence >10% or <90% coverage of the study location) in seventy-six 10 km x 10 km sampling cells. Logistic regression analysis was used to examine the associations and to develop multivariate models to explain avian species occurrence. Avian species were then examined in terms of functional group (*i.e.* landbird, seabird, shorebird, waterfowl) and trophic level (*i.e.* herbivore, carnivore, insectivore, omnivore). Twenty-nine species were significantly associated with the land-cover variables. These species were primarily from the landbird functional group and the omnivore and insectivore trophic groups. There were few discernable patterns in specific metrics used by species, though forest-related variables were associated with species more often than other land-cover types.

This is the first landscape-scale study on avian community ecology on Prince Edward Island. A blended approach to the study of avian communities is useful to wildlife managers, conservation biologists, and ecologists alike. This study has examined several factors that determine species richness and occurrence of birds breeding on Prince Edward Island at a regional spatial scale. What is required now is a process-orientated investigation of some of these factors, especially those associated with anthropogenic activities. Such an approach would be best served by exploring the biology of individual species and how they interact with the physical geography of their environments.

ACKNOWLEDGEMENTS

Any work of this size and complexity can only be created with the assistance of many, many people. To that end, I am going to attempt to acknowledge the most influential and numerous of these contributors. If I do not list your name, do not be offended! In all likelihood, I'll have remembered it the second the thesis goes into print, and have to live that down for the rest of my life. That is why I wrote about the most important person first, even though I placed that person at the end of the list.

I would never have been able to create this document without the constant and helpful influence of my supervisor, Dr. Marina Silva. She was vital from before the very first stage of my MSc, where the ideas of this thesis were first beginning to take root in my mind. In those days, the ecology lab was utterly devoted to mammals. However, due to a fantastic dataset from the Atlantic Canadian Conservation Data Centre, as well as geographic data from the Prince Edward Island provincial government, we had a wonderful opportunity to expand ecological studies at UPEI to include avian species at large spatial scales. This is when I first met Dr. Javier Sanchez in the spring of 2004, and the two of us decided we would sit down and figure out how Geographic Information Systems work. Looking back, we may have seemed a little overambitious, but the success of this thesis shows otherwise. What this thesis does not mention is the enormous investment of time in terms of trial-and-error that we put into this, simply to learn the systems. In sum, I must acknowledge and thank Marina for all of her advice on ecological theory, for the many, many opportunities she allowed me during this degree, and for her friendship. I acknowledge and thank Javier for his technical advice, the opportunity to learn outside the ecological box in the form of epidemiology, his extreme patience and helpfulness (particularly in the last few months of thesis revisions), and also for his friendship. I could not have done this work without these people, and no others could have replaced them. The remaining members of my thesis advisory committee were Pedro Quijon, Jeff Houlahan (the external), and Rob Hurta (chair of the graduate studies committee for Science). These gentlemen were extremely patient and helpful, and gave very good insight into my research, comments that I had not thought of before, or had not looked at from the proper angle. They were courteous and respectful during my MSc defence, which I greatly appreciate, as any MSc student will understand! Dr. Henrik Stryhn was also instrumental in making this thesis statistically sound, and I could not have done this work without his superb guidance.

A number of scholars, while not directly involved with this project, were very influential in the direction of its completion. Sometimes this was as simple as a few comments after a talk at a conference, a quick phonecall, a passing in a university corridor, or an intense philosophical debate at the student pub. Daryl Guignion and Rosemary Curley were influential in their philosophies and my outlook on nature in general and birds in particular. Dr. Sheldon Opps and Dr. James Polson from Physics always kept my spirits up and always provided an interesting way of looking at things. I learned from them that it is important to always think outside the box. Dr. Kevin Teather was important in this research, mostly because he would make random, semi-sarcastic remarks that were rather profound in that they would immediately spark some idea. I doubt that that was the intended effect, but thanks all the same! Dr. Larry Hale was the one who kept me firmly ground in reality, and upheld my faith in the ideals of academia.

That is a man I will always respect, and whose friendship I will cherish; despite the fact that I know no more about genetics than any BSc is expected to know, I learned as much from Larry over the past two years as I did from my own research.

In my experience, the graduate students of Biology are a close-knit bunch compared to the grad students of many other campuses. We look out for each other, help one another out, and we complain and growl about things to one another. In many ways, we are like brothers and sisters that actually get along. I will never forget this tiny community of people, and I am honoured to have been a part of it for even a short time. The ones that were there for the longest time with me were Ryan Barry (we had one hell of a fun place at Queen Street), Carrie Jardine and Billy MacDonald (Duffyvale Trailor Park roommates), Pam MacDonald (00Pam, I still can't believe we drove to Truro), Colleen MacDougal and Eddie Francis , Karen Johnson, and Melissa Burt. This doesn't even begin to mention the rest of the grad students, many of whom have just become grad students recently. Beyond Biology, very good friends that assisted in keeping me sane/helping me with my research in AVC would include Vicky Benson, Nick Tribble, and Fortune Sittol, as well as Faiz Ahmed from Island Studies.

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My mom and dad, Verlie and Guy Mailhiot, were there for me as always, helping their boy reach his full potential. They were always there for my late-night ramblings, where I was trying to figure out if the stress was worth it. They always helped me come to the conclusion that yes, it was. I must also acknowledge my grandparents, Doug and Myrna Pomeroy, because they've always been for me there as well, in the same capacity (though I inflict my late-night rants only to my father. Poor Dad). My parents and my grandparents are very dear to me, and I could not have finished this project without their support.

One person above all had the mighty task of keeping me sane and keeping a smile on my face (usually a besotted, goofy grin). That person is my girlfriend, Kim Gallant, who stuck with me through thick and thin, right up until the very end and beyond. It takes a special kind of girl to date a grad student. It also takes a special kind of girl to date me. It takes a very special one, or one that is clinically insane, to date me while I'm also a grad student. And she did it! So let's say she's very special, and make everyone happy. I could gush more, but this is not the place to do so. In addition to thanking Kim, I'd like to thank her parents, Ronnie and Donna, for letting me stay with them for so long while I was finishing this project. That whole tribe was very nice to me, and the young lady Kimberly is the best of them all. Using the words of my girlfriend, life should be funner now that this project is done, though I think that I will miss my temperamental computer..

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1. INTRODUCTION

The Birds of North America

Anthropogenic activities are known to affect the species richness, abundance and distribution of hundreds of species of birds, all of which vary in their physiology and ecology (Gill, 1994). The avifauna of North America is of special concern due to increasing urban development, loss and fragmentation of habitat, and other human activities (Pimm & Askins, 1995; Boulinier *et al.*, 2001). The effects of these human activities on avian communities have been studied at several spatial scales (*e.g.* Blackburn & Gaston, 1996; Böhning-Gaese, 1997; Rahbek, 1997; Rahbek & Graves, 2000). These studies have been conducted at a variety of spatial scales, such as studies examining impacts affecting entire continents (Mönkkönen & Viro, 1997), and others examining individual species at small, local scales (Rey, 1995). Spatial scale is defined here as the geographic extent and resolution at which a process is examined (Turner *et al.*, 2001a).

The Birds of Prince Edward Island

For at least 150 years, the study of insular systems has led to fundamental interpretations into the relationship between ecological processes and geographical patterns (Drake *et al.*, 2002). Islands have been used as study areas wherein patterns and processes that are affecting large areas may be examined in relatively closed systems (MacArthur & Wilson, 1967). Because it is an island with a landscape that is somewhat typical for an eastern Canadian landscape, Prince Edward Island is an ideal location for the investigation of the patterns of species richness and occurrence of birds at local and landscape spatial scales. Prince Edward Island (henceforth also referred to as "the province" or "the island") covers 5665.6 km^2 of land, and includes a variety of watersheds and ecosystems. The topography of the island primarily consists of rolling hills (van de Poll, 1983), and the province is networked with small streams and rivers (Raymond *et al.*, 1963).

Jacques Cartier was the first European to record the presence of several bird species on the island in 1534. Most of these species were named after birds that occurred in France (Sobey, 2002). Cartier did not conduct complete surveys of the avifauna of the island, but instead focused on species that would be of use to feed his crew (*e.g.* Galliformes; Sobey, 2002). French colonists arrived on Prince Edward Island (known then as Isle St.-Jean) in 1720. Isle St.-Jean formed part of the French colony of Acadia until the end of the Seven Years War in 1755. It is unknown whether the Acadians recorded the presence of avian species, as no manuscripts detailing such activities are known to have survived following the post-war expulsion of the French colonists by the English (Clark, 1959).

Prince Edward Island became a British colony in 1815 after the defeat of France at the end of the Napoleonic Wars. At that time, small-scale agriculture was the main industry, and many wealthy former British officers became landowners. Some of these former officers became interested in the natural history of the island (Sobey, 2002). The earliest surviving documents detailing lists of avian species found on the island were made in those times. These documents have since served to provide an approximation of avian species diversity in the nineteenth century (Stewart, 1806; Bain 1890; Bagster, 1891; Sobey, 2002), though records were incomplete and sometimes contradictory.

Avian Communities

It is often difficult to assess how anthropogenic activities are affecting species richness and species occurrence in avian communities. The first major step in assessing the effects of humans on avian species is to determine the number of species that occur in a given area. This is often followed by an investigation of precisely what species occur in that area. What affects how many avian species are present in a community? What affects the occurrence of particular bird species in a community? These questions are two major areas of ecological research that will be examined in this study. The total number of species in a landscape is defined here as species richness. Occurrence is defined in this study as the presence of a species in a landscape, irrespective of how many individuals of that species are present.

Why examine the occurrence of avian species? Rare and endangered species can be examined to determine if particular land-use practices would be beneficial for their conservation (Caicco *et al.*, 1995; Scott, 1995). Furthermore, the richness and distribution of avian species can be modeled with the purpose of prioritizing certain land-uses for different areas (Peterson *et al.*, 2000). Distributional shifts due to climate change can be predicted if enough information is known as to what affects species occurrence (Aspinall & Matthews, 1994). Likewise, such information could potentially allow scientists to predict where invasive avian species may be likely to colonize (Wadsworth *et al.*, 2000). Empirical knowledge of the species richness of bird communities is important in determining regional levels of biodiversity, and helps in assessing the causes in the variation of species richness (Owens *et al.*, 1999).

Breeding birds are an ideal group to study patterns of species richness and occurrence at large spatial scales. Acquiring reliable data on species counts and distributions can be much easier when using birds than in more cryptic organism guilds such as plankton or arthropods. A reason for this ease is that avian species tend to be morphologically distinct from one another, with little trouble distinguishing species in the field (Gill, 1994). The popularity of watching birds by the general public has led to groups of avid birdwatchers in many parts of North America, many of whom are well-trained at avian identification and are well organized in terms of survey ability. These groups, such as the National Audobon Society, Bird Studies Canada, and United States Geological Survey, have been collecting records of species occurrence of birds in their areas for many years. Various groups in the United States and Canada have been conducting surveys of bird distributions at large spatial scales, which have led to the creation of considerably large databases that can be analyzed for many purposes (Cadman *et al.*, 1988; Erskine, 1992; United States Geological Survey, 2001).

General Concepts about Avian Species Richness and Occurrence

There are many factors that are hypothesized to explain the variation in avian species richness and occurrence in North America, the importance of which can vary with spatial scale (Johnson & Krohne, 2002). Several studies have examined the effects of these factors on avian species richness from different parts of the world, such as North America (H-Acevedo & Currie, 2003; Pearson *et al.*, 2004), South America (Rahbek & Graves, 2000; Rahbek & Graves, 2001), and the British Isles (Gaston & Blackburn, 2000; Gaston & Evans, 2004). At large spatial scales it has been suggested that species richness is determined by climatic factors such as precipitation and temperature (Currie, 1991; Currie *et al.*, 2004). Other factors have also been suggested, such as availability of energy, habitat heterogeneity, and gradients in the amount of land or water available to birds (Brown, 1981; Rapoport, 1982; Stevens, 1992; Brown, 1995; Kerr & Currie, 1999; Taylor & Gaines, 1999; Rahbek & Graves, 2001).

At large spatial scales, the total area a species is known to inhabit on the Earth is known as the geographic range, or geographic distribution (Smith & Smith, 1998). At this scale, it has been shown that the geographic distribution of many animal species, including birds, is strongly correlated with the variety of habitats the population occupies (Ricklefs, 1997; Tews *et al.*, 2004). At the landscape scale, the occurrence of avian species is thought to be primarily determined by the presence or absence of suitable habitat, the nature of which can significantly vary from species to species (Drapeau *et al.*, 2000). Occurrence limits imposed by barriers to long-distance dispersal are not as prevalent among flying birds as among other terrestrial organisms (Gill, 1994). As with species richness, the factors that influence the distribution of species are scale-dependant (Rahbek & Graves, 2001). At the landscape scale, occurrence of avian species can be constrained by factors that may operate at smaller scales than the above examples. For example, Wiens (1973) showed that when the horned lark (*Eremophila alpestris*) was examined at large spatial scales, the species was shown to be distributed throughout North America and more specifically concentrated in the western prairies. However, when the species was examined at small spatial scales, it was more likely to be found in areas where land-use practices promoted heavier cattle grazing. Studies such as this indicate that a multi-scale approach may be more appropriate than single scale studies when examining avian species occurrence (Gaston *et al.*, 1995; Rahbek & Graves, 2001).

Factors affecting Species Richness and Occurrence

1. Latitude and Longitude

Ever since the earliest naturalists began examining gradients in species richness, latitude has played a central role in their observations (Darwin, 1859). No single pattern of biodiversity has been more intensely studied than the trend of increasing species richness with proximity to the tropics (Pianka, 1966; Rohde, 1992; Gaston & Blackburn, 1995a; Rosenzweig, 1995; Gaston & Blackburn, 2000). Recently, Hillebrand (2004) examined 600 recorded latitudinal gradients in species richness. She concluded that the gradient is a general pattern with very few notable exceptions. Hillebrand (2004) found that the strength of the latitudinal gradient varied markedly with the scale of the analysis and it also varied with factors that describe the organism in question (such as trophic level and body size) and the focal habitat (geographic position and habitat type).

Although it is commonly known that the species richness of birds declines with increasing latitude, the mechanisms that explain this pattern are still unclear (Rapoport, 1982; Currie, 1991; Rohde, 1992; Gaston & Blackburn, 2000). Many natural phenomena are highly correlated with latitude, allowing ecologists to use latitude as a surrogate factor for them. Examples of these factors are gradients in solar energy (Currie, 1991), physiological tolerance to variations in temperature and water availability (Currie *et al.*, 2004), primary productivity (Currie & Francis, 1999), average body size (Mein & Dayan, 2003), clutch size (Evans *et al.*, 2005) and habitat area (Rosenzweig, 1995).

Large-scale, global patterns affecting species richness and occurrence are often associated with latitude due to correlations with persistent climatic gradients (Hawkins *et al.*, 2003). However, some ecological patterns related to longitude are known to exist regionally. Avian species diversity has been known to vary with longitude in some locations, with studies showing that topographical variability is the primary reason for this variation (Hillebrand, 2004). Jetz & Rahbek (2001) examined the effects of longitudinal variation in topography on avian species richness and occurrence at the continental edges of Africa. Avian species varied in a longitudinal fashion, due to the north-south alignment of many rivers, mountain ranges, and ecosystem boundaries. Thus, topography can also be the reason for a longitudinal or a latitudinal gradient in species richness and occurrence.

2. Body Size

The distribution of body size can reflect several ecological characteristics in an avian community (Peters, 1983). Body size has been correlated with such ecological attributes as population density and dispersal distances (Maurer & Brown, 1988; Brown, 1995; Gaston & Blackburn, 2000). In bird communities, high species richness is often associated with more species of small body size (Brown *et al.*, 1993), reflecting the tendency of smaller species to become more specialised and to partition resources more finely (Brown, 1995).

The mean body size of a community is known to be associated with the available area avian species can exploit (Peters, 1983; Brown, 1995). Mönkkönen (1992) found that breeding bird species tend to have a larger body size than migrant species, while Southwood (1976) and Peters (1983) found that mean body size is highly correlated with home range size. Because larger birds need larger home ranges, breeding birds may be the most affected by the amount of habitat area that can be exploited in a landscape (Schmiegelow & Mönkkönen, 2002). Also, Enoksson and Nilsson (1983) demonstrated that resident breeding birds are known to adjust winter territory sizes to encompass yet larger areas. Habitat fragmentation can affect the structure of body size distributions in a landscape, as smaller habitat patches may only be able to support subsequently smaller avian species, thus decreasing species richness when habitat patches become too small for larger species (Polo & Carascal, 1999).

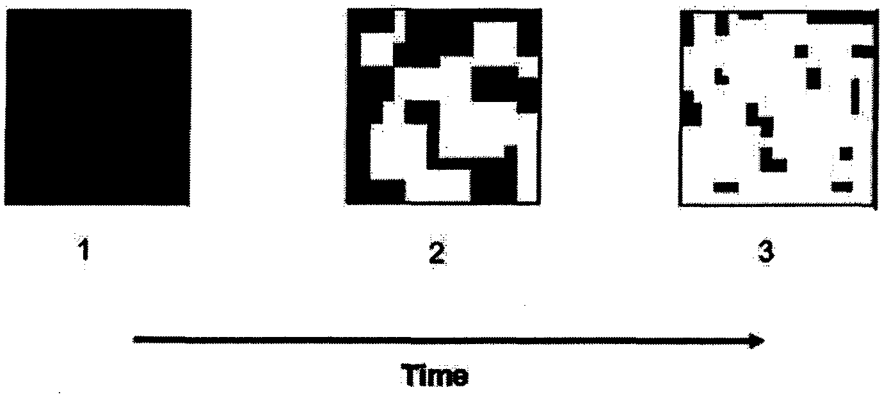
3. Habitat Fragmentation

3.1. Concepts of Habitat Fragmentation

Fragmentation of habitat is one of the most prevalent causes of biodiversity decline in recent years (Wilson, 1996). Habitat fragmentation is defined here as a process during which a large focal habitat area is transformed into several smaller patches, where each patch is isolated from one another by a matrix of habitats that are unlike the focal habitat (Figure 1.1; Wilcove *et al.*, 1986). Numerous studies have demonstrated that habitat fragmentation can alter the patterns of species richness and occurrence in birds (Edenius & Elmberg, 1996; Fahrig, 1997; Estades & Temple, 1999; MacDonald & Kirkpatrick, 2003).

The most visible effect of habitat fragmentation is the direct destruction, or loss of habitat. Some researchers define the level of habitat fragmentation as the amount of habitat that remains on the landscape following a disturbance event (Golden & Crist, 2000; Carlson & Hartman, 2001; Fuller, 2001; Summerville & Crist, 2001; Fahrig, 2003). Habitat loss has been categorized this way by ecologists because fragmentation causes not only the loss of the total amount of habitat, but by creating small, isolated patches it can change the properties of the remaining habitat as well (van den Berg *et al.*, 2001). The destruction of habitat can eliminate avian species in a direct manner, or indirectly by affecting availability of prey species, nesting sites, and cover for avian

Figure 1.1. Diagram illustrating the process of habitat fragmentation over time. Black areas represent habitat and white areas represent matrix. Adapted from Fahrig (2003).



species dependant upon the original habitat. The loss of habitat can affect avian species to the point where some species may not have all of the necessary resources and conditions required for their persistence (see Grinnell, 1917; Elton, 1927; Hutchinson, 1959; James *et al.,* 1984; Schoener, 1988; and Brown, 1995). The species-area hypothesis proposes that species richness will increase with habitat area (Arrhenius, 1921). Consequently, species richness is known to decrease with habitat loss due to habitat fragmentation (Krishnamani *et al.*, 2004).

A consequence of the direct destruction of habitat is the creation of isolated patches of focal habitat. A patch is defined here as a discrete area of habitat. MacArthur and Wilson (1967) took this hypothesis further by demonstrating that on oceanic islands, species richness not only increases with habitat area but also decreases with degree of isolation from the mainland (see also Bruun, 2000; Lomolino, 2000; Haila, 2001; Azeria, 2004). Habitat fragmentation has been known to isolate sections of focal habitat from one another, causing individual patches of similar habitat to lose connectivity. Contrary to many other terrestrial organisms, volant birds are not as likely to be directly affected by poor connectivity in fragmented habitats (Schmiegelow & Mönkkönen, 2002). However, other organisms associated with the presence of avian species may be adversely affected by poor habitat connectivity. For example, Silva *et al.* (2005) found that species richness in small mammals was smaller in habitat patches that were not connected by hedgerows in agricultural landscapes. Ricketts (2001) demonstrated that species richness of butterflies is not only affected by patch isolation, but that the heterogeneity of the matrix may have an effect as well. Other scientists have also examined the effects of patch isolation in association to different animal species, finding that species richness and composition of these species can be affected by patch isolation to varying degrees (e.g., Hobbs *et al.,* 1993; Wiens, 1995; Gascon *et al.,* 1999; Daily *et al.*, 2001). Avian species dependant upon these insects and small mammals as prey animals may therefore be indirectly affected by patch isolation (Golden & Crist, 2000). Fewer species of birds are therefore expected to be able to persist in landscapes dominated by smaller habitat fragments and in landscapes where isolated patches are prevalent.

Habitat fragmentation also involves an "edge effect" (Marini *et al.*, 1995). Edge effect is defined as the effect of the juxtaposition of contrasting environments on an ecosystem (Paton, 1994). It is known that at the point where two distinct habitats coincide, habitats may be altered to a variable and often considerable extent ("ecotone"; Smith & Smith, 1998). Forested landscapes are the most common example used when examining the effects of edge. When the adjacent land in a forest has been removed, creating a boundary of open land and forest, various changes take place within the edge of the forest itself. The penetration of sunlight and wind disturbs the forest to a greater extent than when the forest was not fragmented, drying out the interior of the woodland and encouraging growth of opportunistic plant species at the edge (Kattan *et al.*, 1994). Avian species that are adapted to the forest interior are more likely to become extinct in such fragmented landscapes, causing a loss of regional biodiversity (Wilcox & Murphy, 1985; Harrison & Fahrig, 1995). Also, brood parasitism and nest predation have been found to increase near edges of forests, causing net declines in species richness and occurrence of avian species in woodlands (Andrén *et al.*, 1985; Burkey, 1993; Marini *et al.*, 1995).

Factors other than loss and fragmentation of habitat can affect species richness and distribution at local spatial scales. Interspecific competition has been known to be an important factor affecting avian species occurrence at small spatial scales (Minot, 1981). However, other studies have shown that these factors have reduced effects at the landscape scale, with habitat characteristics appearing to exert a greater influence on species richness and distribution patterns (Wiggins & Mùller, 1997; Donázar *et al.*, 2005).

Habitat heterogeneity can be defined as the structural complexity of a habitat (MacArthur & MacArthur, 1961; Saab, 1999; Gillespie & Walter, 2001; Rahbek & Graves, 2001). Research in the effects of habitat heterogeneity on avian species richness has shown that greater complexity in a habitat tends to yield a higher species richness (MacArthur & MacArthur, 1961). The expansion of agriculture, forestry, and urbanisation has been known to affect habitat heterogeneity in different ways. It is known that the loss of habitat heterogeneity due to clear-cutting and softwood monoculture has had detrimental effects on woodland avian species richness in Prince Edward Island (Makepeace, 1989). Blair (1996) observed that alteration of habitat for human use leads to a net decline in plant diversity, resulting in decline in avian species richness in many places. Sometimes habitat alteration causes an increase in habitat heterogeneity, as an increase in edge habitat has been known to cause a profusion of successional species, many of which are beneficial to many avian species (Fahrig 1997; 2003).

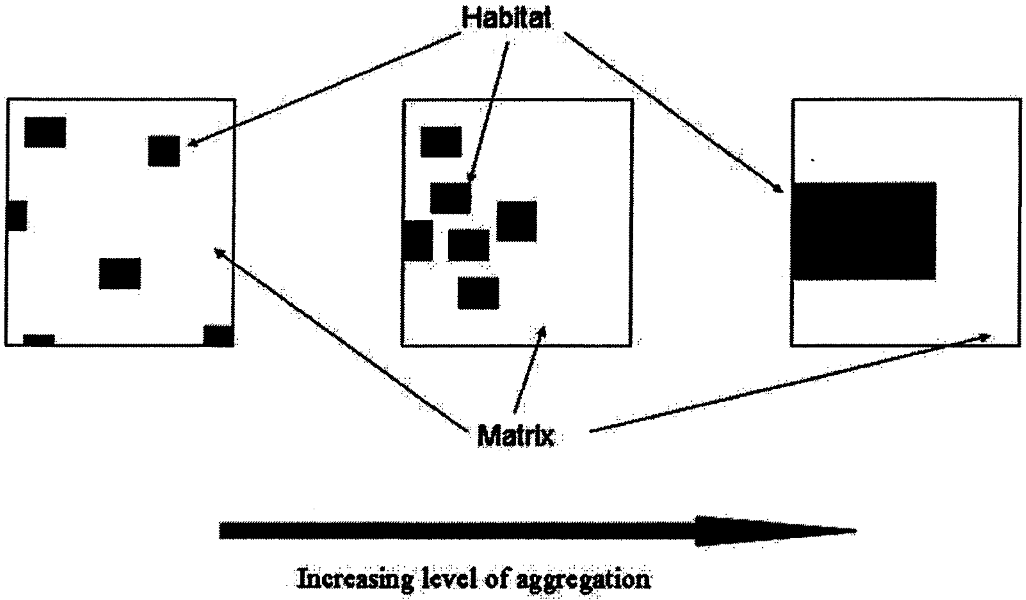
The presence of roads and highways has been known to affect avian species richness and distribution in a variety of habitats. In addition to the effects described above, the presence of roads can cause a deterioration of adjacent habitat due to vehicle emissions (Jaeger *et al.* 2005). Also, recent studies have shown that many species of birds tend to avoid noises associated with vehicles on roads (Reijnen *et al.*, 1995, 1996, 1997).

3.2. Measures of Habitat Fragmentation

In order to examine the association of habitat and matrix structure with the species richness and occurrence of avian species, the habitat and the matrix must both be quantified in some manner. These quantified metrics must be independent from one another in order to meet assumptions of independence among variables (Hargis *et al.*, 1998). Unfortunately, landscape metrics tend to be highly correlated with one another, so achieving complete independence is a difficult, if not impossible task. Turner *et al.* (2001a) reviewed the various methods of quantification of the landscape and found that the three most widely-used and somewhat independent measures of landscape quantification are aggregation, shape and size of habitat patches. There are still correlations among these variables, so interpretations of models involving these variables must keep this lack of independence in mind.

Aggregation is a measure of the spatial configuration of landscape that ranges from clumped to dissected (O'Neill *et al.*, 1988; Li & Reynolds, 1993). For example, it is possible for two different landscapes to have exactly the same amount of forest in terms of area, but have two different levels of aggregation (McGarigal & Marks, 1995). In this example, the landscape with a low aggregation would have small patches of forest scattered throughout its area, while the one with a high aggregation would have all of its vegetation forming one dense mass (Figure 1.2).

Figure 1.2. Diagram illustrating changes in levels of habitat patch aggregation. For example, at the landscape scale a focal habitat with a low aggregation would have habitat patches in a non-clumped, random pattern. With increasing aggregation, the more clumped is the spatial distribution of patches.

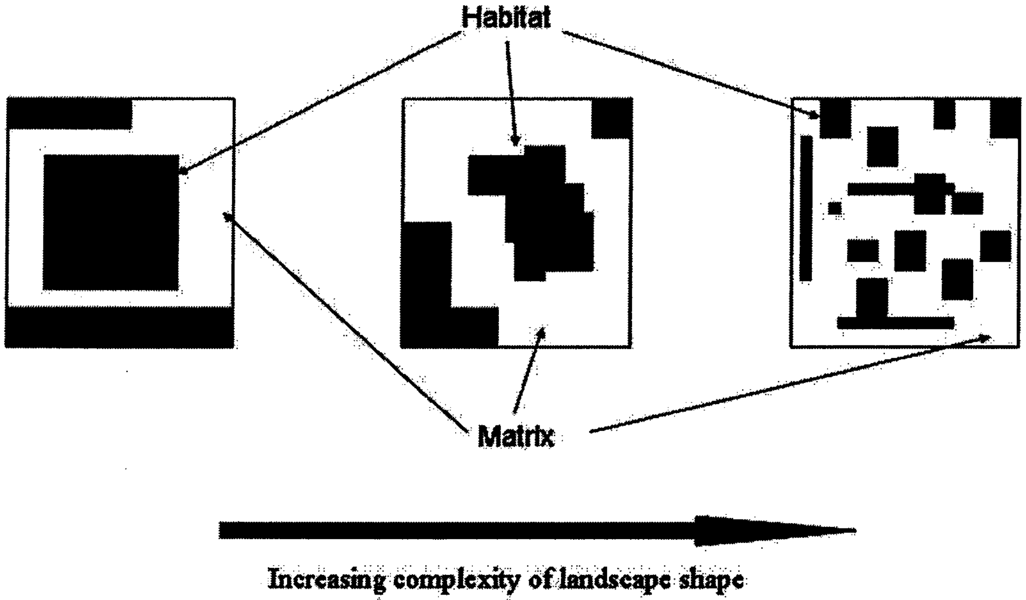


Shape is defined in this study as the spatial complexity of a single land-cover patch, often calculated as a ratio of area and perimeter (Helzer & Jelinski, 1999). The shape of a patch is useful in assessing the level of complexity and fragmentation of a patch (Temple, 1986; Helzer & Jelinski, 1999). A circular patch minimizes the amount of edge habitat and maximizes the land in its core. In contrast, a thin, rectangular patch has only a narrow band of interior habitat. If the strip is narrow enough, there is no interior habitat for species, and ultimately the avian diversity in the strip may be low due to the loss of core-dependant bird species (McIntyre, 1995). Shape can also be examined as a description of a type of landscape over several patches (McGarigal & Marks, 1995; Figure 1.3). Turner *et al.* (2001a) reports that simple area-perimeter ratios are sensitive to the size of the patches used in the calculation, with a large abundance of small habitat patches causing a misrepresentation of the shape of patches over different spatial scales. Some fractal measures mathematically correct for this (McGarigal & Marks, 1995), limiting the effects caused by overabundance of small patches. A fractal index is a scale-invariant dimension that measures the degree of shape complexity (Burrough, 1981; 1986; Krummel *et al.*, 1987; Milne 1991; Olsen *et al.*, 1993). Fractal dimension values vary from 1, which indicates relatively simple shapes such as squares or circles, to 2, which indicate more complex shapes (Lovejoy, 1982). Smaller spatial scales often reveal finer details and affect the perimeter-to-area ratios, necessitating the use of fractal measures (Krummel *et al.*, 1987).

Avian Surveys

Many studies (Brown *et al.*, 1995; Brown *et al.*, 1996; Blackburn & Gaston, 1998; Gaston *et al.*, 2000; Currie *et al.*, 2004; Pautasso & Gaston, 2005; Mönkkönen *et*

Figure 1.3. Diagram illustrating changes in landscape shape. For example, at low landscape complexity individual patches will retain more core habitat in relation to their edge. As the landscape type becomes more complex in terms of shape, smaller fragments with more edge in relation to their core become more prevalent.



al., 2006) make extensive use of databases compiled by thousands of volunteers (*e.g.* Cadman *et al.*, 1988; Erskine, 1992; USGS, 2001). The benefit of these databases is that very large sample sizes of avian species can be examined without the time and money needed for direct sampling. Brown (1981; 1984; 1995) routinely used avian survey data in his examinations of abundance, richness and distribution of avian species, helping to develop his initial theories of macroecology. Gaston and Blackburn (1995a, 1995b, 1996a, 1996b) have also used extensive databases in both Europe and the Americas to examine declining trends in avian diversity. Without the use of these data, our knowledge on many of these topics (abundance-distribution relationships, species-frequency distribution, *etc.*) would be much more limited than it is today.

When scientists and naturalists desired to examine particular locations in greater detail, the breeding bird atlases were created. Breeding bird atlases examine species occupancy at regional spatial scales, allowing for a higher resolution than is possible using breeding bird survey data. Among the first Canadian atlases was one that detailed the breeding birds of Ontario (Cadman *et al.*, 1988). This atlas was soon followed by the Maritime Breeding Bird Atlas (Erskine, 1992), which comprises the database used throughout the rest of our study. The Maritime Breeding Bird Atlas study organized hundreds of volunteers over five years and systematically sampled several hundred cells of 100 m^2 throughout New Brunswick, Nova Scotia and Prince Edward Island (Erskine, 1992). The Breeding Bird Atlas resulted in the first comprehensive database for the breeding birds of Prince Edward Island, and data collection for a second edition began in early 2006.

Surveys were conducted by volunteers using auditory sampling along roads throughout the province. All volunteers were trained and given a field checklist that noted all the birds known and thought to be in the Maritime Provinces at the time. Sampling cells on the island were sampled over five years, the coordinators ascertaining that at least seven party hours were spent in each cell (Erskine, 1992). Party hours were represented by the number of hours per person sampling a given cell. All data submitted to the Atlas coordinators were processed and verified for accuracy in the reporting of species before being included in the final database. The data reported for each species recorded in each of the provinces were then combined to make the Breeding Bird Atlas of the Maritime Provinces (Erskine, 1992), with the raw data being entrusted to the Atlantic Canadian Conservation Data Centre (ACCDC). According to Erskine (1992), 156 avian species were found to breed on the island. Bird species in this study are classified in terms of taxonomy (Sibley & Monroe, 1990), diet, and functional group. Based upon habitat and life-history characteristics, birds can be classified according to a guild structure, known in this study as a functional group (Root, 1967). Such groups include landbirds, seabirds, shorebirds, and waterfowl (Root, 1967; Simberloff & Dayan, 1991; Silva, 1996; Canterbury *et al.,* 2000).

Functional Groups of Avian Species

1. Landbirds

In this study, landbirds are defined as all birds that spend the bulk of their life history associated primarily with terrestrial ecosystems (Hagan *et al.*, 1997). This functional group includes birds from the Orders Passeriformes, Strigiformes and Falconiformes, as well as some species from other orders that live and breed primarily in the forests and meadows of the island (Donovan *et al.*, 2002). Passerine species tend to be very small (~ 10-30 g), with much larger species among the predatory owls, falcons and hawks (Dunning, 1993). One species of hummingbird (*Archilochus colubris*) is also the smallest (~ 3.1 g) bird found on Prince Edward Island (Erskine, 1992).

The diets of the landbirds can be quite varied. Some species of landbird are exclusively insectivorous, some seed-eaters, and others will eat a variety of different foods. For example, the northern shrike (*Lanius excubitor*) is known to eat large insects such as grasshoppers and even other small birds. The red-breasted nuthatch (*Sitta canadensis*) eats seeds from coniferous trees, and birds in the Orders Strigiformes and Falconiformes have diets primarily composed of small mammals, birds, or fish (Erskine, 1992). Some scientists have theorized that one of the most likely reasons for the high diversity of passerine birds in relation to other orders is the small mean body size of the functional group (Hutchinson & MacArthur, 1959; May, 1986; Maurer *et al.*, 1992; Brown *et al.*, 1993), though others have found no similar correlations (Owens *et al.*, 1999). The high species richness in passerine birds relative to other groups is sometimes linked to a high degree of ecological specialization (MacArthur *et al.,* 1966; Gill, 1994). The diets of the falcons, hawks, and owls known to occur in Prince Edward Island tend to be either small passerine birds or small mammals (Erskine, 1992; Gill, 1994).

The effect of habitat composition on landbirds at the scale of the landscape has been studied in recent years (Trzcinski *et al.*, 1999; Villard *et al.*, 1999; Fahrig, 2003). Loss and fragmentation of habitat are thought to have a considerable effect upon the species richness of landbirds, with many studies focusing on increasingly large agricultural fields and a variety of forestry practices (Fahrig, 2003). Habitat fragmentation does not have a wholly negative or positive effect upon species occurrence, with the occurrence of some species responding well, and others badly to disturbed areas (Germaine & Vessey, 1997). Many species of songbirds are considered to be ‘core-forest’ species because they need a critical minimum area of continuous forest to meet their life history requirements (Bayne & Hobson, 1997), though exceptions are common (McGarigal & McComb, 1995; Heske *et al.*, 1999). The reduction of suitable habitat due to habitat loss and fragmentation is likely to result in local extinctions among core-forest avian species (Bellamy *et al.*, 1996), though some forest-dwelling birds are not affected to the same degree (Morrison & Bolger, 2001). Fragmentation of habitat increases habitat edge in relation to the core, creating a broader ecotone between what is usually (on Prince Edward Island) agricultural or pastoral fields and forests. Species from adjoining landscape types can be found within such transitory zones. However, these ecotones may not be ideal breeding habitat for many forest birds, whose populations may need to be maintained through immigration from adjacent patches (Foppen *et al.*, 2000). Therefore, many of these birds can be found within these areas, but this can be explained by source-sink dynamics (Pulliam, 1988; Pulliam & Danielson, 1991), where avian populations are sustained only through immigration from other, more productive areas. Many exotic birds, such as the brood parasite *Molothrus ater* (Rich *et al.*, 1994; Hobson & Villard, 1998), are able to take advantage of heavily fragmented regions, moving into and displacing core-forest species. In some of these cases, the presence of exotic species can actually increase species richness. Thus, even if the species richness of landbirds in a heavily fragmented region may not appreciably change in comparison to a heavily wooded region, actual species composition could be different due to an increase numbers of exotic species and a decrease in the amount of remaining native species.

2. Seabirds

In this study seabirds are defined as those species that feed from saltwater, and spend the bulk of their life cycle living on offshore islands or on coastal cliffs (Schreiber & Burger, 2001). Cormorants, seagulls, and terns are typical representatives of the seabird functional group. In Prince Edward Island, seabirds are normally colonial nesters that live on offshore islands, cliff-faces on the North shore of Prince Edward Island, and in the case of a colony of arctic terns (*Sterna paradisaea*), on abandoned bridge pylons (Erskine, 1992). The body size of seabirds generally varies between 120 g and 1500 g (Dunning, 1993). Seabirds feed predominantly on fish, though some species (*e.g. Larus* spp.) are scavengers, and can take advantage of anthropogenic resources and food cast-offs.

The most common seabird species known to breed on Prince Edward Island are the ubiquitous seagulls (*Larus* spp.; Erskine, 1992). Cormorants *(Phalacrocorax auritus* and *Phalacrocorax carbo*) are also common on the island, though while they are abundant they are also highly concentrated in reclusive colonies (Erskine, 1992). These species are colonial nesting birds that breed in relatively difficult-to-access cliffs or islands, resulting in high population densities wherever they occur (Furness & Monaghan, 1987). Seabirds generally spend most of their time fishing at sea, and may not be present along typical sampling routes.

Habitat loss and fragmentation due to agriculture and forestry is not as likely to have adverse effects upon colonial cliff nesters such as cormorants, therefore species richness may not be strongly affected by changes in landscape composition (Lewis *et al.*, 2001). However, some seabird species (e.g. *Brachyramphus marmoratu*; Raphael *et al.*, 2002) are known to breed inland, in places that could be affected by habitat fragmentation. The effects of habitat fragmentation on these species are little known as of yet and are a current focus of study.

3. Shorebirds

Shorebirds are defined as avian species that spend the bulk of their life cycle on beaches and mudflats (Haig *et al.*, 1998). Shorebirds include birds such as herons, sandpipers, and plovers, all of which nest near beaches or coastlines. Shorebirds are usually small (~ 100 g) when compared to most of the other avian species in the province, though some of the larger wading birds such as the great blue heron (*Ardea herodias*) can weigh as much as 1.4 kg (Dunning, 1993). These birds feed on intertidal invertebrates found on mudflats at low tide, and some are known to subsist on aquatic vegetation. Many of the smaller species (*e.g. Calidrus pusilla*) are often found foraging in very large flocks of 1000 individuals or more (Hicklin, 1987). Shorebirds have been popularized by the media of the public of Prince Edward Island for several years, due to the listing of the piping plover (*Charadrius melodus*) as the only endangered avian species in the province (Haig, 1993; Boyne, 2000; Haig *et al.*, 2005).

4. Waterfowl

Waterfowl are primarily large birds (~ 4000 g) of the Order Anseriformes that spend a significant part of their time in marshy wetlands or in the ocean along the coasts of the province. Waterfowl include freshwater ducks, seawater ducks, mergansers, and geese. The diet of waterfowl species usually consists of fish, aquatic insects, or algae (Scott, 1995). Due to the revenue brought in by tourists, who include both birdwatchers and hunters, the waterfowl functional group is of economic importance to Prince Edward

Island (Federal-Provincial-Territorial Task Force on the Importance of Nature to Canadians, 2000). Waterfowl diversity has declined on Prince Edward Island during the past two centuries due to over-harvesting and the draining of wetlands for agricultural purposes (Rogers & Patterson, 1984). Conservation groups such as Ducks Unlimited have interests in the preservation and augmentation of waterfowl populations, and they have been prominent in obtaining land and creating artificial ponds to protect the local waterfowl (Kadlec & Smith, 1992). In addition, the provincial government has implemented strict harvesting regulations and protocols, particularly concerning which species of duck can be harvested at which particular time (Canadian Wildlife Service Waterfowl Committee, 2004). The purpose of these regulations and protocols is to protect waterfowl during breeding periods, which augments the populations of target species, thus increasing the overall diversity of waterfowl.

2. OBJECTIVES

The main purpose of this thesis is to investigate the patterns of species richness and occurrence of the avifauna of Prince Edward Island. Avian species richness and species occurrence are examined to determine if they are associated with landscape structure. Associated variables such as body size, latitude and longitude are also examined in relation to species richness.

In the following chapter, I investigate the patterns of avian species richness on Prince Edward Island. In particular, I examine the effects of landscape structure, latitude, longitude and body size on the species richness of birds. Following previous studies, I hypothesize that avian species richness will decrease with latitude and will decrease in a non-linear fashion with mean body size of the avian community. In addition, I hypothesize that species richness will increase with forest area and decrease with forest fragmentation.

In chapter four, I examine the relationship of the occurrence of individual avian species to landscape structure. This chapter is an exploratory study, where no *a priori* knowledge is assumed about associations. The purpose of this chapter is to search for associations of landscape structure with avian species occurrence, and to assess which common land-cover variables are important in these relationships. Species will be grouped in terms of habitat and diet (functional and trophic groups). The occurrence of species is expected to be associated to landscape structure in similar ways according to functional and trophic groups.

3. FACTORS DETERMINING AVIAN SPECIES RICHNESS IN PRINCE EDWARD ISLAND AT THE LANDSCAPE SCALE

3.1 ABSTRACT

The aim of this study was to examine the effects of latitude, longitude, mean body size and landscape structure on the species richness of birds breeding in Prince Edward Island, Canada. Spatial data on species counts was obtained from Erskine (1992) and avian body size data was obtained from Dunning (1993). Information on land-cover types (agriculture, forest, wetland, roads, human-used areas) were obtained from the provincial government. ArcView GIS and Fragstats were used to calculate several metrics that characterized the structure and complexity of the different land-cover types (area, shape, and aggregation). Habitat metrics, latitude and longitude, and body size information were related to avian species richness in seventy-six 10 km x 10 km sampling cells. Explanatory variables were related to avian species richness using multiple regression analysis, and models were chosen using Akaike's Information Criterion. Avian species were further examined in terms of functional group (*i.e.* landbird, seabird, shorebird, waterfowl). In total, 156 species were found on the island to breed in Prince Edward Island. Species assemblages varied between 9 and 98 species. Land-cover types, longitude, latitude and body size explained up to 49% of the variation in avian species richness on Prince Edward Island, though each functional group responded differently to particular variables. Overall, our findings show that avian species richness on Prince Edward Island appears to be strongly associated with activities such as the alteration of forest habitat and the expansion of agriculture.

3.2 INTRODUCTION

Loss of species is an important consequence of environmental threats, such as the loss and fragmentation of habitat (Secretariat of the Convention on Biological Diversity, 2001). In order to preserve and enhance biodiversity, measures must be taken to understand what factors drive species richness (Brown & Maurer, 1989). Several studies have examined the patterns of species richness of avian species at different spatial scales (Gaston & Blackburn, 1995a; Gaston *et al.*, 1995; Harrison & Fahrig, 1995; Böhning-Gaese, 1997; Boulinier *et al.*, 2001; Gaston & Evans, 2004). These studies have shown that many biotic and abiotic factors explain patterns of avian species richness, depending upon the spatial scale at which the study is conducted (Rahbek & Graves, 2001). At large spatial scales it has been suggested that species richness is determined by primary productivity, energy, temperature, precipitation or habitat heterogeneity. Surrogates of these variables such as latitude, longitude, and altitude have been used to indirectly study the effects of these variables on species richness at large spatial scales. Studies have also shown that surrogates of these variables such as latitude, altitude, and other related variables such as temperature, and precipitation can also affect species richness (Brown, 1981; Rapoport, 1982; Stevens, 1992; Brown, 1995; Kerr & Currie, 1999; Taylor & Gaines, 1999; Rahbek & Graves, 2001). At smaller spatial scales, patterns of species richness may be related to variation in latitude and longitude due to spatial variation in land-use patterns. It is commonly understood that species richness declines with increasing latitude even though mechanisms that explain this pattern are still controversial (Rapoport, 1982; Krebs, 1985; Currie, 1991; Rohde, 1992; Gaston & Blackburn, 2000). Hillebrand (2004) suggested that latitudinal gradients primarily affect avian species richness at large spatial scales. He also indicated that latitude is not the factor behind avian species richness patterns, but a surrogate for other factors such as energy (Currie, 1991), tolerance to variations in temperature and water availability (Currie *et al.*, 2004), species body size (Mein & Dayan, 2003), and habitat area (Rosenzweig, 1995). Although less studied, longitude is also known to affect the gradient of species diversity, but it is hypothesized that its effect is due to variability in the topography of ecosystems (Jetz & Rahbek, 2001; Hillebrand, 2004).

At local spatial scales, some studies have demonstrated that factors such as habitat fragmentation, habitat loss, and inter- and intraspecific competition are important in explaining variation in avian species richness (Brown, 1984; Rosenzweig, 1995; Villard, 1999). Several studies have also suggested that habitat heterogeneity can also affect avian species richness at local spatial scales (MacArthur & MacArthur, 1961; Saab, 1999; Gillespie & Walter, 2001; Rahbek & Graves, 2001). The expansion of agriculture, forestry, and urbanisation has been known to affect spatial heterogeneity in different way, which in turn can have effects upon avian species richness and occurrence (Saab, 1999; Villard, 1999). Studies have showed that the alteration of habitats due to human activities has led to a decline in the richness of native species, and has allowed non-native species to invade previously impenetrable areas (Estades & Temple, 1999; Debinski & Holt, 2000). It is known that both clear-cutting and softwood monoculture have had detrimental effects on woodland avian species richness, because of fragmentation and loss of habitat (Makepeace, 1989). Specific functional groups have been found to be associated with alteration of habitat in different ways. For example, waterfowl species richness is known to be strongly affected by the presence and size of wetland patches in a sampling area (Virkkala *et al.*, 2005). Also, the number of shorebird species has been known to be constrained by the presence of humans and human-influenced land such as recreational beaches and tourist parks (Naka *et al.*, 2002).

The mean body size of species is known to be inversely related to species richness of birds. This relationship is usually non-linear, with a usual community composition consisting of far more small-bodied species than large-bodied species (Brown, 1995). Numerous studies have demonstrated the role played by body size in terms of determining abundance, species richness, and distribution of avian species (Peters, 1983; Maurer & Brown, 1988; Brown, 1995; Gaston & Blackburn, 2000). Small mean body size in a community is often associated with high species richness (Brown, 1995; Owens *et al.*, 1999). There are several mechanisms that have been postulated to explain this association. For instance, there may be a greater amount of ecological niches for small-sized avian species (Hutchinson & MacArthur, 1959). Differences in species richness have also been associated with reproductive rate and metabolic rate, which are both known to be related to body size of species (Glazier, 1987; Marzluff & Dial, 1991). In addition to the mean body size, the range of body size is also an important metric associated with species richness. A wide variety of species body sizes within a community may allow the exploitation of different resources, permitting more species to co-exist than would otherwise be possible (Peters, 1983; Brown, 1995).

The species-area hypothesis (Arrhenius, 1921; Krishnamani *et al.*, 2004) proposes that species richness increases with habitat area. Furthermore, based on the Island Biogeography Theory, we can expect that species richness will both increase with size of the habitat patch, and decrease with increasing isolation (MacArthur & Wilson, 1967; Bruun, 2000; Lomolino, 2000; Azeria, 2004). Loss and fragmentation of habitat is one of the most prevalent causes of biodiversity decline in recent years (Wilson, 1996), and can create patches whose community dynamics will mimic island dynamics. Many studies have demonstrated that loss and fragmentation of habitats can affect species richness and community composition in birds (Edenius & Elmberg, 1996; Fahrig, 1997; Estades & Temple, 1999; MacDonald & Kirkpatrick, 2003). Reduction in the total habitat area can be detrimental to those species that require large, continuous tracts of habitat to survive (Haskell *et al.*, 2002; Fahrig, 2003).

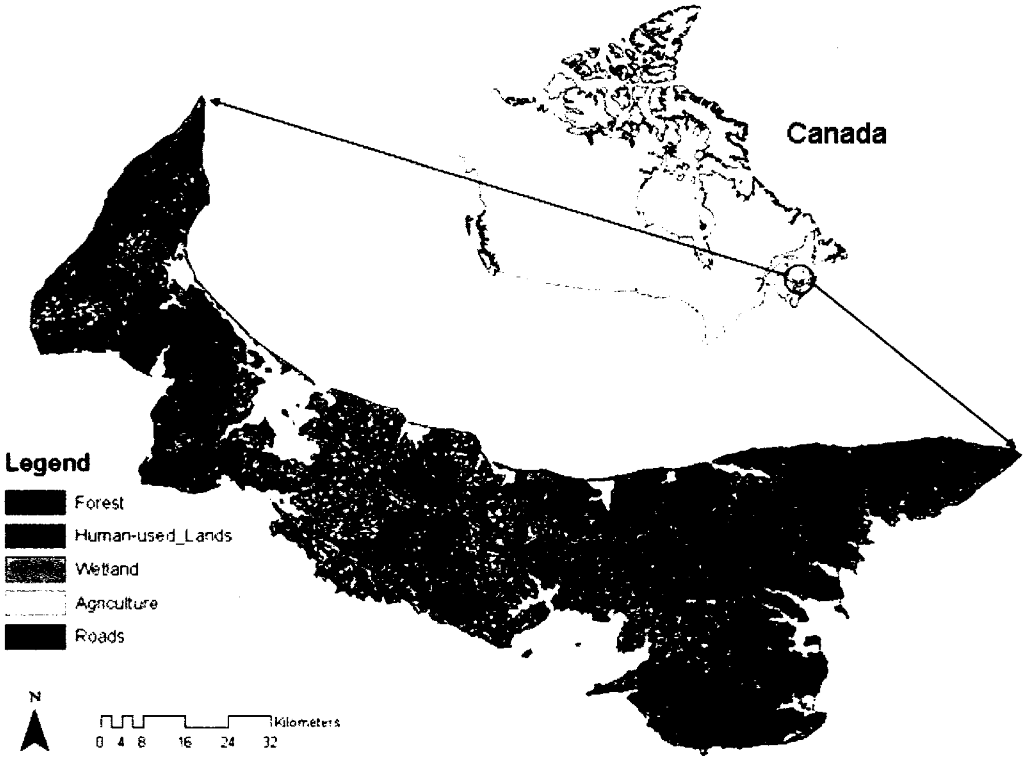
In this paper, we investigate patterns of avian species richness on Prince Edward Island, Canada. In particular, we examine the effects of landscape composition, latitude, longitude and mean body size on the species richness of birds breeding on the island. We hypothesize that (1) species richness will decrease with latitude; (2) that species richness will decrease with the mean body size of the species of birds in the community, and (3) that species richness will increase with habitat area and decrease with forest fragmentation.

3.3 METHODOLOGY

Study Area

Prince Edward Island covers an area of 5665.6 km^2 and is located in the St. Lawrence Basin of Eastern Canada (approximately 46°N, 63°W; Agriculture, Fisheries, Aquaculture and Forestry, 2003; Figure 3.1.). The island is approximately 16 km distant from the mainland at the narrowest gap in the Northumberland Strait, and is relatively flat with a maximum height of 146 m above sea level (Silva *et al.*, 2003). The landscape is composed of approximately 39.4% of agricultural lands used for various crops, especially potatoes. The current forest (48.4% of the island) is a mix of the old-growth

Figure 3.1 Map of Prince Edward Island in relation to Canada (46°N, 63°W). The scale bar refers to Prince Edward Island only. All five land-cover types used in the study are shown here.

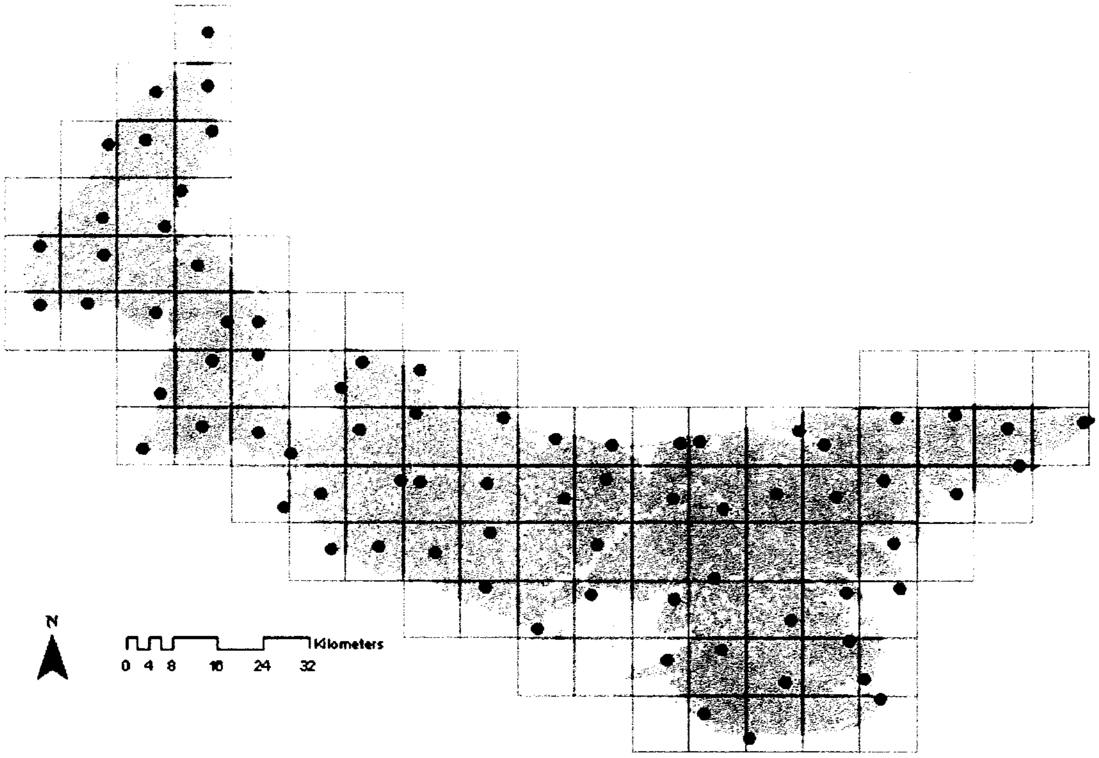


Acadian species, as well as white spruce (*Picea glauca*), black spruce (*Picea mariana*), poplar (*Populus tremuloides*), and other fast-growing, secondary-growth trees. Wetlands comprise 4.2% of the island, within which can be found marshes, bogs, salt marshes, and coastal areas such as sand dunes. Approximately 6% of Prince Edward Island is composed of human-influenced land such as buildings and urban centres. The remaining 2% of the island's land-cover consists of an extensive network of roads. The human population in the province is approximately 134,500 individuals with an increasing rate of 0.5% every five years (Statistics Canada, 2001a).

Avian Species Data

Data on avian species counts and distributions were obtained from the Maritime Breeding Bird Atlas (Erskine, 1992). Bird censuses were undertaken in all seasons by volunteers from 1986 to 1990. Data of bird occurrences were collected using auditory and visual identification. Sampling locations were designed in order to sample as much of the landscape of the island as possible (Figure 3.2). Sampling proceeded in each location until samplers had detected at least 75% of the species expected to exist in the region, with 38% of the expected number being confirmed to breed within (Erskine, 1992). Sampling effort (hours per individual per sampling cell) varied depending on remoteness of the sampling cell and the availability of volunteers. Only confirmed sightings of breeding birds were used in this study, and confirmations were mostly made in July due to breeding cycles of species (Erskine, 1992). For identification, we followed Sibley and Monroe's (1990) avian taxonomic classification. Each avian species was also classified into a functional group according to diet and life history (*i.e.* landbird, shorebird, seabird, or waterfowl). Body size (grams) information was obtained from

Figure 3.2. Map detailing the 97 sampling cells (10 km x 10 km) used in the study to divide Prince Edward Island into sampling units. The black dots represent the main communities in each of the sampling locations as detailed in the Atlas of the Breeding Birds of the Maritime Provinces (Erskine, 1992). There were avian sampling locations within 76 cells in this study.



Dunning (1993). Body size values were also $\log_{10}$ transformed in order to normalize the data. Only adult size values were used in order to provide a single body size value for each species. This may be a limitation in the study, as a proportion of the individuals of each species in the study may be of a smaller, juvenile stage.

Spatial Scale

The spatial scale at which this study was conducted was established using the same sampling grain that was used for the Maritime Breeding Bird Atlas (Erskine, 1992). Prince Edward Island was divided into 97 cells of 10 km x 10 km to maximize the number of sampling cells on the island that reported avian species observations (Figure 3.2). Sampling cells were generated using the "randompoly" extension of ArcView^{TM} (ESRI, version 3.3, Redlands, CA), where a grid was generated and superimposed upon the study area determined in Erskine (1992). Sampling of species occurrences took place throughout the sampling cells, each of which was labelled with the name of the primary human community within the cell. While sampling was recorded as distributed throughout each cell, it was likely concentrated near to the main communities listed. At this spatial scale, species richness was calculated as the number of bird species counted in each sampling cell. Latitudinal and longitudinal coordinates of the main community of each sampling cell were added to the dataset, the surroundings of which presumably the greatest concentration of sampling was performed. These coordinates were used throughout the rest of the study where latitude and longitude were investigated.

Land Cover

Land-cover types of the province were quantified using ArcView™ (ESRI, version 3.2, Redlands, CA), ArcGIS™ (ESRI, version 8.1, Redlands, CA) and the 1990 forest inventory data prepared by the government of Prince Edward Island. Suitability of land-cover layers would be assessed using Pearson correlation analysis. This exploratory analysis consisted in examining the relationship between the area of land-cover types in a sampling cell and avian species richness; the land-covers that had the strongest associations with species richness were retained. Area of a land-cover type was calculated as a percentage of the sum of all the land-covers in a sampling cell. Initially a finely grained analysis was attempted, using several different land-cover types (*e.g.* salt marsh, coniferous forest, potato field, *etc.*). The exploratory analysis showed weak relationships between species richness and many of these variables at a fine scale. Further examination of variables revealed that a reducing the number of variables yielded higher relations to species richness. A coarse delineation of the land-cover types (*e.g.*, agriculture, forest, human-used areas, roads, and wetlands) was chosen for the analysis. These five land-cover types were used throughout the rest of the study.

Landscape Metrics

Following the recommendations of Turner *et al.* (2001a), metrics of area, shape and aggregation were obtained for each land-cover type in each sampling cell using Fragstats *v.* 3.3 (McGarigal & Marks, 1995). In order to use Fragstats, all land-cover layers were converted from a vector (polygon) format into a raster (pixel) format using ArcGIS *v.* 8.1 (Spatial Analyst Extension). To calculate metrics of land-cover size, the "Percentage of Landscape" class metric was obtained. This quantified the proportional abundance of each land-cover type per cell. The "Clumpiness Index" was calculated to assess aggregation of habitat within sampling cells. Clumpiness ranges from a maximally disaggregated value to a completely aggregated value, and is calculated from examining adjacent pixels in a matrix. Adjacent pixels of similar land-cover type result in higher aggregation values. The "Perimeter-Area Fractal Dimension" was used to assess land-cover shape. Fractals have been used in landscape ecology for many years (Sugihara & May, 1990; Krummel *et al.*, 1997) and have been shown to be a powerful measure of habitat fragmentation (Spies *et al.*, 1994). We calculated the fractal dimension for all land-covers to test if complexity of the habitat had an effect on species richness (Equation 3.1).

$$\mathrm{PAFRAC} = \frac{2}{\dfrac{\left[n_i \sum_{j=1}^{n} (\ln p_{ij} \cdot \ln a_{ij})\right] - \left[\left(\sum_{j=1}^{n} \ln p_{ij}\right)\left(\sum_{j=1}^{n} \ln a_{ij}\right)\right]}{\left(n_i \sum_{j=1}^{n} \ln p_{ij}^{2}\right) - \left(\sum_{j=1}^{n} \ln p_{ij}\right)^{2}}}$$

Equation 3.1 Perimeter-Area Fractal Dimension. a_{ij} = area (m^2) of patch ij. p_{ij} = perimeter (m) of patch ij. n_i = number of patches in the landscape of land-cover i. (McGarigal *et al.*, 2002)

A resulting fractal dimension of greater than one demonstrates an increasing complexity of the land-cover. The fractal dimension approaches 1 for land-covers composed of simple shapes such as circles and squares, and it approaches 2 for very complex shapes. For instance, an elongated forest patch such as a hedgerow would have a fractal dimension that approaches 2.

Data Analysis

Pearson correlation analysis was conducted among the variables generated by these metrics. Land-cover metrics that were significantly correlated to one another ($r > 0.7$) were individually plotted against species richness using simple linear regression. Of these correlated variables, those with a stronger correlation to species richness were kept and used in subsequent analyses. Possible relationships between sampling effort and the land-cover metrics were also assessed using Pearson correlation analysis.

We used an information-theoretic approach to select models that were both parsimonius and that well-explained avian species richness (Akaike, 1973; Burnham & Anderson, 1998). My primary goal was to determine associations between the species richness of four avian functional groups with: mean body size, latitude, longitude, and landscape structure variables. We used least squares regression to estimate parameters for the candidate models. Candidate models were nested from a model consisting of all explanatory variables used in the study (the "full model"). The Akaike's Information Criterion (AIC) process calculates lower AIC values for models that increasingly balance predictive power with parsimony. As a rule of thumb, $\Delta AIC < 2$ suggests substantial support for a model with this number. Values between 3 and 7 indicate that the model has considerably less support, and $\Delta AIC > 10$ indicates that the model is very unlikely (Burnham & Anderson, 1998). For each functional group, we determined the most parsimonious and highly predictive models by calculating differences in AIC values (ΔAIC) between each candidate model and the model with the lowest AIC value (The "best model"; Johnson & Collinge, 2004). The five models with the lowest AIC value in each functional group were examined. The standardized residuals of each of the models were examined in order to ascertain fulfillment of assumptions necessary for multiple regression analysis. Unexpected results were examined in further detail, by removing outliers from analyses and by examining univariate associations between variables. All statistical analyses in this study were performed using SAS (SAS Institute, Inc., version 8.02, Carey, NC) unless otherwise stated.

3.4 RESULTS

The five land-cover types used in this study were deemed to be the most biologically relevant to birds. A total of 156 breeding bird species were recorded to breed in Prince Edward Island (Appendix 1). Among these species were 123 landbirds, 7 seabirds, 10 shorebirds, and 16 waterfowl. Species richness in sampling cells ranged between 9 and 98 species when all species were pooled together (Figure 3.3). Descriptive statistics of all explanatory variables used in the study were obtained and recorded (Table 3.1).

Thirteen land-cover variables were used in this study, with three variables (percentage of agriculture, fractal dimension of roads, and clumpiness of wetlands) being dropped due to high correlations ($r > 0.7$; $p < 0.05$) with the remaining land-cover variables (Appendix 2; Appendix 3). While the remaining variables were not as highly correlated as the ones that were dropped, there were still many with significant, albeit not strong correlations ($0.5 < r < 0.7$). Due to this lack of complete independence among variables, the interactions of these variables with one another and with species richness must be cautiously interpreted. The fractal dimension of roads was not used in the study because the interconnectedness of the roads invalidated the function by treating all roads

Figure 3.3. Total number of avian species observed in each 10 km x 10 km sampling cell. The sampling cells are shown overlaying the landscape composition of Prince Edward Island. Blank spaces were non-sampled areas.

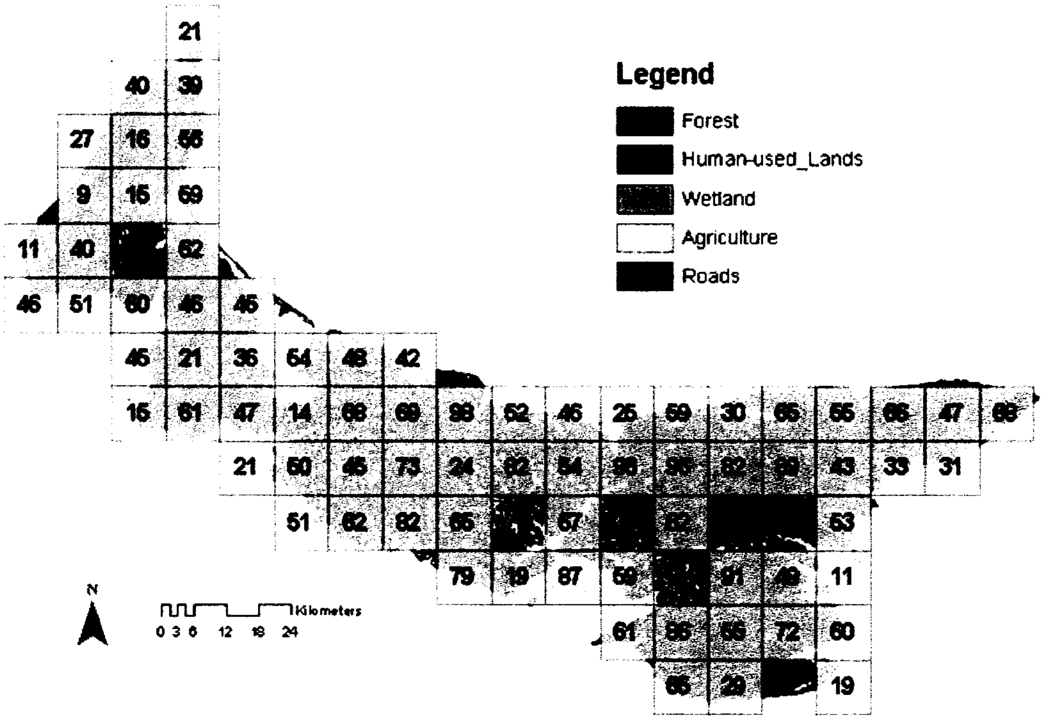


Table 3.1 Descriptive statistics of variables used in this study.

Variable	N	Mean	Standard Deviation of Mean	Minimum	Median	Maximum
Total Area (km^2)	76	6672	3130	322	7155	10000
Total area (km^2; $\log_{10}$)	76	3.74	0.32	2.51	3.85	4
Percentage of Agriculture	76	38.86	19.2	8.7	32.73	75.24
Fractal Dimension of Agriculture	75	1.26	0.04	1.1773	1.27	1.35
Clumpiness of Agriculture	76	0.94	0.01	0.91	0.95	0.9638
Percentage of Forest	76	47.28	20	11.35	48.36	81.28
Fractal Dimension of Forest	76	1.28	0.05	1.15	1.28	1.38
Clumpiness of Forest	76	0.94	0.01	0.91	0.94	0.97
Percentage of Human-used lands	76	6.42	4.8	1.12	4.69	31.1
Fractal Dimension of Human used lands	75	1.30	0.05	1.19	1.3	1.44
Clumpiness of Human-used lands	76	0.92	0.01	0.89	0.92	0.95
Percentage of Wetlands	76	5.37	5.69	0.1	3.82	35.46
Fractal Dimension of Wetlands	75	1.29	0.06	1.19	1.28	1.5
Clumpiness of Wetlands	76	0.93	0.04	0.74	0.94	0.99
Percentage of Roads	76	2.06	0.37	1.16	2.08	2.94
Clumpiness of Roads	76	0.70	0.01	0.67	0.70	0.74
Longitude	76	-63.31	0.66	-64.37	-63.35	-61.99
Latitude	76	46.42	0.24	45.95	46.41	47.06
Latitude X Longitude	76	-2938.8	42.7	-3011.5	-2934.5	-2874.1

Table 3.1 (Continued) Descriptive statistics of variables used in this study.

Variable	N	Mean	Standard Deviation of Mean	Minimum	Median	Maximum
Sampling Effort (Hours/Individual/Cell)	76	35.21	26.5	2	35	100
Sampling Effort ($\log_{10}$)	76	1.39	0.43	0.3	1.54	2
Pooled Species Richness	76	51.01	22.8	9	51.5	98
Species Richness of Landbirds	76	42.34	19.9	8	40	81
Species Richness of Seabirds	76	0.92	1.4	0	0	7
Species Richness of Shorebirds	76	2.5	0.17	0	2.5	8
Species Richness of Waterfowl	76	5.2	3.3	0	5	12
Mean body size of pooled species (g; $\log_{10}$)	76	2.33	0.19	1.6	2.3	2.8
Mean body size of pooled species (g; $\log_{10})^2$	76	5.49	0.86	2.6	5.5	8.0
Mean body size of landbirds (g; $\log_{10}$)	76	2.11	0.22	1.49	2.11	2.70
Mean body size of landbirds (g; $\log_{10})^2$	76	4.52	0.90	2.21	4.47	7.27
Mean body size of seabirds (g; $\log_{10}$)	76	1.2	1.4	0	0	3.32
Mean body size of seabirds (g; $\log_{10})^2$	76	3.3	4.14	0	0	11
Mean body size of shorebirds (g; $\log_{10}$)	76	1.87	0.807	0	2.01	3.38
Mean body size of shorebirds (g; $\log_{10})^2$	76	4.13	2.3	0	4.07	11.41
Mean body size of waterfowl (g; $\log_{10}$)	76	2.93	0.0132	0	2.89	3.14
Mean body size of waterfowl (g; $\log_{10})^2$	76	7.66	2.71	0	8.34	9.87

in a sampling cell as one land-cover patch. Sampling effort and total area were significant in multivariate analysis of species richness in most of the models throughout this chapter. These two variables were included in the analyses as a correction factor to account for the time spent sampling and for the amount of land in a cell, in order to more accurately reflect species richness in a given area. Sampling effort and total area were both $\log_{10}$-transformed and tended to show positive relationships with avian species richness. Species richness tended to be increasingly higher until the maximum amount of land was sampled. Increases of species richness with total area reflect the larger amount of territory that had to be covered by the samplers, with an increased chance to find a particular species as a function of the amount of land sampled. Many of the sampling cells had a high proportion of land (29 with greater than 90% land) in relation to the amount of ocean, while 11 cells had less than 10% land. The number of bird species observed tended to increase with sampling effort, but the relationship was non-linear. As time was spent making observations in a sampling cell, samplers eventually reached the maximum number of species they were likely to find, at which point sampling ceased. This sampling trend was reflected in the results obtained in this study. The land-cover variables in the models selected by Akaike's Information Criterion explained up to 44% of the variation in the species richness of all bird species pooled together (Table 3.2), though the variables significantly associated with species richness differed among functional groups. The best explanatory models for the pooled species consisted of variables explaining the mean body size of the species assemblages, longitude, and variables from all of the land-types. Species richness increased in relation to the proportion of human-used lands, and decreased in relation to an increased percentage of forest in a cell, though these variables were only significant in three of the five models

Table 3.2. Table showing the coefficients and standard error of the five best models for explaining species richness of all birds in Prince Edward Island, as determined by Akaike's Information Criterion. These models relate avian species richness with the land-cover variables, latitude and longitude, total area in a cell, and sampling effort. All body size values are $\log_{10}$ transformed. Sample size, adjusted-R^2, and the ΔAIC for each of these models are shown. Where blank spaces are shown, associations were tested and were found non-significant ($p < 0.05$).

Full Model	Model-1	SE	Model-2	SE	Model-3	SE	Model-4	SE	Model-5	SE
Intercept	568.96	391.1	439.6	341.7	680.4	387.4	309.4	356.4	680.0	487.3
Percentage of Forest	-0.28	0.18			-0.23	0.18				
Percentage of Human-used land	1.43	0.69	1.12	0.62			1.5	0.7		
Percentage of Wetland									0.74	0.42
Percentage of Roads										
Fractal Dimension of Agriculture	117.10	58.0	122.8	58.7	122.1	58.4	118.8	58.6	101.7	58.3
Fractal Dimension of Forest	-162.24	66.1	-103.55	48.7	-162.95	66.7	-93.6	49.2	-64.2	42.8
Fractal Dimension of Human-used	-120.86	46.2	-97.0	45.1	0.99	0.6	-109.6	46.1	-85.7	43.6
Fractal Dimension of Wetlands					-104.3	45.2				
Clumpiness of Agriculture					-655.3	217.3				
Clumpiness of Forest	445.19	301.0					369	300		
Clumpiness of Human-used land	-825.86	244.3	-638.8	218.1	-655.3	217.3	-777.6	244.8	-405.5	169.4
Clumpiness of Roads										
Total area of land-cover in cell (km^2; $\log_{10}$)	25.8	9.5	24.3	9.4	26.6	9.5	23.2	9.4	24.1	9.2
Sampling Effort ($\log_{10}$)	15.5	6.18	14.4	5.7	12.4	5.9	17.2	6.1	12.6	5.9
Latitude									-18.3	9.5
Longitude	9.16	3.8	6.0	3.5	7.9	3.7	6.8	3.5		
Latitude x Longitude										
Mean Body Size (g; $\log_{10}$)	455.6	137.6	508.0	136.3	498.2	135.8	474.2	138.6	493.2	136.8
Mean Body Size^2 (g; $\log_{10}$)	-102.3	30.2	-113.3	29.9	-112.2	29.8	-105.3	30.5	-110.0	30.0
ΔAIC	-									
n	75		75		75		75		75	
p	< 0.0001		< 0.0001		< 0.0001		< 0.0001		< 0.0001	
Adjusted-R^2	0.44		0.42		0.43		0.43		0.42	

examined among pooled species. Note that these directional trends are contrary to what may be expected to occur, and may be results of sampling artefacts or correlation among variables. Species richness was positively related to the fractal dimension of agriculture, indicating that more species may be found in areas where long, narrow fields dominate over large, round fields. Also of note were results that species richness tended to be higher in areas where forest patches and human-used areas were less spatially complex, as represented by a low fractal dimension. The number of avian species was positively related to high aggregation of forest patches as denoted by the clumpiness index. This relation makes sense in that more aggregated patches will tend to have higher area in relation to their perimeter. This variable is related to the percentage and shape of patches, and so it may have an influence on the curious negative relation of richness to the proportion of forest. Longitude was positively related to species richness, indicating that more species were observed in the eastern portion of Prince Edward Island than in the west. Latitude did not have a significant effect upon the species richness of all birds pooled together, nor did the interaction of latitude and longitude. The mean body size of the avian assemblages had a non-linear relationship with species richness. A fitted-line plot was made to further illustrate this relationship (Fig. 3.4). As demonstrated in this figure and partially supporting our hypotheses, species richness does decrease with increasing body size. However, initially species richness increases with body size, up until ~ 50 g. At this point, avian species richness begins to decrease with mean body size. Standardized residuals of all three models shown were normally distributed and no severe outliers were observed.

The landbird functional group was associated with landscape structure, latitude, longitude, and body size in a similar fashion to that of the pooled species (Table 3.3).

Figure 3.4 (*Top*) Linear regression examining the non-linear association of the species richness of all species pooled together (Richcell) with the mean body size of the community ($\log_{10}$ transformed). (*Bottom*) Corresponding normal probability plot of the residuals of the above regression.

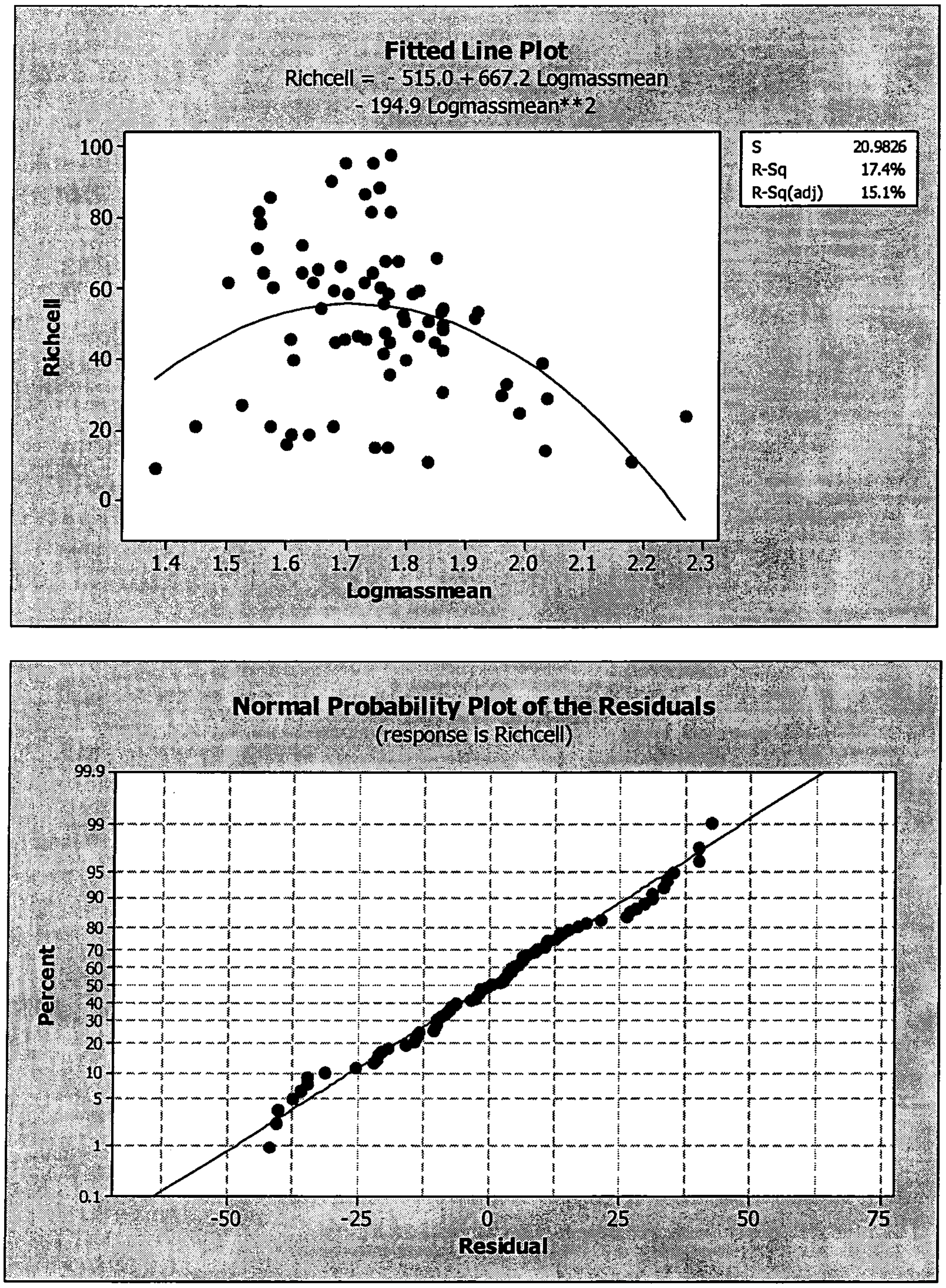


Table 3.3. Table showing coefficients and the standard error of the five best models for explaining species richness of landbirds in Prince Edward Island, as determined by Akaike's Information Criterion. These models relate avian species richness with the land-cover variables, latitude and longitude, total area in a cell, and sampling effort. All body size values are $\log_{10}$ transformed. Sample size, adjusted-R^2, and the ΔAIC for each of these models are shown. Where blank spaces are shown, associations were tested and were found non-significant ($p < 0.05$).

Full Model	Model-1	SE	Model-2	SE	Model-3	SE	Model-4	SE	Model-5	SE
Intercept	125.7	406	-68.8	312.2	290.6	426.8	-7.98	311.3	235.0	427.8
Percentage of Forest										
Percentage of Human-used land			1.5	0.6			1.3	0.6		
Percentage of Wetland	0.79	0.35			0.87	0.36			0.75	0.37
Percentage of Roads										
Fractal Dimension of Agriculture	123.6	49.5	141.6	49.3	124.2	49.2	138.8	49.6	129.5	49.3
Fractal Dimension of Forest	-44.9	36.6	-79.4	41.9	-51.6	36.9	-84.2	42.1	-55.0	36.9
Fractal Dimension of Human-used	-47.8	35.4	-93.4	39.3	-61.5	37.1	-88.5	39.5	-64.9	37.0
Fractal Dimension of Wetlands	52.6	29.8	40.5	29.2	51.2	29.7			42.5	30.4
Clumpiness of Agriculture										
Clumpiness of Forest			418.2	254.1			384.0	254.8		
Clumpiness of Human-used land			-560.7	209.4	-171.2	141.3	-547.9	210.7	-192.7	141.9
Clumpiness of Roads										
Total area of land-cover in cell (km^2; $\log_{10}$)	27.2	7.2	23.5	7.8	28.8	7.3	24.9	7.8	25.9	7.7
Sampling Effort ($\log_{10}$)			11.4	5.1			12.4	5.0	6.0	5.0
Latitude	-16.9	7.8			-16.6	7.8			-13.7	8.13
Longitude			4.9	2.9			4.5	2.9		
Latitude x Longitude										
Mean Body Size (g; $\log_{10}$)	468.6	91.9	401.0	96.0	465.3	91.6	385.6	96.1	428.9	96.1
Mean Body Size^2 (g; $\log_{10}$)	-110.3	21.9	-94.4	22.9	-109.8	21.8	-90.5	22.8	-101.4	22.8
ΔAIC	-									
n	75		75		75		75		75	
p	< 0.0001		< 0.0001		< 0.0001		< 0.0001		< 0.0001	
Adjusted-R^2	0.44		0.46		0.45		0.45		0.45	

The three best models as selected by the AIC procedure primarily consisted of the same variables as one another, though there were minor differences. The adjusted-R^2 of these models was the same at 0.45, with corresponding high significance values ($p < 0.0001$). This was not unexpected, as the landbirds comprise the bulk of the species present on Prince Edward Island. Because of the many similarities between the pooled species and the landbird functional group, it is more efficient to speak about how the landbirds differed from the pooled birds rather than discuss them on their own. The percentage of forest was not a significant explanatory variable for the species richness of landbirds, though the clumpiness and fractal dimension of forest still exhibited the same trends. This indicates to me that the percentage of forest is not necessarily a weak or nonsignificant variable, but that it may be interacting with other variables. This interaction may be influencing the percentage of forest variable, causing it to be non-significant in the models chosen by the AIC method.

Landbirds were also significantly affected by metrics of wetland, variables that were not common in the pooled species models. Landbird species richness in three models were positively associated with the percentage of wetland in a cell. Species richness was also positively associated with the fractal dimension of wetlands, implying that there may be a large number of landbird species in cells where there is a large amount of spatially simple wetland patches. For example, cells like this may have a profusion of round ponds or bogs. Latitude was found to be negatively related to species richness in two of the three models, while longitude was positively related with species richness. There was no interaction detected between latitude and longitude in the models examined for this functional group. These results demonstrate high species richness in the southeast part of Prince Edward Island, which is logical and is likely a result of the natural topography of the area. Residual analysis showed results similar to those found when examining all species pooled together, and so assumptions for multiple regression analysis were upheld.

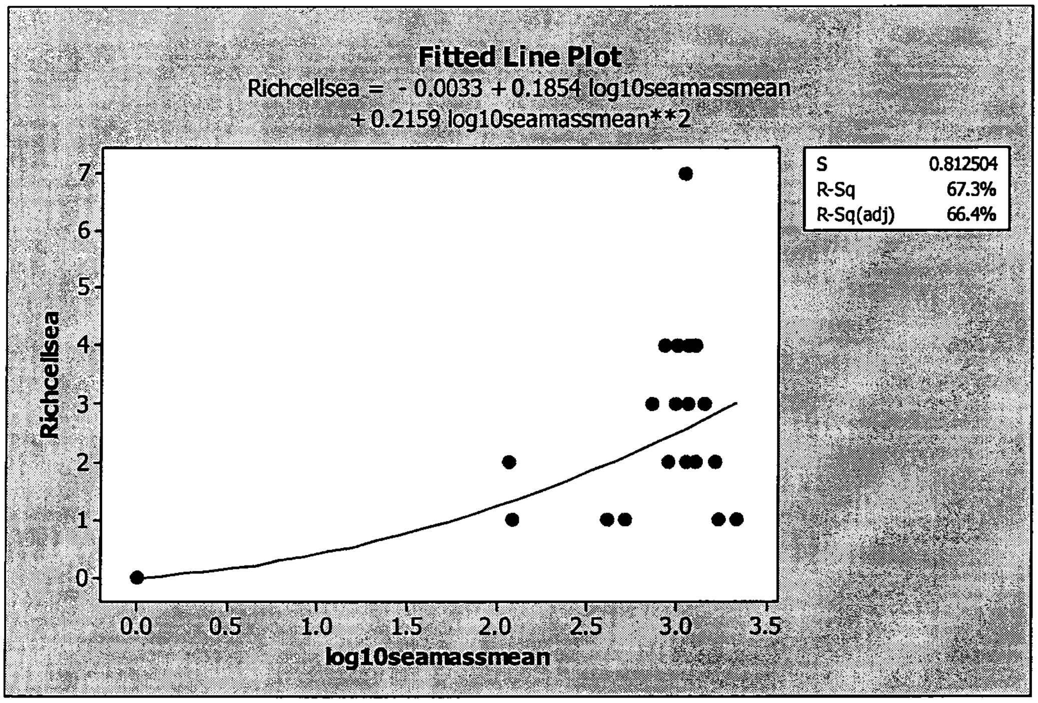
The seabird functional group was distinct in that seabirds were observed in fewer cells (31) than any other functional group. Due to this, possible biases in results due to small sample sizes should be taken into consideration when examining this group. Species richness of seabirds increased with proportion to the amount of wetlands and forest patches (Table 3.4). The species richness of this group was also positively related to simple-shaped forest patches, and agricultural patches with complex edges. Additionally, seabird species richness increased with aggregation of forest patches, and decreased with aggregation of agricultural patches. Species richness of seabirds was negatively related to longitude and latitude, which may be related to the trend observed with the total area; there are more sampling cells in the south and east that are completely land-locked. Species richness was non-linearly related to mean body size among the seabirds, but these variables proved to be non-significant in each of the models examined for seabird species. The resulting non-significance of these variables may be the cause for heteroscedasticity observed among the residual analysis, and for a possible inflation of the adjusted-R^2 beyond what could be reasonably expected. Small sample size could be another factor in the irregularity of results concerning body size in this functional group, though there were few deviations from normality as shown in the residual analysis of the multivariate models (Fig. 3.5).

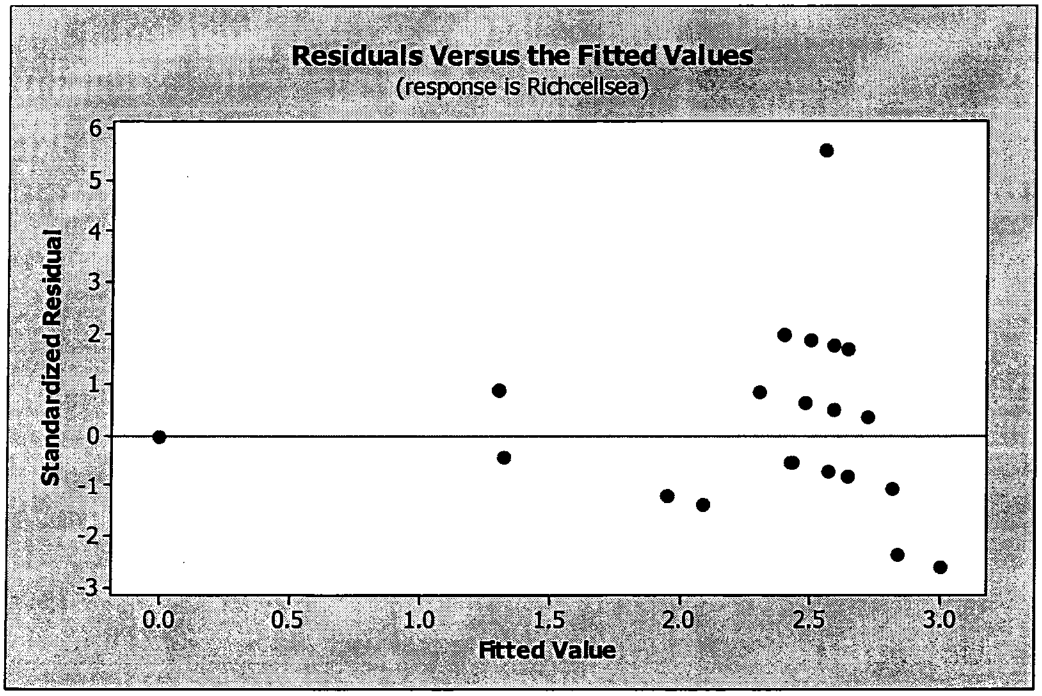
The species richness of shorebirds was primarily related to the shape of patches in the landscape, rather than their size and clumpiness. However, correlation among landscape variables makes this a less definitive statement. Only three candidate models

Table 3.4. Table showing the five best models for explaining species richness of seabirds in Prince Edward Island, as determined by Akaike's Information Criterion. These models relate avian species richness with the land-cover variables, latitude and longitude, total area in a cell, and sampling effort. All body size values are $\log_{10}$ transformed. Sample size, significance ($p < 0.05$), adjusted-R^2, and the ΔAIC for each of these models are shown. Coefficients and standard errors are shown for each model. Where blank spaces are shown, associations were tested and were found non-significant ($p < 0.05$).

Full Model	Model-1	SE	Model-2	SE	Model-3	SE	Model-4	SE	Model-5	SE
Intercept	85.1	21.0	87.3	21.0	81.6	20.7	86.9	20.9	84.5	21.0
Percentage of Forest	0.02	0.008	0.02	0.008	0.02	0.008			0.02	0.008
Percentage of Human-used land										
Percentage of Wetland	0.04	0.02	0.05	0.02	0.04	0.02	0.04	0.02	0.04	0.02
Percentage of Roads										
Fractal Dimension of Agriculture	-3.6	2.4	-3.2	2.4			-3.7	2.4	-4.0	2.4
Fractal Dimension of Forest	6.0	2.6	5.9	2.6	4.9	2.5	6.7	2.6	6.6	2.7
Fractal Dimension of Human-used			-2.2	1.8	-2.5	1.8	-2.5	1.8		
Fractal Dimension of Wetlands										
Clumpiness of Agriculture	-36.0	12.6	-38.9	12.8	-37.3	12.8			-34.7	12.7
Clumpiness of Forest	18.6	12.3	20.3	12.3	16.9	12.2	21.7	12.4	19.5	12.4
Clumpiness of Human-used land										
Clumpiness of Roads										
Total area of land-cover in cell (km^2; $\log_{10}$)							-0.45	0.37	-0.36	0.36
Sampling Effort ($\log_{10}$)										
Latitude	-2.38	0.55	-2.40	0.5	-2.28	0.5	-2.4	0.5	-2.35	0.55
Longitude	-0.59	0.2	-0.63	0.2	-0.62	0.2	-0.6	0.2	-0.56	0.21
Latitude x Longitude										
Mean Body Size (g; $\log_{10}$)	0.27	0.39	0.25	0.39	0.25	0.39	0.30	0.38	0.32	0.39
Mean Body Size^2 (g; $\log_{10}$)	0.21	0.13	0.22	0.13	0.22	0.13	0.20	0.13	0.19	0.13
ΔAIC	-									
n	75		75		75		75		75	
p	< 0.0001		< 0.0001		< 0.0001		< 0.0001		< 0.0001	
Adjusted-R^2	0.74		0.74		0.74		0.45		0.45	

Figure 3.5 (*Top*) Linear regression of the species richness of seabirds (Richsellsea) plotted against the $\log_{10}$-transformed mean body size of seabirds (logseamassmean) and its quadratic transformation (logseamassmean**2). (*Bottom*) Plot of the standardized residuals versus the fitted values of the previous regression.





had an ΔAIC < 2, which is why only three are shown in Table 3.5. Of these three models, species richness appeared to be higher in areas where wetland and human-used patches were simple in perimeter and with large areas.

The species richness of the waterfowl functional group was reasonably well-predicted in the best three models selected by the AIC process (Table 3.6; adjusted-R^2 = 0.37 - 0.39). Residual analysis of these models revealed that assumptions of normality were upheld and procedure assumptions were properly met. Specific variables that affected the species richness of waterfowl included each of the forest variables, the clumpiness of human-used land, latitude and longitude, and body size. The signs of these variables did not change regardless of removal of the outliers. The species richness of waterfowl was negatively associated with the percentage of forest and to the fractal dimension of forest in a cell, and was positively related to the clumpiness of forest in a cell. As was noted with other functional groups, the close correlations between the forest variables may distort their individual effects, and so the negative relation between species richness and percentage of forest should be viewed with caution. The clumpiness of human-used lands was negatively related to species richness, indicating that sampling cells with heavily aggregated human areas may result in observations of less waterfowl species. As clumpiness is slightly correlated with the proportion of land for this land-cover type, this may also reflect an avoidance of human-dominated lands by waterfowl. Latitude and longitude were both positively associated with the species richness of waterfowl, indicating that more species were found on the north-eastern part of Prince Edward Island than elsewhere. Mean body size was significantly related to waterfowl species richness, exhibiting a linear trend among these models.

Table 3.5. Table showing coefficients and standard errors for the three best models explaining species richness of shorebirds in Prince Edward Island, as determined by Akaike's Information Criterion. These models relate avian species richness with the land-cover variables, latitude and longitude, total area in a cell, and sampling effort. All body size values are $\log_{10}$ transformed. Sample size, adjusted-R^2, and the ΔAIC for each of these models are shown. Coefficients and standard errors are shown for each model. Where blank spaces are shown, associations were tested and were found non-significant ($p < 0.05$).

Full Model	Model-1	SE	Model-2	SE	Model-3	SE
Intercept	-7.41	7.18	-43.3	33.1	-20.1	16.3
Percentage of Forest						
Percentage of Human-used land						
Percentage of Wetland						
Percentage of Roads						
Fractal Dimension of Agriculture	11.8	3.9	12.7	4.0	-20.1	16.3
Fractal Dimension of Forest						
Fractal Dimension of Human-used	-5.2	2.9	-5.6	2.9	-5.87	3.04
Fractal Dimension of Wetlands	-4.6	2.4	-4.4	2.4	-4.66	2.4
Clumpiness of Agriculture						
Clumpiness of Forest						
Clumpiness of Human-used land						
Clumpiness of Roads						
Total area of land-cover in cell (km^2; $\log_{10}$)	1.11	0.58	1.13	0.58	1.12	0.58
Sampling Effort ($\log_{10}$)	0.93	0.38	1.03	0.39	1.0	0.39
Latitude			0.75	0.67		
Longitude						
Latitude x Longitude						
Mean Body Size (g; $\log_{10}$)	1.24	0.20	1.30	0.20	1.25	0.20
Mean Body Size^2 (g; $\log_{10}$)						
ΔAIC	-					
n	75		75		75	
p	< 0.0001		< 0.0001		< 0.0001	
Adjusted-R^2	0.49		0.49		0.49	

Table 3.6. Table showing coefficients and standard errors for the three best models explaining species richness of waterfowl in Prince Edward Island, as determined by Akaike's Information Criterion. These models relate avian species richness with the land-cover variables, latitude and longitude, total area in a cell, and sampling effort. All body size values are $\log_{10}$ transformed. Sample size, adjusted-R^2, and the ΔAIC for each of these models are shown. Coefficients and standard errors are shown for each model. Where blank spaces are shown, associations were tested and were found non-significant ($p < 0.05$).

Full Model	Model-1	SE	Model-2	SE	Model-2	SE
Intercept	-55.2	64.67	-39.6	65.9	-37.6	68.1
Percentage of Forest	-0.07	0.02	-0.08	0.03	-0.08	0.03
Percentage of Human-used land						
Percentage of Wetland						
Percentage of Roads						
Fractal Dimension of Agriculture	-18.6	8.4			-22.0	8.9
Fractal Dimension of Forest			-21.4	8.7		
Fractal Dimension of Human-used					-7.4	6.8
Fractal Dimension of Wetlands						
Clumpiness of Agriculture						
Clumpiness of Forest	51.9	34.9	60.9	35.7	71.3	39.0
Clumpiness of Human-used land			-27.4	23.8	-40.3	26.6
Clumpiness of Roads						
Total area of land-cover in cell (km^2; $\log_{10}$)						
Sampling Effort ($\log_{10}$)	1.64	0.83	1.8	0.8	1.8	0.84
Latitude	3.3	1.8	3.6	1.8	3.8	1.8
Longitude	1.89	0.68	2.05	0.69	2.0	0.7
Latitude x Longitude						
Mean Body Size (g; $\log_{10}$)	1.65	0.38	1.65	0.38	1.7	0.4
Mean Body Size^2 (g; $\log_{10}$)						
ΔAIC	-					
n	75		75		75	
p	< 0.0001		< 0.0001		< 0.0001	
Adjusted-R^2	0.39		0.39		0.37	

3.5 DISCUSSION

The primary goal of this study was to examine the effects of latitude and longitude, mean body size, and the structure of the landscape on the species richness of birds breeding in Prince Edward Island. In our study, latitude and longitude were significant, predictors of avian species richness, though longitude was more prevalent among candidate models. Latitude is also known to be a surrogate of climatic factors including temperature, evapotranspiration, and energy (Currie *et al.*, 2004). Studies such as this have shown that latitude tends to operate at larger spatial scales than that of our study, so direct correlations of species richness with climatic variability are unlikely to produce strong associations (Pianka, 1966; Gaston *et al.,* 1995; Hurlbert & Haskell, 2002; Hawkins *et al.*, 2003). A similar pattern describing the association of species richness and longitude was found by Jetz & Rahbek (2001) when they examined African avian species. The likeliest reasons for the latitudinal and longitudinal gradients in species richness observed in this study are likely topographical in nature. The general increase in richness with longitude may be due to there being more forest, more wetland, and less human-used land in the eastern part of the island. There are known association of many landbird and waterfowl species to wetlands and forested habitats (Gill, 1994), and these sorts of areas are more prevalent in the eastern part of Prince Edward Island than in the west (Clark, 1959; Raymond *et al.*, 1963; van de Poll, 1983). Additionally, there is simply more land in the eastern part of Prince Edward Island. Due to the shape of the island, an increase in species richness in an eastward direction would result in a corresponding southward trend, as observed in many of the models constructed in this study. Though no significant interactions were detected between latitude and longitude, an underlying interaction between latitude and longitude is suspected to be evident, but is possibly masked by other variables.

The mean body size of the avian community was an important explanatory variable in our study, being significant in all functional groups. Brown (1995) and Owens *et al.* (1999) showed that at the level of the community, low mean body size is related to high species richness, though this is a non-linear trend where species richness is highest at a low-mid mean body size. Our study supported the findings of these scientists when examining the landbird functional group, as we found a non-linear relationship between species richness and mean body-size, with the highest species richness at low-mid mean body size. Assemblages with very small or large mean body-sizes tended to exhibit low species richness, while the most species occurred where the mean body size of the community was approximately 50 g. At continental spatial scales, Blackburn *et al.* (1999) and Cardillo (2002) observed that the species richness of birds was strongly related to both the mean body size and landscape structure. Our study supports these results, following the quadratic trends that were seen in these earlier studies. A variable that could explain more of the relationship between species richness and body size is the range of body size, which may allow more insight into the composition of the avian community, particularly with regard to its largest species. Though this study did not make use of this variable due to a desire to examine the mean in particular, the range will be examined in future studies.

In comparison to our study, other studies have found stronger relationships between avian species richness and land-cover variables where R^2 exceeds 0.5, though rarely by large value (Edenius & Elmberg, 1996; Bayne & Hobson, 1997; Böhning-Gaese, 1997; Germaine & Vessey, 1997). The relatively low strength of association found in our study may be related to the spatial scale of our analysis, inadequate delineation of the land-covers, or there was simply a true weak association. It is possible that if land-use was delineated in a different fashion, particularly in the wetland land-types and forest land-types, specie richness may be better explained. Avian species may respond differently to bogs than they would to marshes and salt marshes, and to deciduous forests differently than to coniferous forests. The difficulty in defining land-types in this fashion lies in finding metrics to explain their attributes. For example, defining coniferous and deciduous stands as different land-types may result in a perceived discontinuity of land-cover that may not be perceived by avian species. The edges between two closely-related land-types may not be as clearly defined as in coarser landscape delineations. Because of this, the shape as defined by the fractal dimension may not be as accurate when land-types are delineated in too fine a fashion, and the aggregation of habitat as defined by the clumpiness metric becomes a less clear measure. The five land-cover types used in this study were the most distinguishable habitat types that we could delineate using indices of size, shape, and aggregation, and adding or removing different land-cover types would have to be done with caution.

The accuracy of specific variables may also be in question when examining the results of this study. For example, when the landscape structure was examined in relation to the species richness of the pooled avian species, a striking result was that species richness was not often associated with the percentage of forest. Note, however, that percentage of forest, fractal dimension and the clumpiness of forest were also both associated with avian species richness, and that these variables are moderately correlated ($r > 0.2$) with one another. Therefore, the signs of individual variables must be interpreted with caution. The best interpretation may be to conclude that the forest variables have the greatest effect on the pooled species richness of all of the land-cover variables, but that the specific effects of the metrics explaining forest structure are difficult to explain.

While keeping the correlation of variables in mind, some results can still be examined. As Burrough (1986) showed, high avian species richness tended to occur in areas where forest patches had high area in relation to their perimeter, as quantified by the fractal dimension. Our findings suggest that the diversity of avian species in Prince Edward Island may be strongly dependant on the occurrence of birds that occupy forest habitats with a high area to edge ratio, which supports the results found in some other studies (Greenwood *et al.*, 1996; Mönkkönen *et al.*, 2006). Many of the avian species that inhabit these sorts of areas are small passerine birds, which may help explain the relationship between species richness, body size and landscape composition. Correspondingly, this trend is reversed when examining agriculture. As quantified by the fractal dimension of agriculture in this study; the more complex in shape agricultural fields become, the more birds can be found in the sampling cell. St. Claire *et al.* (1998) showed that greater complexity in the shape of agricultural fields can increase avian species richness. The mechanism they suggested to explain this trend was a behavioural response of species to field shape. Agricultural patches with low area-perimeter ratios may reduce the amount of time forest birds have to be away from cover in order to forage in what can sometimes be very productive edges of agricultural fields. The results of this study indicate that landbird species are more likely to be observed in areas where there is a high proportion of human-used land that is both well dispersed in a cell and is relatively simply shaped. It as also found that the shape of several different land-cover types, as quantified by the perimeter-area fractal dimension, was strongly associated with species richness of birds. Similar results were obtained by Sugihara & May (1990) and Milne (1991). As these sorts of interactions are examples of habitat fragmentation, habitat fragmentation could be a major driving force of avian species richness patterns on Prince Edward Island. However, further studies involving a more intense examination of habitat aggregation and other biotic interactions would have to be undertaken before this could be conclusively said (Turner *et al.*, 2001a).

The avian functional groups of Prince Edward Island revealed interesting information when they were examined separately. When examining avian species richness in Scotland, French & Picozzi (2002) separated avian species in their study into functional groups. They found clear differences among functional groups in the association of species richness to landscape structure. Scotland covers a much larger area than Prince Edward Island, and though French & Picozzi (2002) used a similar sampling grain as that of our study, the sampling extent was much larger. The limitations of our dataset may have biased the survey in favour of landbirds, in that they were easier to observe and may occur more extensively throughout the island regardless of habitat. The resulting skew in favour of a high amount of landbird species in contrast to other groups may encourage a reassessment of the sampling technique in future studies. The landbird functional group was associated to landscape structure in a similar fashion to that of the pooled species, with the addition of the wetland variable in one of the models. The species richness of breeding seabirds on Prince Edward Island was significantly associated to the landscape structure on the island. However, residual analysis and a low sample size indicate that these results should be interpreted with caution at best. Similar results were obtained when examining shorebirds. Though R^2 values were fairly high for the shorebird functional group, subsequent residual analysis revealed heteroscedastic trends, likely due to non-significance of the body size variables. Any interpretations that could be made from their associations with landscape structure would have to be treated with caution. Waterfowl species were affected by the presence of forest in the sampling cell, and was negatively affected by the aggregation of human-influenced lands. Though waterfowl species richness was not strongly associated with landscape structure ($R^2 = 0.39$), the models were significant and residual analysis showed that the analysis was acceptable.

The goal of this chapter was to examine the effects of latitude, longitude, body size, and landscape structure upon the species richness of birds on Prince Edward Island. Many significant associations were found among these variables to the species richness of two of the four functional groups in addition to all the species pooled together. Any interpretations must be examined with the understanding that there was correlation, and therefore a lack of independence, among the land cover variables (Turner *et al.*, 2001a). Analytical techniques that would eliminate these correlations, such as Principal Components Analysis, are recommended for future studies. Based upon our results, focus on the shape of agricultural and forest patches is recommended for further study, and the relationship of body size, longitude and latitude to land-cover variables should be examined in future works. Advice to landscape managers desiring to increase species richness in Prince Edward Island would be to preserve forest patches with large areas in relation to their perimeters. When new agricultural fields are needed, the results of this study lead to a recommendation that long, narrow fields are more associated with higher avian species richness than broad, short fields.

4. THE EFFECTS OF LANDSCAPE STRUCTURE ON THE OCCURRENCE OF BREEDING BIRDS

4.1 ABSTRACT

The aim of this study was to examine the effects of landscape structure on the occurrence of avian species breeding on Prince Edward Island, Canada. Spatial data on species counts were obtained from Erskine (1992) and information on land-cover types (agriculture, forest, wetland, roads, human-used areas) were obtained from the provincial government. ArcView GIS and Fragstats were used to calculate several metrics that characterized the structure and complexity of the different land-cover types (area, shape, and aggregation). Habitat metrics were related to the occurrence of 102 avian species in seventy-six 10 km x 10 km sampling cells. Logistic regression analysis was used to examine the associations and to develop multivariate models to explain avian species occurrence. Avian species were then examined in terms of functional group (*i.e.* landbird, seabird, shorebird, waterfowl) and trophic level (*i.e.* herbivore, carnivore, insectivore, omnivore). Twenty-nine species were significantly associated with the land-cover variables. These species were primarily from the landbird functional group and the omnivore and insectivore trophic groups. There were few discernable patterns in specific metrics used by species, though forest-related variables were associated with species more often than other land-cover types.

4.2 INTRODUCTION

Loss of species is an important consequence of environmental threats, such as the loss and fragmentation of habitat (Secretariat of the Convention on Biological Diversity, 2001). The study of species occurrence is of great importance in ecology, biogeography, wildlife management, and conservation biology. For instance, investigations of the factors that determine the occurrence of rare and endangered species can be useful to identify particular land-use practices that may be beneficial for their conservation (Caicco *et al.*, 1995; Scott *et al.*, 1995). The occurrence of avian species can also be modeled with the purpose of prioritizing natural areas for conservation (Peterson *et al.*, 2000). Potential distributional shifts of avian species resulting from climatic changes may also be predicted if sufficient information on factors affecting species occurrence is known (Aspinall & Matthews, 1994). Information on factors determining species occurrence may also be useful to predict, or control invasive species (Wadsworth *et al.*, 2000).

Several factors have been hypothesized to explain occurrence of avian species breeding in North America, including energy, climate, habitat heterogeneity, and habitat fragmentation (Brown, 1981; Rapoport, 1982; Stevens, 1992; Brown, 1995; Kerr & Currie, 1999; Taylor & Gaines, 1999; Rahbek & Graves, 2001; Johnson & Krohne, 2002). However, the influence of these and other factors in terms of determining the occurrence of a given avian species depends upon the spatial scale at which the study is conducted. Several studies have examined the effects of these factors on avian species occurrence from different parts of the world (Gaston & Blackburn, 2000; Rahbek & Graves, 2000; Rahbek & Graves, 2001; H-Acevedo & Currie, 2003; Gaston & Evans, 2004; Pearson *et al.*, 2004). At large spatial scales, the total area wherein a species is known to occur on the Earth is known as the geographic range, or geographic distribution (Smith & Smith, 1998). At this scale, it has been shown that the geographic distribution of many animal species, including birds, is strongly correlated with the amount of land and the variety of habitats the population occupies (Ricklefs, 1997; Tews *et al.*, 2004). At the landscape scale, the occurrence of avian species is thought to be primarily determined by the presence or absence of suitable habitat, the nature of which can significantly vary from species to species (Drapeau *et al.*, 2000). Species that are closely related or that have similar dietary or habitat needs (*i.e.* trophic and functional groups; French & Picozzi, 2002) are expected to be influenced by the availability of habitat in similar ways (Brown, 1984). At large spatial scales it has been suggested that the occurrence of many avian species is determined by climatic factors such as precipitation and temperature, because species have differential tolerances to the amount of water and the heat in a given area (Currie, 1991; Currie *et al.*, 2004). It has also been postulated that occurrence limits imposed by barriers to long-distance dispersal are not as prevalent among flying birds as they are for other terrestrial vertebrates (Gill, 1994). For example, Wiens (1973) showed that when the horned lark (*Eremophila alpestris*) was examined at large spatial scales, its distribution covered much of North America, with some aggregation in the western prairies. However, when the same species was examined at small spatial scales, it was more likely to be found in areas where land-use practices promoted heavier cattle grazing. Therefore, different factions will be important in determining the occurrence of this species, depending on the spatial scale at which its occurrence is investigated. These studies also suggest that a multi-scale approach may be optimal when examining the occurrence of a given species (Gaston *et al.*, 1995; Rahbek & Graves, 2001).

Habitat loss is the process where areas with specific features important to the presence of species is destroyed or otherwise made unsuitable for habitation. Habitat fragmentation is a process whereby a continuous habitat type is partially removed, resulting in a change of configuration of the initial landscape above and beyond the fragmentation that is associated with habitat loss (Villard *et al.*, 1999). Habitat loss and fragmentation has been shown to affect the occurrence of avian species at the scale of the landscape (100 km^2 - 1000 km^2; McGarigal & McComb, 1995; Edenius & Elmberg, 1996). The habitat types in a landscape can be quantified in terms of landscape composition and landscape configuration (McGarigal & Marks, 1995). Landscape composition refers to the number or proportion of features in a landscape (Rodewald & Yahner, 2001). Landscape composition is not spatially explicit, in that landscape composition is unaffected by patch shape. Landscape configuration is a spatially defined concept that relates the physical location of a landscape patch to that of other patches (McGarigal & McComb, 1995). Landscape configuration is often defined by metrics such as patch shape and contagion indices (Hargis *et al.*, 1998). In this study, we followed McGarigal and Marks (1995)'s definition and used several variables that describe the composition and configuration of landscapes to quantify landscape structure.

To my knowledge, the effect of landscape structure on the occurrence of avian species at small spatial scales has only been studied recently (Trzcinski *et al.*, 1999; Villard *et al.*, 1999; Fahrig, 2003). Loss and fragmentation of habitat resulting from agricultural practices and forestry have often been found to have an adverse effect on the occurrence of many avian species (McIntyre, 1995; Trzcinski *et al.*, 1999; Villard *et al.*, 1999; Rickets, 2001; Rodewald & Brittingham, 2002; Stanislaw, 2002; Fahrig, 2003).

Many songbird species are considered to be "core-forest species" because they need a critical minimum area of continuous forest to meet their life history requirements (Bayne & Hobson, 1997). Therefore, the reduction of suitable habitat due to habitat loss and fragmentation is likely to result in local extinctions of core-forest species. Fragmentation of a forest patch increases its edge or the edge habitat in relation to the core, creating a broader ecotone between the forested area and the matrix habitat (*i.e.*, the nonhabitat surrounding the native habitat patches of interest; Ricketts, 2001). Although species from adjoining landscape types can be found within such transition zones, these ecotones may not be ideal breeding habitat for many core-forest species, whose populations may need to be maintained through immigration from adjacent patches (Foppen *et al.,* 2000). Consequently, this phenomenon can be explained by source-sink dynamics rather than by an affinity to the habitat in question (Pulliam, 1988; Pulliam & Danielson, 1991). In source-sink dynamics, avian populations are sustained only through immigration from other, more productive areas. Many exotic birds such as the brood parasite *Molothrus ater* are able to take advantage of heavily fragmented regions, moving into and displacing core-forest species (Rich *et al.* 1994; Hobson & Villard, 1998).

The objectives of this study are: (1) to identify the associations between landscape structure descriptors (metrics) and the occurrence of individual species; (2) to search for trends in the relation between occurrence and landscape structure among functional groups and (3) trophic groups. This is an exploratory study that seeks to find relations between these variables and species occurrence in a broad, encompassing way.

4.3. METHODOLOGY

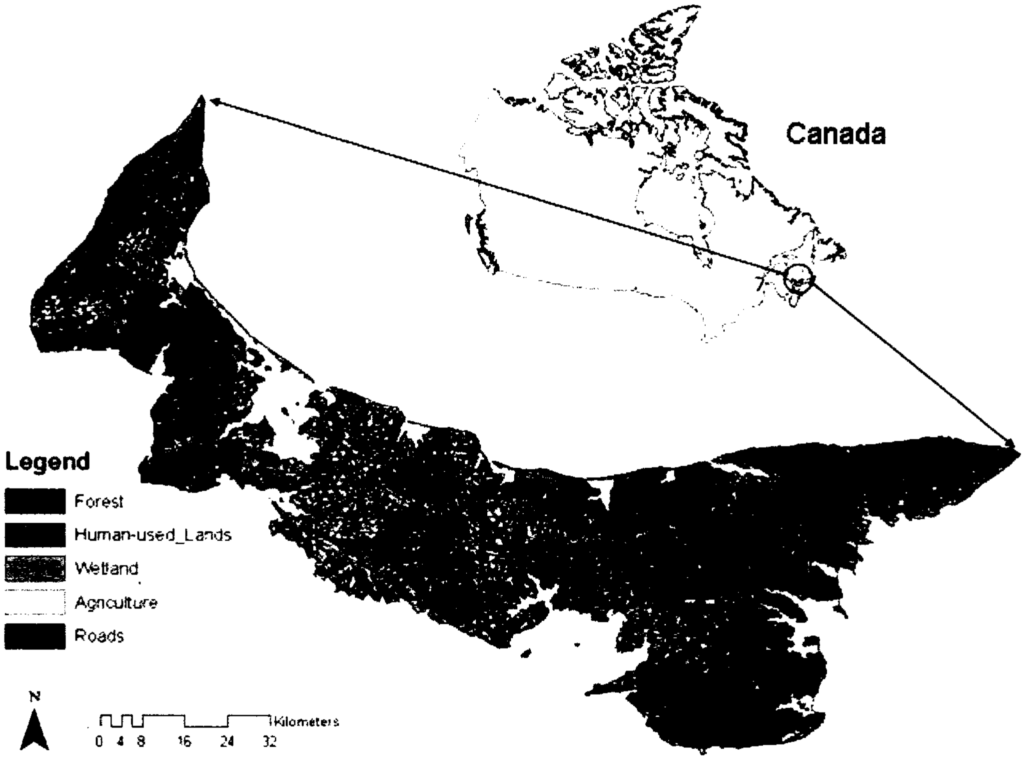
Study Area

Prince Edward Island covers an area of 5665.6 km^2 and is located in the St. Lawrence Basin of Eastern Canada (approximately 46°N, 63°W; Agriculture, Fisheries, Aquaculture and Forestry, 2003; Figure 4.1.). The island is approximately 16 km distant from the mainland at the narrowest gap in the Northumberland Strait, and is relatively flat with a maximum height of 146 m above sea level (Silva *et al.*, 2003). The landscape is composed of a number of land-types, including approximately 39.4% of agricultural lands used for various crops, especially potatoes. The forests cover 48.4% of the island, and are a mix of the old-growth Acadian species, as well as other species such as white spruce (*Picea glauca*), black spruce (*Picea mariana*), poplar (*Populus tremuloides*), and other fast-growing, secondary-growth trees. Wetlands comprise 4.2% of the island, within which we can find marshes, bogs, salt marshes, and coastal areas such as sand dunes. Approximately 6% of Prince Edward Island is composed of human-used areas such as buildings and urban centres. The remaining 2% of the island's land-cover consists of an extensive network of roads. The human population in the province is approximately 134,500 individuals with an increasing rate of 0.5% every five years (Statistics Canada, 2001a).

Avian Species Data

Data on avian species occurrence were obtained from the Maritime Breeding Bird Atlas (Erskine, 1992). Bird censuses were undertaken in all seasons by volunteers from 1986 to 1990, who were organised and assigned sampling cells by an overseeing committee of experienced avian samplers. Sampling locations were designed in order to

Figure 4.1. Map of Prince Edward Island in relation to Canada (46°N, 63°W). The scale bar refers to Prince Edward Island only. All five land-cover types used in the study are shown here.

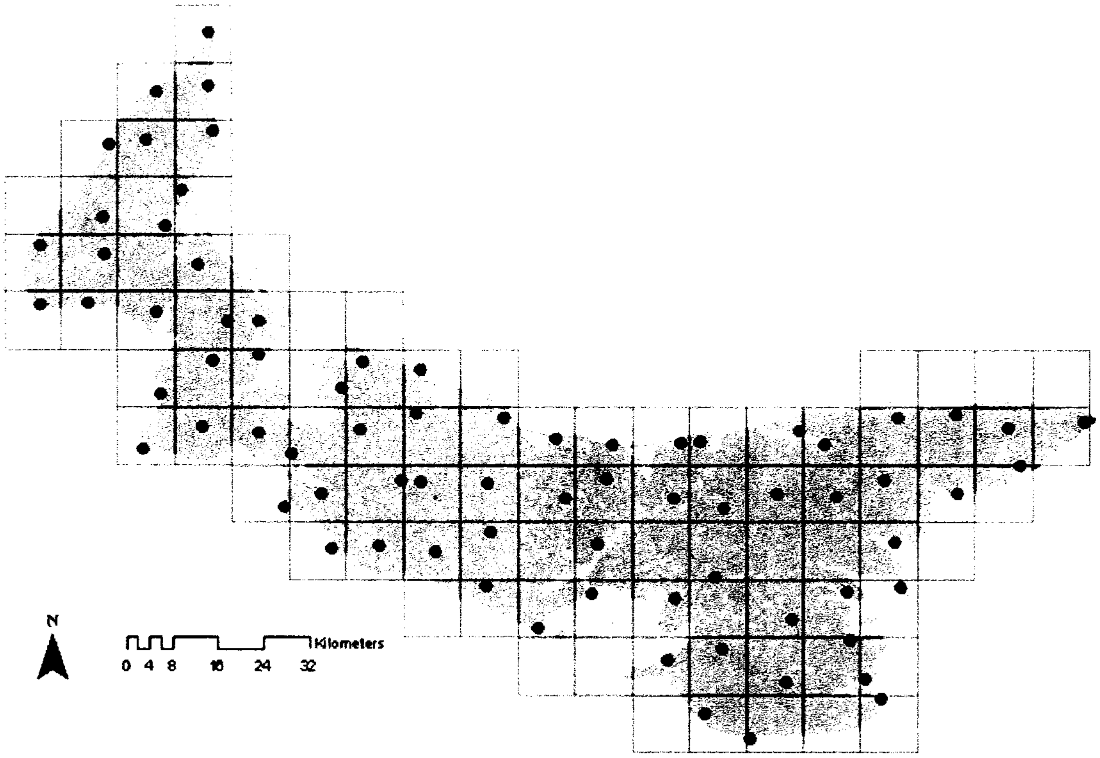


sample as much of the landscape of the island as possible, and each cell was sampled at least twice during the sampling period (Figure 4.2). Sampling proceeded in each location until samplers had detected at least 75% of the species expected to exist in the region, with 38% of the expected number being confirmed to breed within (Erskine, 1992). Sampling effort (hours per individual per sampling cell) varied depending on remoteness of the sampling cell and the availability of volunteers. Only confirmed sightings of breeding birds were used in this study, and confirmations were mostly made in July due to breeding cycles of species (Erskine, 1992). For identification, we followed Sibley and Monroe's (1990) avian taxonomic classification. Each avian species was also classified into a functional group according to habitat preferences and life history (*e.g.* landbird, shorebird, seabird, or waterfowl). Shorebirds are defined as avian species that spend the bulk of their life cycle on beaches and mudflats. In this study a seabird is defined as any bird that feeds from saltwater, and spends the bulk of its life cycle living on offshore islands or on coastal cliffs (Schreiber & Burger, 2001). Waterfowl are primarily large birds (~ 4000 g) of the Order Anseriformes that spend a significant part of their time in marshy wetlands or in the ocean along the coasts of the province. In this study, landbirds are defined as all birds that spend the bulk of their life history associated primarily with terrestrial ecosystems. Avian species were also classified based on diet into four trophic groups: carnivore, omnivore, herbivore, and insectivore (which in this study included species consuming arthropods and annelids). Body size (g) information was estimated from Dunning (1993).

Spatial Scale

The spatial scale at which this study was conducted was established using the

Figure 4.2. Map showing the 97 sampling cells (10 km x 10 km) that were used in this study, created using the RandomPoly extension of ArcView 3.3. The black dots represent the original sampling locations as detailed in the Atlas of the Breeding Birds of the Maritime Provinces (Erskine, 1992). There were avian sampling locations within 76 cells in the study.



same sampling grain that was used for the Maritime Breeding Bird Atlas (Erskine, 1992). Prince Edward Island was divided into 97 cells of 10 km x 10 km to maximize the number of sampling cells on the island that reported avian species observations (Figure 4.2). Sampling cells were generated using the "randompoly" extension of ArcView™ (ESRI, version 3.3, Redlands, CA), where a grid was generated and superimposed upon the study area determined in Erskine (1992). Sampling took place throughout the sampling cells, each of which was labelled with the name of the primary human community within the cell. While sampling was recorded as distributed throughout each cell, it was likely concentrated near to the main communities listed. Latitudinal and longitudinal coordinates of the main community of each sampling cell were added to the dataset, the surroundings of which presumably the greatest concentration of sampling was performed. These coordinates were used throughout the rest of the study where latitude and longitude were investigated.

Landscape Types

Land-cover types of the province were quantified using ArcView™ (ESRI, version 3.2, Redlands, CA) and ArcGIS™ (ESRI, version 8.1, Redlands, CA) based on the Prince Edward Island 1990 Forest Inventory. This inventory was created from aerial photographs that were taken during July and August 1990 at a scale of 1/17,500 scale, using false colour infrared film. Photographs were ground-truthed in order to determine the composition of landscape before being entered into the geographic information system database, particularly with regards to the species composition of the forests.

Because it was expected that there would be significant correlations among the metrics used to define landscape structure, we decided to conduct a Pearson correlation analysis to define land-cover layers. The relationships between a variety of land-cover types and avian species richness were examined in this fashion, and the land-covers that had the strongest associations with species richness were retained. Initially a finely grained analysis was attempted, using several different land-cover types (*e.g.* salt marsh, coniferous forest, potato field, etc.). Ultimately a coarse delineation of five land-cover types was chosen (agriculture, forest, human-used areas, roads, and wetlands) based on their better association with species richness. Another reason why we followed the methodology used in Chapter 3 was because we were interested in examining the effects of the same landscape variables that were associated with species richness.

Data Analysis

Following recommendations made by Turner *et al.* (2001a), we obtained metrics of area, shape and aggregation for each landscape type. These metrics were generated using Fragstats (*v.* 3.3; McGarigal & Marks, 1995), and consisted of the "percentage of landscape", the "patch-area fractal dimension", and the "clumpiness index". In order to use Fragstats, all land-cover layers were converted from a vector (polygon) format into a raster (pixelated) format using ArcGIS *v.* 8.1 (Spatial Analyst Extension). The "percentage of landscape" metric quantified the proportional abundance of each land-cover type per cell. The "clumpiness index" was used to assess aggregation of a given land-cover type within a sampling cell. Clumpiness ranges from a maximally disaggregated value to a completely aggregated value, and is calculated from examining adjacent pixels in a matrix. Adjacent pixels of similar land-cover type result in higher aggregation values. The precise calculation of clumpiness is equal to the proportional deviation from the proportion of like adjacencies that involve corresponding land-type from that expected under a spatially random distribution (McGarigal & Marks, 1995). If the proportion of these like adjacencies (G_i) is less than the proportion of the land-cover that comprises the focal land-type (P_i), and $P_i < 0.5$, then the clumpiness index equals G_i minus P_i, divided by P_i. If P_i is greater than 0.5, the clumpiness index equals $(G_i - P_i) / (1 - P_i)$. The "Perimeter-Area Fractal Dimension" was used to assess land-cover shape. Fractals have been used in landscape ecology for many years (Sugihara & May, 1990; Krummel *et al.*, 1997) and have been shown to be a powerful tool to describe spatial patterns of landscape elements (Spies *et al.*, 1994). We calculated the fractal dimension for all land-covers in each sampling cell to test if complexity in the shape of a land-type had any significant effect on species occurrence. (Equation 3.1).

$$\mathrm{PAFRAC} = \frac{2}{\dfrac{\left[n_i \sum_{j=1}^{n} (\ln p_{ij} \cdot \ln a_{ij})\right] - \left[\left(\sum_{j=1}^{n} \ln p_{ij}\right)\left(\sum_{j=1}^{n} \ln a_{ij}\right)\right]}{\left(n_i \sum_{j=1}^{n} \ln p_{ij}^{2}\right) - \left(\sum_{j=1}^{n} \ln p_{ij}\right)^{2}}}$$

Equation 3.1 Perimeter-Area Fractal Dimension. a_{ij} = area (m^2) of patch ij. p_{ij} = perimeter (m) of patch ij. n_i = number of patches in the landscape of land-cover i. (McGarigal *et al.*, 2002)

The perimeter-area fractal dimension equals 2 divided by the slope of the regression line obtained by regressing the logarithm of patch area (m^2) against the logarithm of patch perimeter (m). A fractal dimension of higher than one indicates an increasing complexity of the land-cover. The fractal dimension approaches 1 for land-covers composed of simple shapes such as circles and squares, and it approaches 2 for very complex shapes. The fractal dimension index is only meaningful when the log-log relationship between perimeter and area is constant over the complete range of areas, and so this relationship was tested as well.

Pearson correlation analysis was conducted among the variables generated by these metrics. Metrics that were significantly correlated to one another with $r \geq 0.7$ were individually plotted against species richness using simple linear regression. Variables with a stronger relation to species richness as defined in the previous chapter were kept and used in subsequent analyses. All other variables that were not related to one another to a strong a degree (*i.e.* $r < 0.7$) were kept in the analyses. It should be noted that the remaining variables are likely to have some correlation, and so should not be regarded as completely independent. Therefore, interpretations derived from these variables must be made with caution.

In this study, occurrence is defined as the presence of a species in a landscape, irrespective of how many individuals of that species are present. We calculated the percentage of occurrence for each bird species by counting the number of sampling cells each species was observed in. Following Gaston & Blackburn (2000), we only included species that had occupancy of greater than 10% and less than 90%. Avian species with less than 10% occupancy were considered in this study to be too spatially restricted to be adequately assessed at the spatial scale of the landscape. Species with greater than 90% occupancy may have too abundant to see emerging patterns in their occurrence, which is why they were also excluded from the study. Though excluding the species with less than 10% occurrence may remove rare species from the analysis that may benefit from this kind of study, interpretations that could be made from so few data points would be vague at best.

The occurrence of avian species was related to the landscape structure of Prince Edward Island using a series of stepwise forward logistic regression analyses. This and all subsequent data analyses were performed using the SAS statistical software package (SAS Institute, Inc., version 8.02, Carey, NC). We developed an explanatory model for each one of the examined avian species. Explanatory variables were selected using a significance level where $p = 0.05$, and were chosen from all uncorrelated land-cover variables as well as sampling effort.

To compare and assess the significance of each of the logistic models, the likelihood-ratio test was used. The likelihood ratio test of a model determines the significance of the difference between -2(log-likelihood) of a candidate model and -2(log-likelihood) for the null model. This is a comparison of a model that only has the constant with a model that that has the constant plus all of the predictive variables. In the case in which predictors are not significantly related to the outcome found when the variables are added to the model, the predictors are considered to be unrelated to the outcome.

We used the Hosmer and Lemeshow goodness-of-fit test to determine whether the distribution of probabilities produced by our model fit the logistic probability distribution (Hosmer & Lemeshow, 1989). When the Hosmer and Lemeshow goodness-of-fit statistic exceeded 0.05, we did not reject the null hypothesis that there is no significant difference between observed and model-predicted values. This implies that the estimate of the model fits the data at an acceptable level. Avian species that were found to be significant for this test ($p \leq 0.05$) did not fit the logistic probability distribution, and so did not have well-fitting models.

In this study, the logistic R^2 used was Nagelkerke's R^2 (Nagelkerke, 1991). Nagelkerke's R^2 is a standard output in statistical programs, and is one of the most commonly used measures of strength of association in logistic regression studies (Guisan & Zimmermann, 2000; Harrell, 2001). This type of R^2 is an attempt to imitate the interpretation of multiple R^2 values based on the likelihood, and the measure is divided by its maximum to obtain values varying between 0 and 1. Nagelkerke's R^2 will tend to run lower than an equivalent ordinary least-square R^2. Possible trends in the importance of specific landscape variables in relation to species occurrence were also examined from the perspective of functional and trophic groups. This was accomplished visually by a direct examination of significant land-cover variables within all logistic models of occurrence.

4.4. RESULTS

The five land-cover types (*e.g.*, agriculture, forest, human-used areas, roads and wetlands) used in this study were the best correlated to avian species richness as determined in Chapter 3. Thirteen land-cover variables were used in this study, with three variables (percentage of agriculture, fractal dimension of roads, and clumpiness of wetlands) being dropped due to high correlations ($r > 0.7$; $p \leq 0.05$) with the remaining land-cover variables (Appendix 2; Appendix 3). Descriptive statistics of all explanatory variables used in the study are presented in Table 4.2. Sampling effort and total area were significant predictors of species occurrence in many of the models throughout this chapter. These two variables were included in the analyses as a correction factor to account for the time spent sampling and for the amount of land in a cell, in order to more accurately reflect species richness in a given area. Many of the sampling cells had

Table 4.1 Land-cover variables examined. Abbreviations are provided to assist in explaining statistical models in subsequent tables.

Land-Cover Variable	Abbreviation
Total area of land-cover in cell ($\log_{10}$)	TA ($\log_{10}$)
Fractal Dimension of Agriculture	PAFracAgr
Clumpiness of Agriculture	ClumpyAgr
Percentage of Forest	PLandFor
Fractal Dimension of Forest	PAFracFor
Clumpiness of Forest	ClumpyFor
Percentage of Human-used lands	PLandInf
Fractal Dimension of Human-used lands	PAFracInf
Clumpiness of Human-used lands	ClumpyInf
Percentage of Wetland	PLandWet
Fractal Dimension of Wetlands	PAFracWet
Percentage of Roads	PLandRoad

Table 4.2 Descriptive statistics of variables examined.

Variable	N	Mean	Standard Error of Mean	Minimum	Median	Maximum
Total Area (km^2)	76	6672	359	322	7155	10000
Total area (km^2; log$_{10}$)	76	3.744	0.0361	2.5075	3.8546	4
Fractal Dimension of Agriculture	75	1.2605	0.00444	1.1773	1.2686	1.3497
Clumpiness of Agriculture	76	0.94431	0.00131	0.9139	0.9459	0.9638
Percentage of Forest	76	47.28	2.3	11.35	48.36	81.28
Fractal Dimension of Forest	76	1.2777	0.00595	1.1526	1.2817	1.3806
Clumpiness of Forest	76	0.94127	0.00119	0.9068	0.9428	0.9669
Percentage of Human-used lands	76	6.423	0.554	1.121	4.688	31.096
Fractal Dimension of Human used lands	75	1.3022	0.00597	1.1859	1.2987	1.4389
Clumpiness of Human-used lands	76	0.9169	0.00156	0.8879	0.9154	0.9536
Percentage of Wetlands	76	5.373	0.654	0.1	3.815	35.462
Fractal Dimension of Wetlands	75	1.2864	0.00736	1.1894	1.277	1.5005
Percentage of Roads	76	2.062	0.043	1.1567	2.0781	2.9397
Clumpiness of Roads	76	0.70023	0.00165	0.6687	0.70145	0.7396
Longitude	76	-63.308	0.0761	-64.374	-63.346	-61.992
Latitude	76	46.419	0.028	45.955	46.41	47.057
Latitude X Longitude	76	-2938.8	4.9	-3011.5	-2934.5	-2874.1
Minimum body size of pooled species (g)	76	5.915	0.311	3.15	6.2	14.1
Maximum body size in assemblage (g)	76	2355	161	114	1659	4740
Mean body size in assemblage (g)	76	234.6	11.5	39.1	225.7	669.7

Table 4.2 (Continued) Descriptive statistics of variables examined.

Variable	N	Mean	Standard Error of Mean	Minimum	Median	Maximum
Sampling Effort (Hours/Individual/Cell)	76	35.21	3.04	2	35	100
Sampling Effort ($\log_{10}$)	76	1.3901	0.0491	0.301	1.5441	2
Pooled Species Richness	76	51.01	2.61	9	51.5	98
Species Richness of Landbirds	76	42.34	2.28	8	40	81
Species Richness of Seabirds	32	2.188	0.244	1	2	7
Species Richness of Shorebirds	66	2.924	0.189	1	3	8
Species Richness of Waterfowl	68	5.824	0.359	1	5.5	12
Mean body size of pooled species (g; $\log_{10}$)	76	1.751	0.0179	1.3798	1.7551	2.2733
Mean body size of pooled species (g; $\log_{10})^2$	76	3.09	0.0645	1.9037	3.0804	5.1678
Mean body size of landbirds (g; $\log_{10}$)	76	2.1147	0.025	1.4862	2.1133	2.6968
Mean body size of landbirds (g; $\log_{10})^2$	76	4.519	0.104	2.209	4.466	7.273
Mean body size of seabirds (g; $\log_{10}$)	32	2.7584	0.0769	2.0607	2.9509	3.3242
Mean body size of seabirds (g; $\log_{10})^2$	32	7.792	0.401	4.246	8.708	11.05
Mean body size of shorebirds (g; $\log_{10}$)	66	0.4043	0.0297	0	0.4771	0.9031
Mean body size of shorebirds (g; $\log_{10})^2$	66	0.221	0.0233	0	0.2276	0.8156
Mean body size of waterfowl (g; $\log_{10}$)	68	2.924	0.0132	2.5866	2.904	3.1415
Mean body size of shorebirds (g; $\log_{10})^2$	68	8.5616	0.0769	6.6904	8.4332	9.8692

a high proportion of land (29 with greater than 90% land) in relation to the amount of ocean, while 11 cells had less than 10% land. As time was spent making observations in a sampling cell, samplers eventually reached the maximum number of species they were likely to find, at which point sampling ceased. This sampling trend was reflected in the results obtained in this study. A total of 156 breeding bird species were recorded in Prince Edward Island (Appendix 1) in 76 sampling cells (Figure 4.3.). Of these species, 52 were observed to occur in less than 10% of Prince Edward Island, while 2 species (*Melospiza melodia* and *Turdus migratorius*) covered an area of greater than 90%, leaving 102 species to be analyzed in this study. Both before and after excluding these species from subsequent analyses, the occurrence of avian species exhibited a right-skewed frequency distribution (Figure 4.4.), indicating that there are many more species with a low occurrence than a high occurrence.

Logistic regression analysis resulted in significant associations between occurrence and our explanatory variables for 48 avian species, according to the likelihood-ratio test. Of these 48 species, 47 were considered to adequately fit the data based upon Hosmer and Lemeshow's goodness-of-fit test. Of the 47 remaining avian species, 19 were significantly associated only to total area and/or sampling effort, with no significant associations with any of the land-cover variables. The 29 species that remained were considered to be significantly associated with landscape structure (Table 4.3.1 and 4.3.2), and R^2 varied from 0.12 to 0.37.

With the exception of the aggregation of wetland patches, all landscape metrics examined in this study were associated to the occurrence of at least one avian species (Table 4.4). However, no single land-cover variable was significantly related to more than six species. Due to the correlations discovered in the land-cover metrics, it may be

Figure 4.3. The 76 sampling cells of 10 km x 10 km where avian species were observed in this study. The sampling cells are shown overlaying the landscape composition of Prince Edward Island. Blank spaces were non-sampled areas.

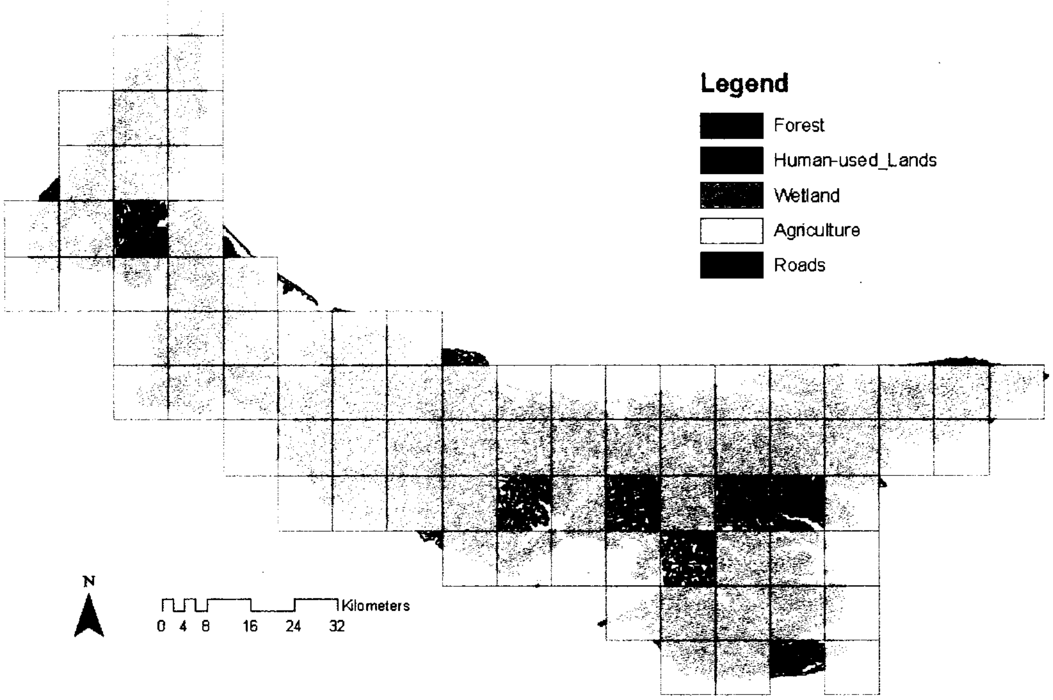


Figure 4.4. Frequency distribution of the percentage of occurrence of avian species breeding on Prince Edward Island. This figure includes all species observed in the study, and illustrates the amount of land each species was found to occur within.

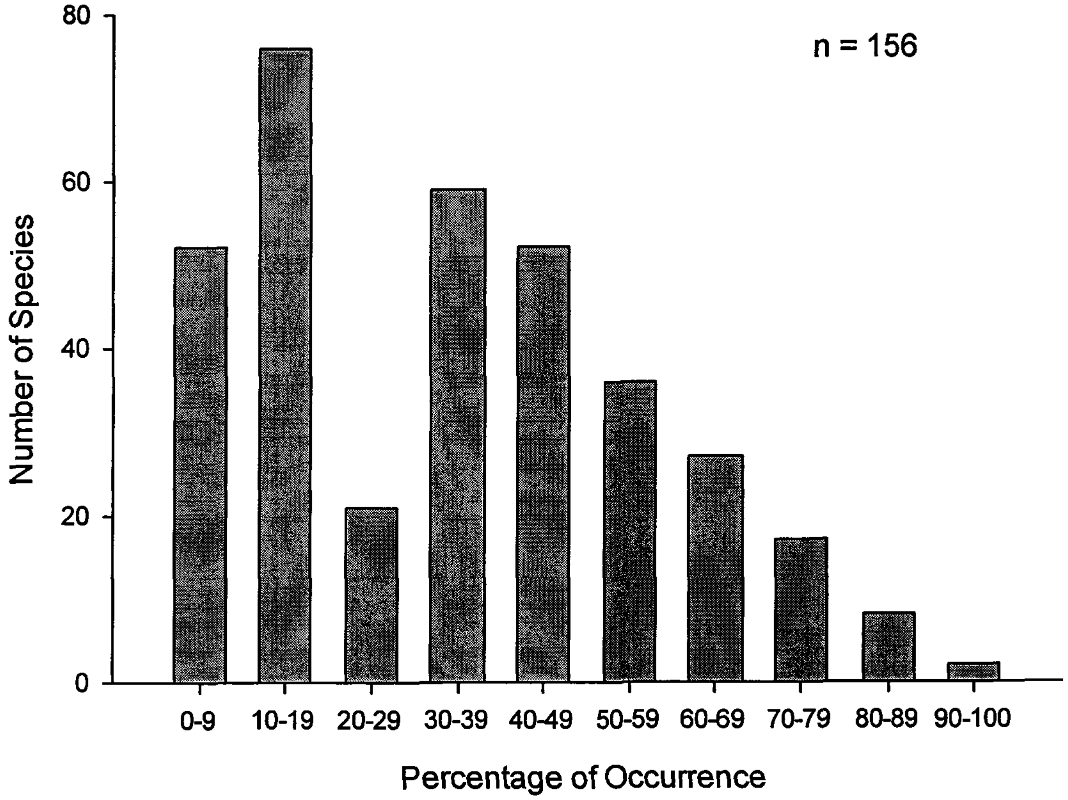


Table 4.3.1 Avian species models developed in this study using logistic regression, sorted by functional group (L = Landbird, W = Waterfowl, Sh = Shorebird, Se = Seabird). Included in this table is the list of variables used in this study (See Table 4.1. for the key to abbreviations). ClumpyWet was nonsignificant for all species, and is not shown in this table. Variables chosen in models are shown as coefficients, with signs to indicate the effect (positive or negative) on species occurrence. Also included is sampling effort (Hours per individual per sampling cell) and the model Y-intercept. Model statistics such as Hosmer and Lemeshow's goodness-of-fit test and the likelihood ratio test are shown in the following tables. Table is continued on subsequent page.

Species	Functional Group	Model Y- Intercept	Sampling Effort ($\log_{10}$)	TA ($\log_{10}$)	PAFracAgr	ClumpyAgr	PLandFor	PAFracFor	ClumpyFor	PLandInf	PAFracInf	ClumpyInf	PLandWet	PAFracWet	PLandRoad
Bubo virginianus	L	87.99	-0.53	.	.	.	.	.	-92.87	.	.	.	-0.17	.	.
Haliaeetus leucocephalus	L	9.16	3.04	.	.	.	0.04	.	.	.	.	.	.	-13.28	.
Strix varia	L	152.31	-0.33	.	.	.	.	.	-162.38	-0.16	.	.	.	.	.
Perdix perdix	L	58.85	0.93	.	.	-64.74	.	.	.	.	.	.	.	.	.
Contopus virens	L	-16.11	1.35	.	.	.	.	11.21	.	.	.	.	.	.	.
Dendroica fusca	L	8.21	1.96	.	.	.	.	.	.	.	.	.	.	-9.10	.
Dendroica pensylvanica	L	14.32	1.63	.	.	.	.	-14.00	.	.	.	.	.	.	.
Dendroica virens	L	-1.75	1.57	.	.	.	.	.	.	-0.16	.	.	.	.	.
Passerculus sandwichensis	L	-28.26	2.00	2.19	.	.	.	15.29	.	.	.	.	.	.	.
Regulus satrapa	L	87.65	0.13	3.57	.	.	.	-19.40	-81.48	.	.	.	.	.	.
Sphyrapicus varius	L	69.10	0.39	.	.	-71.13	.	.	.	.	.	.	.	.	-1.81
Vermivora ruficapilla	L	-3.86	0.82	.	.	.	0.03	.	.	.	.	.	.	.	.
Dumetella carolinensis	L	-5.24	1.35	.	.	.	0.04	.	.	.	.	.	.	.	.

Table 4.3.1 Continued

Species	Functional Group	Model Y- Intercept	Sampling Effort (log$_{10}$)	TA (log$_{10}$)	PAFracAgr	ClumpyAgr	PLandFor	PAFracFor	ClumpyFor	PLandInf	PAFracInf	ClumpyInf	PLandWet	PAFracWet	PLandRoad
Euphagus carolinus	L	0.24	1.46	.	.	.	.	.	.	.	.	.	.	.	-2.11
Melospiza georgiana	L	-15.73	0.72	.	.	.	.	.	.	.	.	.	.	11.68	.
Molothrus ater	L	85.77	1.29	.	.	-76.86	.	.	.	.	-12.15	.	.	.	.
Parula americana	L	6.49	1.15	2.03	.	.	.	.	.	.	.	.	.	-12.22	.
Passer domesticus	L	20.26	0.43	.	.	.	.	.	.	.	.	.	.	-15.20	.
Phasianus colchicus	L	74.89	0.27	.	.	.	.	.	-82.16	.	.	.	.	.	.
Pheucticus iudovicianus	L	1.14	0.76	.	.	.	-0.03	.	.	.	.	.	.	.	.
Quiscalus quiscula	L	56.42	1.10	.	-42.81	.	.	.	.	.	.	.	.	.	.
Sturnus vulgaris	L	-5.62	1.00	.	.	.	.	.	.	.	.	.	.	.	3.60
Colaptes auratus	Sh	36.01	0.65	.	-27.86	.	.	.	.	.	.	.	.	.	.
Scoiopax minor	Sh	59.43	-1.03	2.95	.	.	.	.	.	.	.	-77.03	.	.	.
Catoptrophorus semipalmatus	Sh	64.55	0.84	.	.	.	.	.	.	.	.	-73.83	.	.	.
Gallinago delicata	Sh	71.70	0.47	.	.	.	.	.	-76.59	.	.	.	.	.	.
Mergus serrator	W	-67.32	-0.67	.	-19.79	.	.	.	96.29	.	.	.	0.16	.	.
Anas americana	W	-0.12	2.09	.	.	.	.	.	.	.	.	.	.	.	-1.42
Anas crecca	W	24.33	1.06	.	-16.50	.	.	.	.	.	.	.	.	.	-2.16

Table 4.3.2. Table depicting model statistics for species detailed in Table 4.3.1, sorted by functional group. The likelihood ratio test (model accepted if $p \leq 0.05$) determines the significance of the nested model in comparison to the constant-only model. The Hosmer-Lemeshow test determines whether the model fits the data (model fits if score ≥ 0.05). Nagelkerke's R^2 provides an approximation of the amount of variance explained in the model. Characteristics of the species are shown, such as Functional Group (L = Landbird, W = Waterfowl, Sh = Shorebird, Se = Seabird), Trophic Group (C = Carnivore, O = Omnivore, H = Herbivore, I = Insectivore).

Species	Likelihood ratio test	Hosmer-Lemeshow	Nagelkerke's R^2	Functional Group	Trophic Group
Bubo virginianus	0.006	0.538	0.22	L	C
Haliaeetus leucocephalus	0.001	0.445	0.3	L	C
Strix varia	0.002	0.964	0.31	L	C
Perdix perdix	0.004	0.798	0.19	L	H
Contopus virens	0.004	0.481	0.18	L	I
Dendroica fusca	0.006	0.685	0.17	L	I
Dendroica pensylvanica	0.008	0.387	0.18	L	I
Dendroica virens	0.002	0.679	0.2	L	I
Passerculus sandwichensis	0.002	0.281	0.35	L	I
Regulus satrapa	0.001	0.831	0.3	L	I
Sphyrapicus varius	0.020	0.481	0.19	L	I
Vermivora ruficapilla	0.039	0.729	0.12	L	I
Dumetella carolinensis	0.034	0.318	0.14	L	O
Euphagus carolinus	0.041	0.443	0.15	L	O
Melospiza georgiana	0.007	0.334	0.17	L	O
Molothrus ater	0.001	0.594	0.26	L	O
Parula americana	0.004	0.765	0.22	L	O
Passer domesticus	0.004	0.174	0.21	L	O
Phasianus colchicus	0.053	0.780	0.14	L	O
Pheucticus ludovicianus	0.035	0.126	0.12	L	O
Quiscalus quiscula	0.015	0.062	0.31	L	O
Sturnus vulgaris	0.019	0.692	0.23	L	O
Colaptes auratus	0.005	0.670	0.21	Sh	I
Scolopax minor	0.003	0.674	0.26	Sh	I
Catoptrophorus semipalmatus	0.026	0.158	0.16	Sh	O
Gallinago delicata	0.007	0.573	0.17	Sh	O
Mergus serrator	0.000	0.641	0.37	W	C
Anas americana	0.043	0.857	0.22	W	O
Anas crecca	0.002	0.142	0.24	W	O

Table 4.4. Table listing the number of times each land-cover metric was significantly associated to avian species occurrence in this study. Of the total observations, positive and negative associations are also listed.

Land-Cover Variable	Total number of species associated with variable	Number of positive associations	Number of negative associations
Percentage of Forest	4	3	1
Percentage of Human-used land	2	0	2
Percentage of Wetland	2	1	1
Percentage of Roads	5	1	4
Fractal Dimension of Agriculture	4	0	4
Fractal Dimension of Forest	4	2	2
Fractal Dimension of Human-used land	1	0	1
Fractal Dimension of Wetlands	5	1	4
Clumpiness of Agriculture	3	0	3
Clumpiness of Forest	6	1	5
Clumpiness of Human-used land	2	0	2
Clumpiness of Wetland	0	0	0

more informative to examine the relationships between landscape structure and species occurrence in terms of the type of land: Forest variables were significant among 13 species, agriculture and wetland variables were both significant for 7 species, while human-used lands and roads were significant for 5 species each.

Functional Groups and Trophic Groups

Due to the small amount of avian species for which occurrence was significantly explained in this study, trends were difficult to examine in terms of functional group (Table 4.3.1 and 4.3.2) and trophic group (Table 4.5.1 and 4.5.2). The most apparent trends were of which birds were predicted, rather than which variables were found to be important.

Out of the 29 species for which occurrence models were developed, 22 were landbirds, 4 were shorebirds, 3 were waterfowl, and no seabirds were significantly related to land-cover at all. Far more landbirds were associated with landscape structure than any other group, with many of these species being forest species of the Order Passeriformes. This is expected, as there are far more land-bird species on the island than any of the other functional groups. Although there were individual species differences, the 22 landbird species tended to relate to agricultural and forest variables more than other land-cover types.

The association between occurrence and the land-cover metrics did not show any discernable pattern among species when occurrence was examined by trophic group. Of the 29 species that showed association with the land-cover metrics, 4 were carnivores, 10 were insectivores, 14 were omnivores, and one was an herbivore. These insectivores and omnivores were primarily composed of the Order Passeriformes. Species did not appear

Table 4.5.1 Avian species models developed in this study using logistic regression, sorted by trophic group (C = Carnivore, O = Omnivore, H = Herbivore, I = Insectivore). Included in this table is the list of variables used in this study (See Table 4.1. for the key to abbreviations). ClumpyWet was nonsignificant for all species, and is not shown in this table. Variables chosen in models are shown as coefficients, with signs to indicate the effect (positive or negative) on species occurrence. Also included is sampling effort (Hours per individual per sampling cell) and the model Y-intercept. Model statistics such as Hosmer and Lemeshow's goodness-of-fit test and the likelihood ratio test are shown in the following tables. Table is continued on subsequent page.

Species	Trophic Group	Model Y- Intercept	Sampling Effort ($\log_{10}$)	TA ($\log_{10}$)	PAFracAgr	ClumpyAgr	PLandFor	PAFracFor	ClumpyFor	PLandInf	PAFracInf	ClumpyInf	PLandWet	PAFracWet	PLandRoad
Bubo virginianus	C	87.99	-0.53	.	.	.	.	.	-92.87	.	.	.	-0.17	.	.
Haliaeetus leucocephalus	C	9.16	3.04	.	.	.	0.04	.	.	.	.	.	.	-13.28	.
Strix varia	C	152.31	-0.33	.	.	.	.	.	-162.38	-0.16	.	.	.	.	.
Mergus serrator	C	-67.32	-0.67	.	-19.79	.	.	.	96.29	.	.	.	0.16	.	.
Perdix perdix	H	58.85	0.93	.	.	-64.74	.	.	.	.	.	.	.	.	.
Contopus virens	I	-16.11	1.35	.	.	.	.	11.21	.	.	.	.	.	.	.
Dendroica fusca	I	8.21	1.96	.	.	.	.	.	.	.	.	.	.	-9.10	.
Dendroica pensylvanica	I	14.32	1.63	.	.	.	.	-14.00	.	.	.	.	.	.	.
Dendroica virens	I	-1.75	1.57	.	.	.	.	.	.	-0.16	.	.	.	.	.
Passerculus sandwichensis	I	-28.26	2.00	2.19	.	.	.	15.29	.	.	.	.	.	.	.
Regulus satrapa	I	87.65	0.13	3.57	.	.	.	-19.40	-81.48	.	.	.	.	.	.
Sphyrapicus varius	I	69.10	0.39	.	.	-71.13	.	.	.	.	.	.	.	.	-1.81
Vermivora ruficapilla	I	-3.86	0.82	.	.	.	0.03	.	.	.	.	.	.	.	.
Colaptes auratus	I	36.01	0.65	.	-27.86	.	.	.	.	.	.	.	.	.	.

Table 4.5.1 Continued

Species	Trophic Group	Model Y- Intercept	Sampling Effort ($\log_{10}$)	TA ($\log_{10}$)	PAFracAgr	ClumpyAgr	PLandFor	PAFracFor	ClumpyFor	PLandInf	PAFracInf	ClumpyInf	PLandWet	PAFracWet	PLandRoad
Scolopax minor	I	59.43	-1.03	2.95	.	.	.	.	.	.	.	-77.03	.	.	.
Dumetella carolinensis	O	-5.24	1.35	.	.	.	0.04	.	.	.	.	.	.	.	.
Euphagus carolinus	O	0.24	1.46	.	.	.	.	.	.	.	.	.	.	.	-2.11
Melospiza georgiana	O	-15.73	0.72	.	.	.	.	.	.	.	.	.	.	11.68	.
Molothrus ater	O	85.77	1.29	.	.	-76.86	.	.	.	.	-12.15	.	.	.	.
Parula americana	O	6.49	1.15	2.03	.	.	.	.	.	.	.	.	.	-12.22	.
Passer domesticus	O	20.26	0.43	.	.	.	.	.	.	.	.	.	.	-15.20	.
Phasianus colchicus	O	74.89	0.27	.	.	.	.	.	-82.16	.	.	.	.	.	.
Pheucticus ludovicianus	O	1.14	0.76	.	.	.	-0.03	.	.	.	.	.	.	.	.
Quiscalus quiscula	O	56.42	1.10	.	-42.81	.	.	.	.	.	.	.	.	.	.
Sturnus vulgaris	O	-5.62	1.00	.	.	.	.	.	.	.	.	.	.	.	3.60
Catoptrophorus semipalmatus	O	64.55	0.84	.	.	.	.	.	.	.	.	-73.83	.	.	.
Gallinago delicata	O	71.70	0.47	.	.	.	.	.	-76.59	.	.	.	.	.	.
Anas americana	O	-0.12	2.09	.	.	.	.	.	.	.	.	.	.	.	-1.42
Anas crecca	O	24.33	1.06	.	-16.50	.	.	.	.	.	.	.	.	.	-2.16

Table 4.5.2 Table depicting model statistics for species detailed in Table 4.4.1, sorted by trophic group. The likelihood ratio test (model accepted if $p \leq 0.05$) determines the significance of the nested model in comparison to the constant-only model. The Hosmer-Lemeshow test determines whether the model fits the data (model fits if score ≥ 0.05). Nagelkerke's R^2 provides an approximation of the amount of variance explained in the model. Characteristics of the species are shown, such as Functional Group (L = Landbird, W = Waterfowl, Sh = Shorebird, Se = Seabird), Trophic Group (C = Carnivore, O = Omnivore, H = Herbivore, I = Insectivore). Table is continued on subsequent pages.

Species	Likelihood ratio test	Hosmer-Lemeshow	Nagelkerke's R^2	Functional Group	Trophic Group
Bubo virginianus	0.006	0.538	0.22	C	L
Haliaeetus leucocephalus	0.001	0.445	0.3	C	L
Strix varia	0.002	0.964	0.31	C	L
Mergus serrator	0.000	0.641	0.37	C	W
Perdix perdix	0.004	0.798	0.19	H	L
Contopus virens	0.004	0.481	0.18	I	L
Dendroica fusca	0.006	0.685	0.17	I	L
Dendroica pensylvanica	0.008	0.387	0.18	I	L
Dendroica virens	0.002	0.679	0.2	I	L
Passerculus sandwichensis	0.002	0.281	0.35	I	L
Regulus satrapa	0.001	0.831	0.3	I	L
Sphyrapicus varius	0.020	0.481	0.19	I	L
Vermivora ruficapilla	0.039	0.729	0.12	I	L
Colaptes auratus	0.005	0.670	0.21	I	Sh
Scolopax minor	0.003	0.674	0.26	I	Sh
Dumetella carolinensis	0.034	0.318	0.14	O	L
Euphagus carolinus	0.041	0.443	0.15	O	L
Melospiza georgiana	0.007	0.334	0.17	O	L
Molothrus ater	0.001	0.594	0.26	O	L
Parula americana	0.004	0.765	0.22	O	L
Passer domesticus	0.004	0.174	0.21	O	L
Phasianus colchicus	0.053	0.780	0.14	O	L
Pheucticus ludovicianus	0.035	0.126	0.12	O	L
Quiscalus quiscula	0.015	0.062	0.31	O	L
Spizella passerina	0.010	0.452	0.12	O	L
Sturnus vulgaris	0.019	0.692	0.23	O	L
Catoptrophorus semipalmatus	0.026	0.158	0.16	O	Sh
Gallinago delicata	0.007	0.573	0.17	O	Sh
Anas americana	0.043	0.857	0.22	O	W
Anas crecca	0.002	0.142	0.24	O	W

to respond to landscape structure in any discernable pattern, although insectivores were associated to marginally more forest-related variables than the others.

4.5 DISCUSSION

Overall, this study showed that landscape structure significantly affected the occurrence of many avian species in Prince Edward Island, and to varying degrees. We explored the effects of several land-cover metrics on the occurrence of avian species known to breed in Prince Edward Island. The occurrence of 29 out of 156 avian species was associated with landscape structure, which was considerably less than was anticipated. Earlier avian studies on Prince Edward Island were conducted at small spatial scales (Makepeace, 1989). While the findings in these studies were suitable to answer specific questions regarding small-scale occurrence and watershed-level issues, they were not designed to examine questions about broad-scale variability in the occurrence of species (Weins, 1989). Other studies focused on particular focal groups such as waterfowl, and ignored the remaining avifauna on the island (Dibblee & Guignion, 1974; Bateman & Dibblee, 2000; Stevens *et al.*, 2003). Thus, this is the first study that was designed to examine the patterns of occurrence of avian species at a large or regional spatial scale in Prince Edward Island.

Fifty-four species were removed from the analysis because they occurred in less than 10% or more than 90% of our sampling cells. Most species that occurred in less than 10% of sampling cells were rare (23) or uncommon (13) as denoted by ACCDC (2004; Table 4.6), while a few were possibly under sampled. Most of the species that were excluded from this study were rare or uncommon. Therefore, the findings in this study do not reflect the patterns of occurrence of rare avian species. In further studies, a larger

Table 4.6. List of species removed from the analysis due to high (> 90%) or low (< 10%) occurrence, in alphabetical order. Characteristics of the species are shown, such as Functional Group (L = Landbird, W = Waterfowl, Sh = Shorebird, Se = Seabird), Trophic Group (C = Carnivore, O = Omnivore, H = Herbivore, I = Insectivore) and mean body size. S-Ranks denote provincial status from ACCDC (2004). S-rankings are: (S1) extremely rare; (S2) rare; (S3) uncommon; (S4) usually widespread; (S5) demonstrably widespread; (SE) exotic; (SZ) zero occurrences; (B) breedings; (N) non-breeding; (S?) Unranked; (SA) Accidental; (SZ) long-distance migrant. Multiple entries indicate no consensus on S-Rank delineation. Table is continued on subsequent page.

Species	Proportion of Occupancy	Functional Group	Trophic Group	S-Rank
Accipiter gentilis	0.09	L	C	S4B
Aegolius acadicus	0.09	L	C	S5B,S2N
Anas clypeata	0.06	W	O	S3B
Ardea herodias	0.08	Sh	C	S4B
Asio flammeus	0.02	L	C	S1,S2B
Asio otus	0.01	L	C	S1,S2
Aythya americana	0.02	W	H	SAN
Aythya marila	0.01	W	O	SAB,S3M,S1N
Bartramia longicauda	0.02	Sh	I	S1B
Buteo jamaicensis	0.05	L	C	S2B
Buteo platypterus	0.01	L	C	S1B
Carduelis pinus	0.08	L	H	S2B,S3,S4N
Carpodacus mexicanus	0.03	L	H	SE
Catharus minimus	0.02	L	O	SAN
Cepphus grylle	0.07	Se	C	S2B
Certhia americana	0.07	L	I	S5B
Chaetura pelagica	0.01	L	I	S1B
Charadrius semipalmatus	0.03	Sh	I	S5N
Chordeiles minor	0.03	L	I	S1,S2B
Coccyzus erythropthalmus	0.02	L	I	S4B
Dendroica caerulescens	0.07	L	I	S4B
Dendroica striata	0.01	L	I	SAN
Dryocopus pileatus	0.02	L	I	S2
Empidonax flaviventris	0.07	L	I	S5B
Empidonax traillii	0.02	L	I	S1B

Table 4.6 Continued

Species	Proportion of Occupancy	Functional Group	Trophic Group	S-Rank
Eremophila alpestris	0.02	L	O	S2B,S5N
Fulica americana	0.01	L	O	S2B
Hirundo pyrrhonota	0.01	L	I	S3B
Icterus galbula	0.05	L	I	S2B
Larus argentatus	0.08	Se	O	S5B,S5N
Larus delawarensis	0.03	Se	O	S1B,S5N
Loxia curvirostra	0.01	L	H	S2,S3
Melospiza melodia	0.93	L	H	S5B
Mergus merganser	0.01	W	C	S4N
Mimus polyglottos	0.03	L	O	S2B
Myiarchus crinitus	0.01	L	I	SAB
Numida meleagris	0.01	L	H	S
Passerella iliaca	0.02	L	I	SZB
Perisoreus canadensis	0.09	L	O	S3
Phalacrocorax auritus	0.08	Se	C	S5B
Phalacrocorax carbo	0.08	Se	C	S3B
Picoides arcticus	0.09	L	I	S3
Picoides tridactylus dorsa	0.01	L	I	S1
Pinicola enucleator	0.04	L	O	S2,S3
Pooecetes gramineus	0.06	L	H	S1,S2B
Rallus limicola	0.02	L	O	S2B
Seiurus noveboracensis	0.08	L	C	S3B
Sialia sialis	0.02	L	I	S1B
Sitta carolinensis	0.06	L	H	S5
Sterna paradisaea	0.05	Se	O	S1?B
Turdus migratorius	0.93	L	O	S5B
Tympanuchus phasianellus	0.05	L	H	SE
Vireo philadelphicus	0.04	L	I	S2B
Wilsonia pusilla	0.04	L	I	S4B

spatial scale extent may be needed to examine these species in more detail (Vaughan & Ormerod, 2003).

Similarly to the previous chapter in this thesis, landscape structure explained less of the variation in species occurrence than we had originally expected. The relatively low number of species successfully associated with landscape structure in our study may be related to the spatial scale of our analysis, inadequate delineation of the land-covers, or there was simply a true weak association. It is possible that more finely divided delineations may have yielded more accurate explanations, particularly in the wetland land-type, and possibly in the forest land-type. Avian species may respond differently to bogs than they would to marshes and salt marshes, and to deciduous forests differently than to coniferous forests. The difficulty in defining land-types in this fashion lies in finding metrics to explain their attributes. For example, defining coniferous and deciduous stands as different land-types may result in a perceived discontinuity of land-cover that may not truly exist. The edges between two closely-related land-types may not be as clearly defined as in coarser landscape delineations. Because of this, the shape as defined by the fractal dimension may not be as accurate when land-types are delineated in too fine a fashion, and the aggregation of habitat as defined by the clumpiness metric becomes a less clear measure. The five land-cover types used in this study were the most distinguishable habitat types that we could delineate using indices of size, shape, and aggregation, and adding or removing different land-cover types would have to be done with caution.

Functional Groups

Shorebird species can be common on Prince Edward Island, due to the broad, sandy shores surrounding most of the province. In general, landscape structure was not a major determinant of the occurrence of shorebird species. Also, because only four species were significantly associated with landscape structure, no meaningful trends in important variables could be assessed. This is not to imply that landscape structure is not important to this functional group, but that precisely which metrics that directly affect occurrence are not possible to interpret using our data and methodology. Human-influenced land in the form of recreational beaches has known to have a strong effect on the survival of shorebird populations (Flemming *et al.*, 1988; MacIvor *et al.*, 1990), but this was not reflected in our results.

In Prince Edward Island, seabirds are normally colonial nesters that live on offshore islands, cliff-faces on the North shore of Prince Edward Island (Schreiber & Burger, 2001). Few seabirds are known to breed on Prince Edward Island, and none were significantly associated with landscape structure in this study. The most common species are the seagulls (*Larus* spp.) that are found ubiquitously throughout the island, and cormorants *(Phalacrocorax auritus* and *Phalacrocorax carbo*), that live in colonies on cliff-faces of the northern shore of Prince Edward Island (Erskine, 1992). Habitat loss and fragmentation due to agriculture and forestry is not likely to have adverse effects upon colonial cliff-nesting seabirds such as cormorants, simply because they are not generally in the same regions. This may explain why we didn't find significant associations between the land-cover metrics species studied here. However, some seabird species (*e.g. Brachyramphus marmoratu*; Raphael *et al.*, 2002) are known to breed inland, in places that could be affected by habitat fragmentation. Therefore, though seabirds were not significantly associated with landscape structure in this study, these results do not mean they should be discounted in studies of habitat fragmentation.

Waterfowl diversity has declined through the past two centuries in Prince Edward Island, which is thought to be due to over-harvesting and the conversion of wetlands into agricultural fields (Stevens *et al.*, 2003). Waterfowl species have been linked to wetland habitats in Prince Edward Island, both in terms of diet and preferred breeding habitat (Stevens *et al.*, 2003). In our study, only three waterfowl species were significantly associated with landscape structure. Surprisingly, only one species was associated with a wetland metric. One possibly explanation for this finding is the coarseness of the landscape classification scheme used in this study. MacFaden & Capen (2002) found that more specific land-classifications at smaller scales yielded greater predictions of species occurrence. In our study, dunes, salt-marshes, bogs and marshes were grouped together in order to create a parsimonious representation of the wetlands of Prince Edward Island. It is possible that this amalgamation has diluted the effect that any particular wetland type may have on avian species occurrence (Turner *et al.*, 2001a; Beever *et al.*, 2006).

As expected, more landbird species were associated with landscape structure than any other functional group. These findings also support other studies that have demonstrated relationships between landscape structure and the occurrence of avian species (Trzcinski *et al.*, 1999; Rodewald & Brittingham, 2002; Fahrig, 2003; Estrada & Coates-Estrada, 2004; Rodewald & Matthews, 2005). Though there were more landbird species associated to landscape structure than the other functional groups, there were still few discernable trends as to which metrics were more important than others. Also, rarely were species affected by more than two specific landscape metrics. Very generally, it can be seen that variables related to forest configuration (shape, size, and aggregation of patches) were important for many landbird species, but due to correlation among variables, importance of specific metrics should not be interpreted above the importance of the overall land-type. Some of the forest metrics were inversely proportional to metrics related to the agriculture land-type. Therefore, they may still be important in relation to avian species occurrence, despite their lack of representation within the occurrence models. Occurrence of landbirds has been known to be positively related to the fractal dimension of agricultural fields, indicating that landbirds in some other places are likely to occur in agricultural areas where the perimeter of the fields is much larger than the area of agricultural patches (Hughes *et al.*, 2002; Naidoo, 2004).

Trophic Groups

No specific trends were observed within the trophic groups. Due to the small number of species successfully associated with landscape structure in this study, there is too little information to make definitive statements as to what groups respond to which variable in a consistent manner. For example, only one herbivore (*Perdix perdix*) was significantly associated with landscape structure in this study, and it was negatively associated with the aggregation of agriculture. However, without many more species of this functional group, no trends could be adequately analyzed. This is also true of the other trophic groups to a lesser extent, but some general observations can still be made.

Carnivores seemed to be less dependent on landscape structure than other bird groups, as there were only four species significantly associated with landscape structure in this study. Of those four species, variables related to wetland and forest land-types seemed to be the most important metrics. It is important to recognize that in this study, piscivorous species were included within the carnivore trophic group, and so results may change should these groups be examined separately (Brawley *et al.*, 1998; Benoit & Askins, 2002). It is also possible that the occurrence of many carnivorous species on the island may be independent of landscape structure, and be more related to characteristics that describe their prey species (Haskell *et al.*, 2002).

Several landscape metrics were significantly associated with the occurrence of the omnivorous avian species in this study. The observations of specific variables associated with omnivore occurrence were similar in nature to that of the landbird functional group, in that few species were associated with more than two given land-cover metrics. They were more random in relation to landscape structure than insectivores, possibly due to their more generic diets.

Insectivores were found throughout the province, and along with omnivores are some of the most easily recognized and abundant avian species on Prince Edward Island (Domm, 2002). Insectivores were primarily related to forest variables in this study, and should be considered to be a subset of the landbird functional group in that they are primarily small species of the Order Passeriformes (Erskine, 1992). It is likely that this result is related to the food resources that insectivores rely upon (Jones *et al.*, 2005). Bélisle *et al.*, (2001) found similar results when examining the dispersal of avian insectivores at small spatial scales. Their studies demonstrated that birds would forage for insects in the agricultural fields while rarely straying too far from the protective edges of the forest. Similar results were found by Gaston and Evans (2004), who examined songbird abundance in English farm fields. They found high abundances of insectivorous songbirds were found along ecotones that border both woodlots and agricultural fields, with insect abundance increasing with greater edge complexity.

5. GENERAL DISCUSSION

The conclusion of any project, and more specifically this thesis, can be turned into a profitable affair by considering future opportunities; both what needs to be done in order to make similar projects more successful in the future, and also the types of research that can follow from the findings of a project. The first and most evident of these is to supplement the dataset. Due to the large number of avian species that were considered in this study, it was inevitable that there would be missing information. It should be mentioned that this is typical of most macroecological studies (Brown, 1995). However, it is important to recognize that even though this lack of information might not have significantly altered the trends observed in this study for common species, our findings do not provide much information on the factors that determine the occurrence of rare or uncommon species. This is important because it has been recently been suggested that that the factors that determine the abundance and occurrence of rare species differ from those that determine the abundance and occurrence of common species (La Sorte, 2006). Therefore, it is clear that future studies should consider focusing on rare and uncommon species by collecting more thorough data on their abundance, as well the factors that determine their presence or absence.

It is also especially pertinent that attention be drawn to the biasing effect of sampling effort in Erskine (1992), as Bird Studies Canada is currently in the process of collecting data using an identical methodology for an updated publication. The atlas would have even greater applications if it contained more accurate estimates of population abundances (within provinces).

With respect to the methodology, the inclusion of many biologically relevant variables meant there were issues of collinearity between similar variables. A different approach to analyze the patterns of species richness which may warrant investigation, if only for comparative purposes, would be to use *Principal Components* (McGarigal *et al.*, 2000) in combination with multiple regression. This would remove the effects of collinearity, and amalgamate the variables into compound variables that could act as broad surrogates for such insular descriptor categories as 'physical', 'ecological' and 'human effects'. However, biological interpretation of principal component axes is not always easy, and any analysis would have to be carefully planned to obtain biologically relevant results.

This study has examined several factors that determine species richness and occurrence of birds breeding on Prince Edward Island at a regional spatial scale. What is required now is a process-orientated investigation of some of these factors, especially those associated with anthropogenic activities. Such an approach would be best served by exploring the biology of individual species (autoecology) and how they interact with the physical geography of their environments.

General Observations

The combined study of species richness and species occurrence in avian species is not a common procedure in ecology. Examining these two processes is usually for very separate purposes. Ecologists often examine species richness in order to assess overall biodiversity, often in conjunction with measures of population abundance. Species occurrence is most often examined for particular species to determine relative commonness or rarity. This is done to investigate whether or not a species is in danger of extinction, and to determine which species are in need of protection or of further study. The difficulty in combining these two different patterns is a problem of both disparate spatial scales and of finding adequate landscape metrics to fully describe both patterns. Additionally, agricultural variables were known to be inversely related to forest variables in many places on Prince Edward Island, and so their effects would be necessary to examine at the same time as forest variables.

Species Richness

Landscape structure was not as powerful a predictor of avian species richness on Prince Edward Island as was originally expected. Due to the collinearity of the many of the explanatory variables, generalizations had to be made as to what specific variables were important in explaining species richness. The shape, size, and aggregation of forest patches were important for many groups of birds, with the result that any studies involving avian species richness on Prince Edward Island must keep the spatial composition of the forests firmly in mind. Body size and latitude added considerable explanatory power to the models explaining variation in species richness, both factors which are usually thought to explain larger-scale patterns in species richness.

Species Occurrence

The investigation into the effects of landscape structure on avian species occurrence yielded results that may fuel future studies of avian species occurrence upon Prince Edward Island. Though few species were successfully associated with landscape structure in this study (29 out of a possible 102), many rare species were not examined for methodological reasons, which should be rectified in the future. Species that were associated with landscape structure tended to show now trends, other than a tendency for forest variables to be important in landbirds, omnivores and insectivores (many of the latter two of which belong to the first group). Although community-based trends were not apparent, the knowledge of how each of the 29 species were associated with landscape structure in this study can be the basis for many further studies, in effort to refine and improve these models. Altogether, this study marks the first broad-scale quantitative study at the species level for birds on Prince Edward Island. The information found in this study will provide baseline knowledge for the use of future studies in landscape ecology in the province.

Conservation Implications and Philosophical Significance

This is the first landscape-scale study on avian community ecology on Prince Edward Island. A blended approach to the study of avian communities is useful to wildlife managers, conservation biologists, and ecologists alike. The study of species richness and occurrence attempt to answer different and yet related questions: Why do we have so many species in one place and not another (Hutchinson, 1959), and why is a particular species in one place and not another (MacArthur, 1972)?

Wildlife managers and conservation biologists may seek to increase the biodiversity of a region, or may desire to protect a specific endangered species. Knowledge of what determines the species richness and occurrence of species is not complete, therefore every study performed in answer to these questions will help these managers and biologists perform their tasks with more efficiency. Studies have been performed globally in response to these questions, from the Galapagos (Darwin, 1859) to the Red Sea (Azeria, 2004), to Australia (Rozensweig, 1995) and beyond. The knowledge that many patterns of species richness and occurrence vary with spatial scale (Rahbek and Graves, 2001) has been acknowledged. Ecologists have since examined variation in species richness and occurrence across spatial scales, allowing a more complete answer to the questions of Hutchinson and MacArthur than has previously been known (Brown & Maurer, 1989; Currie, 1991; Currie & Francis, 1999; Cardillo, 2002). Each of these studies may therefore indirectly help increase the biodiversity of an area, or save an endangered species from local extinction. Recommendations given to landscape managers and ecologists would vary depending upon their focus and intentions. The dual nature of this thesis lends itself to two very different directions. For purposes of conservation, our findings show that the highest species richness of birds on Prince Edward Island is likely to occur (albeit with a large margin of error) in areas with an abundant amount of forests with plenty of core area in relation to their perimeter, and areas of complex agricultural fields with a low perimeter-to-area ratio.

Altogether, this study marks the first broad-scale quantitative study at the landscape level for birds on Prince Edward Island. The simultaneous examination of species richness and occurrence is not a new approach (Rahbek, 2001; Jetz & Rabhbek, 2002), but is not one that is widespread. Combining these two studies has given a broader and more comprehensive examination of the ecological effects of landscape structure, body size and latitude on avian species. These findings may prove useful for conservationists, in that managers wishing to use the landscape structure of Prince Edward Island to optimize the diversity of birds can use the models found within to assist in doing so. In addition, those that wish to find the impacts of landscape change on particular species can do so in a similar fashion. These findings may also be of use to ecologists in general, in that Prince Edward Island has now successfully been used as a case-study region in landscape ecology.

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7. APPENDICES

Appendix 1. List of avian species used in this study.

Table 7.1 Attribute information of each species used in the study.

Species name	Common name	Family	Order	Functional Group	Mean mass (g)	Trophic Group
Accipiter striatus	Sharp-shinned Hawk	Accipitridae	Falconiformes	Landbird	138.5	Carnivore
Aix sponsa	Wood Duck	Anatidae	Anseriformes	Waterfowl	658	Omnivore
Ammodramus caudacutus	Nelson's Sharp-tailed Sparro	Emberizidae	Passeriformes	Landbird	19.25	Omnivore
Anas americana	American Wigeon	Anatidae	Anseriformes	Waterfowl	755.5	Omnivore
Anas crecca	Green-winged Teal	Anatidae	Anseriformes	Waterfowl	341	Omnivore
Anas platyrhynchos	Mallard	Anatidae	Anseriformes	Waterfowl	1082	Omnivore
Anas strepera	Gadwall	Anatidae	Anseriformes	Waterfowl	919.5	Herbivore
Bombycilla cedrorum	Cedar Waxwing	Bombycillidae	Passeriformes	Landbird	31.85	Omnivore
Bonasa umbellus	Ruffed Grouse	Phasianidae	Galliformes	Landbird	576.5	Omnivore
Botaurus lentiginosus	American Bittern	Ardeidae	Ciconiiformes	Shorebird	706	Carnivore
Branta canadensis	Canada Goose	Anatidae	Anseriformes	Waterfowl	3564	Herbivore
Bubo virginianus	Great Horned Owl	Strigidae	Strigiformes	Landbird	1543	Carnivore
Carduelis tristis	American Goldfinch	Fringillidae	Passeriformes	Landbird	12.9	Omnivore
Carpodacus purpureus	Purple Finch	Fringillidae	Passeriformes	Landbird	24.9	Omnivore
Catharus guttatus	Hermit Thrush	Turdidae	Passeriformes	Landbird	31	Omnivore
Catharus ustulatus	Swainson's Thrush	Turdidae	Passeriformes	Landbird	30.8	Omnivore
Catoptrophorus semipalmatu	Willet	Scolopacidae	Charadriiformes	Shorebird	215	Omnivore
Charadrius melodus	Piping Plover	Charadriidae	Charadriiformes	Shorebird	55.2	Invertivore
Charadrius vociferus	Killdeer	Charadriidae	Charadriiformes	Shorebird	96.55	Omnivore
Coccothraustes vespertinus	Evening Grosbeak	Fringillidae	Passeriformes	Landbird	11.25	Omnivore
Colaptes auratus	Northern Flicker	Picidae	Piciformes	Landbird	132	Invertivore
Columba livia	Rock Dove	Columbidae	Columbiformes	Landbird	354.5	Omnivore
Contopus borealis	Olive-sided Flycatcher	Tyrannidae	Passeriformes	Landbird	32.1	Invertivore
Contopus virens	Eastern Wood-Pewee	Tyrannidae	Passeriformes	Landbird	14.1	Invertivore
Corvus brachyrhynchos	American Crow	Corvidae	Passeriformes	Landbird	448	Omnivore
Cyanocitta cristata	Blue Jay	Corvidae	Passeriformes	Landbird	86.8	Omnivore
Dendroica castanea	Bay-breasted Warbler	Parulidae	Passeriformes	Landbird	12.6	Omnivore
Dendroica coronata	Yellow-rumped Warbler	Parulidae	Passeriformes	Landbird	12.55	Omnivore
Dendroica fusca	Blackburnian Warbler	Parulidae	Passeriformes	Landbird	9.75	Invertivore
Dendroica magnolia	Magnolia Warbler	Parulidae	Passeriformes	Landbird	8.7	Invertivore
Dendroica palmarum	Palm Warbler	Parulidae	Passeriformes	Landbird	10.3	Invertivore
Dendroica pensylvanica	Chestnut-sided Warbler	Parulidae	Passeriformes	Landbird	9.6	Invertivore

Table 7.1 Continued

Species name	Common name	Family	Order	Functional Group	Mean mass (g)	Trophic Group
Dendroica petechia	Yellow Warbler	Parulidae	Passeriformes	Landbird	9.5	Invertivore
Dendroica tigrina	Cape May Warbler	Parulidae	Passeriformes	Landbird	11	Invertivore
Dendroica virens	Black-throated Green Warbler	Parulidae	Passeriformes	Landbird	8.8	Invertivore
Dumetella carolinensis	Gray Catbird	Mimidae	Passeriformes	Landbird	36.9	Omnivore
Empidonax alnorum	Alder Flycatcher	Tyrannidae	Passeriformes	Landbird	12.9	Invertivore
Empidonax minimus	Least Flycatcher	Tyrannidae	Passeriformes	Landbird	10.3	Invertivore
Euphagus carolinus	Rusty Blackbird	Icteridae	Passeriformes	Landbird	59.75	Omnivore
Falco columbarius	Merlin	Falconidae	Falconiformes	Landbird	190.5	Carnivore
Falco sparverius	American Kestrel	Falconidae	Falconiformes	Landbird	115.5	Carnivore
Gallinago delicata	Wilson's Snipe	Scolopacidae	Charadriiformes	Shorebird	122	Omnivore
Haliaeetus leucocephalus	Bald Eagle	Accipitridae	Falconiformes	Landbird	4740	Carnivore
Junco hyemalis	Dark-eyed Junco	Emberizidae	Passeriformes	Landbird	19.6	Omnivore
Larus marinus	Great Black-backed Gull	Laridae	Charadriiformes	Seabird	1658.5	Omnivore
Loxia leucoptera	White-winged Crossbill	Fringillidae	Passeriformes	Landbird	26.55	Herbivore
Megaceryle alcyon	Belted Kingfisher	Alcedinidae	Coraciiformes	Landbird	148	Carnivore
Melospiza georgiana	Swamp Sparrow	Emberizidae	Passeriformes	Landbird	17	Omnivore
Melospiza lincolnii	Lincoln's Sparrow	Emberizidae	Passeriformes	Landbird	17.4	Omnivore
Mergus serrator	Red-breasted Merganser	Anatidae	Anseriformes	Waterfowl	1021.5	Carnivore
Mniotilta varia	Black-and-White Warbler	Parulidae	Passeriformes	Landbird	10.8	Invertivore
Molothrus ater	Brown-headed Cowbird	Icteridae	Passeriformes	Landbird	43.9	Omnivore
Oporornis philadelphia	Mourning Warbler	Parulidae	Passeriformes	Landbird	12.5	Invertivore
Pandion haliaetus	Osprey	Pandionidae	Falconiformes	Landbird	1485.5	Carnivore
Parula americana	Northern Parula	Parulidae	Passeriformes	Landbird	8.6	Invertivore
Parus atricapillus	Black-capped Chickadee	Paridae	Passeriformes	Landbird	10.8	Omnivore
Parus hudsonicus	Boreal Chickadee	Paridae	Passeriformes	Landbird	9.8	Omnivore
Passer domesticus	House Sparrow	Passeridae	Passeriformes	Landbird	503.5	Omnivore
Passerculus sandwichensis	Savannah Sparrow	Emberizidae	Passeriformes	Landbird	20.05	Invertivore
Perdix perdix	Gray Partridge	Phasianidae	Galliformes	Landbird	389.5	Herbivore
Phasianus colchicus	Ring-necked Pheasant	Phasianidae	Galliformes	Landbird	1135	Omnivore
Pheucticus ludovicianus	Rose-breasted Grosbeak	Emberizidae	Passeriformes	Landbird	45.6	Omnivore
Picoides pubescens	Downy Woodpecker	Picidae	Piciformes	Landbird	27	Invertivore
Picoides villosus	Hairy Woodpecker	Picidae	Piciformes	Landbird	66.25	Invertivore
Podilymbus podiceps	Pied-billed Grebe	Podicipedidae	Podicepediformes	Waterfowl	453	Carnivore
Regulus calendula	Ruby-crowned Kinglet	Regulidae	Passeriformes	Landbird	6.65	Invertivore
Regulus satrapa	Golden-crowned Kinglet	Regulidae	Passeriformes	Landbird	6.2	Invertivore

Table 7.1 Continued

Species name	Common name	Family	Order	Functional Group	Mean mass (g)	Trophic Group
Riparia riparia	Bank Swallow	Hirundinidae	Passeriformes	Landbird	14.6	Invertivore
Scolopax minor	American Woodcock	Scolopacidae	Charadriiformes	Shorebird	197.5	Invertivore
Seiurus aurocapillus	Ovenbird	Parulidae	Passeriformes	Landbird	19.4	Invertivore
Setophaga ruticilla	American Redstart	Parulidae	Passeriformes	Landbird	8.3	Omnivore
Sitta canadensis	Red-breasted Nuthatch	Sittidae	Passeriformes	Landbird	9.8	Omnivore
Sphyrapicus varius	Yellow-bellied Sapsucker	Picidae	Piciformes	Landbird	50.3	Invertivore
Spizella passerina	Chipping Sparrow	Emberizidae	Passeriformes	Landbird	18.98	Omnivore
Sterna hirundo	Common Tern	Laridae	Charadriiformes	Seabird	120	Carnivore
Strix varia	Barred Owl	Strigidae	Strigiformes	Landbird	716.5	Carnivore
Sturnus vulgaris	European Starling	Sturnidae	Passeriformes	Landbird	82.3	Omnivore
Tachycineta bicolor	Tree Swallow	Hirundinidae	Passeriformes	Landbird	20.1	Omnivore
Tringa macularia	Spotted Sandpiper	Scolopacidae	Charadriiformes	Shorebird	40.4	Invertivore
Troglodytes troglodytes	Winter Wren	Troglodytidae	Passeriformes	Landbird	8.9	Invertivore
Tyrannus tyrannus	Eastern Kingbird	Tyrannidae	Passeriformes	Landbird	43.6	Omnivore
Vermivora peregrina	Tennessee Warbler	Parulidae	Passeriformes	Landbird	10	Omnivore
Vermivora ruficapilla	Nashville Warbler	Parulidae	Passeriformes	Landbird	8.75	Invertivore
Vireo olivaceus	Red-eyed Vireo	Vireonidae	Passeriformes	Landbird	16.7	Omnivore
Wilsonia canadensis	Canada Warbler	Parulidae	Passeriformes	Landbird	10.4	Invertivore
Zonotrichia albicollis	White-throated Sparrow	Emberizidae	Passeriformes	Landbird	32	Omnivore

Appendix 2. Scatterplots of the pooled species richness of birds on Prince Edward Island against land-cover variables.

Figure 7.1 Scatterplot of Species Richness and Total Area of Land in Sampling Cell

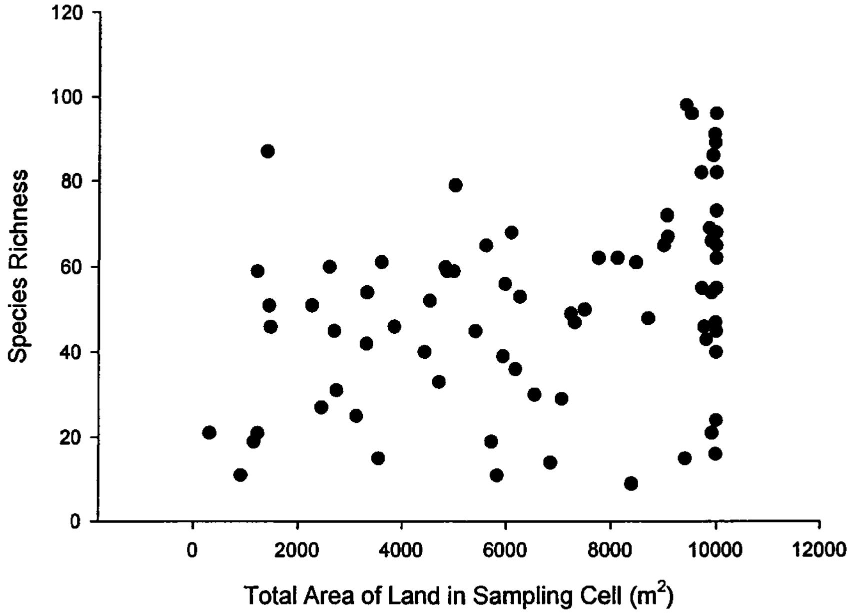


Figure 7.2 Scatterplot of Species Richness and Percentage of Forest

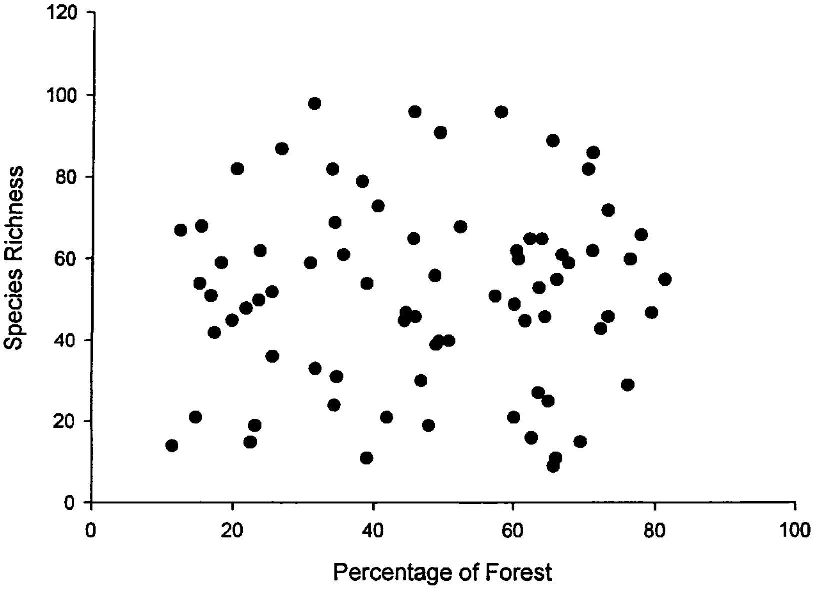


Figure 7.3 Scatterplot of Species Richness and Percentage of Human-Influenced Lands

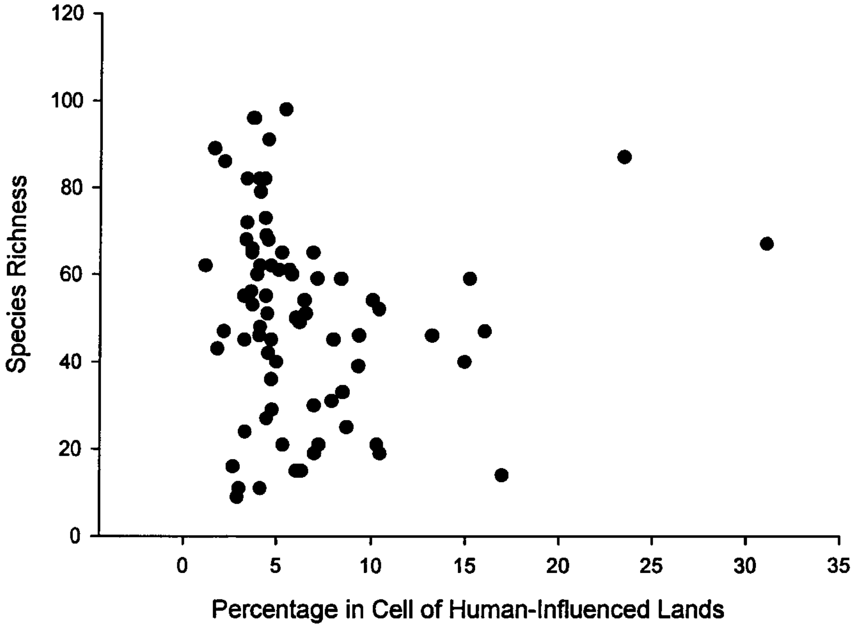


Figure 7.4 Scatterplot of Species Richness and Percentage of Wetlands

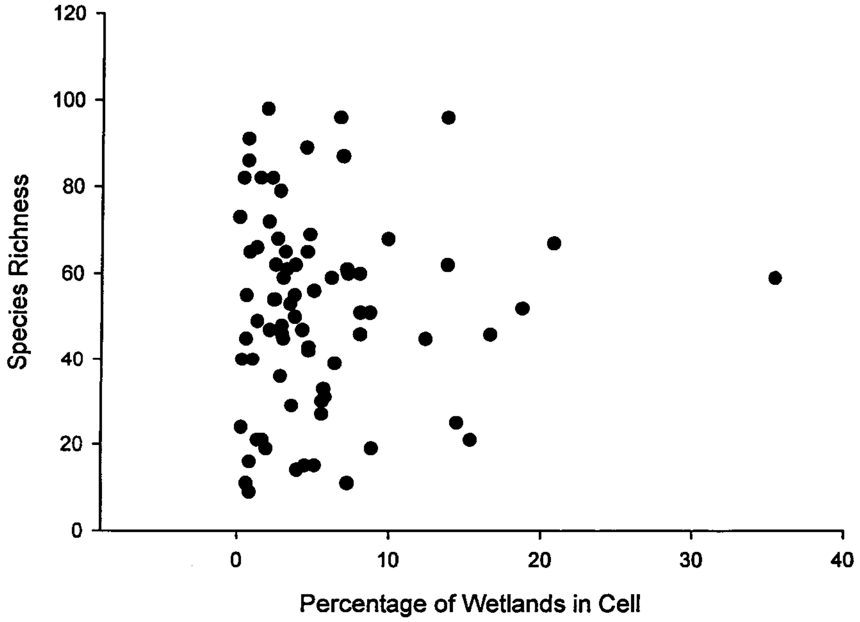


Figure 7.5 Scatterplot of Species Richness and Percentage of Roads

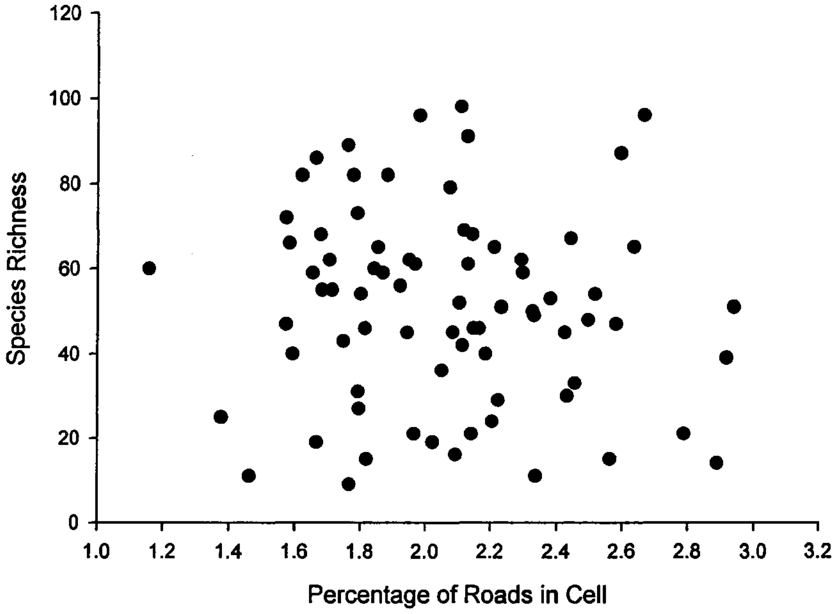


Figure 7.6 Scatterplot of Species Richness and Fractal Dimension of Agriculture

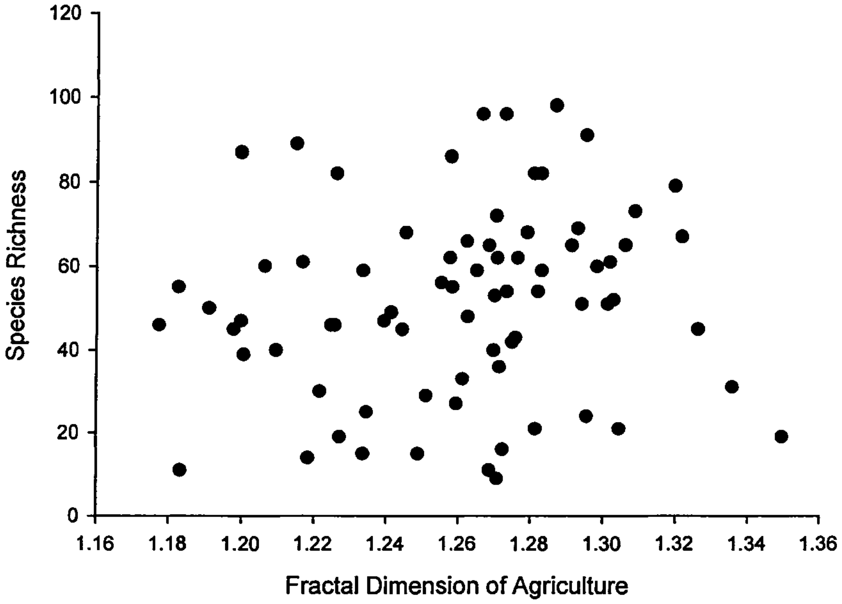


Figure 7.7 Scatterplot of Species Richness and Fractal Dimension of Forest

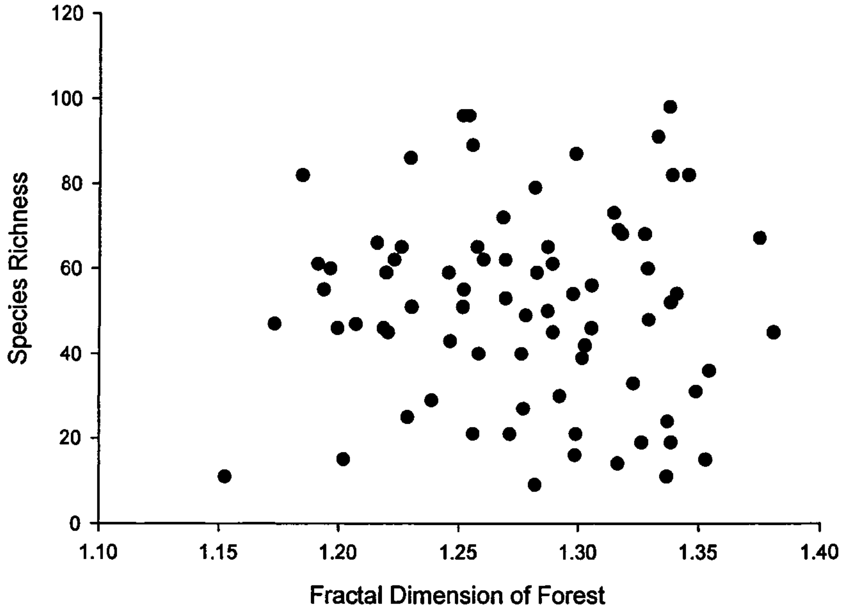


Figure 7.8 Scatterplot of Species Richness and Fractal Dimension of Human-Influenced Lands

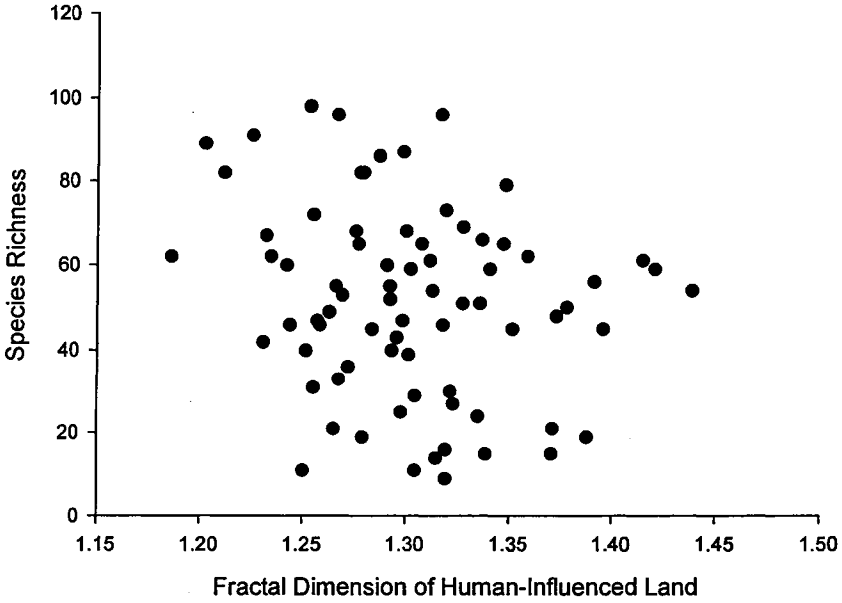


Figure 7.9 Scatterplot of Species Richness and Fractal Dimension of Wetlands

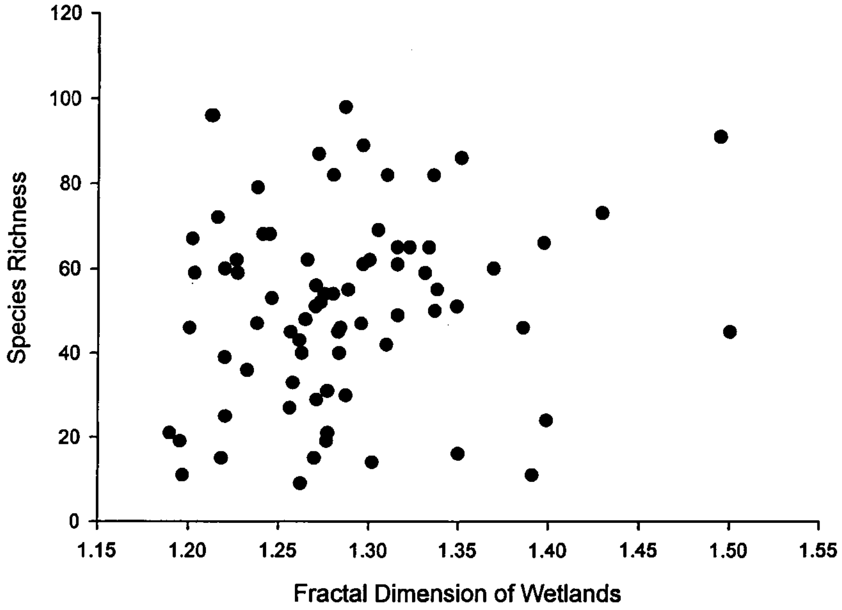


Figure 7.10 Scatterplot of Species Richness and Clumpiness of Agriculture

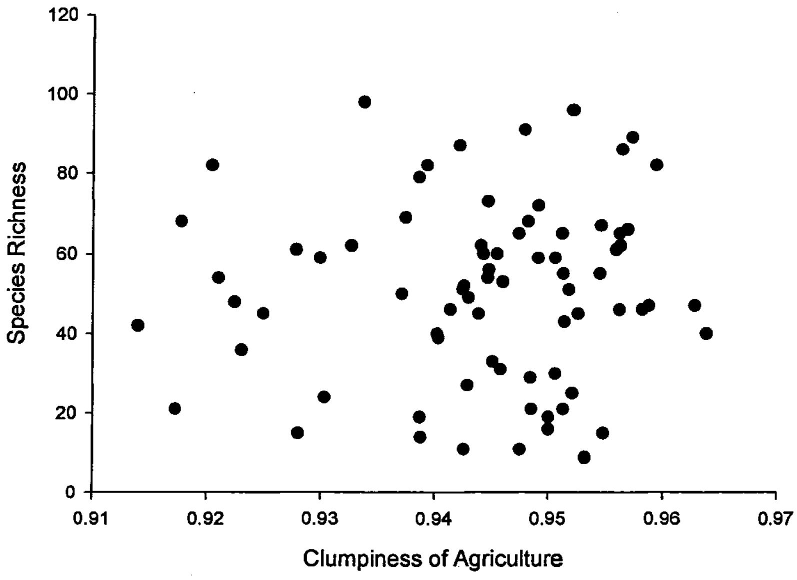


Figure 7.11 Scatterplot of Species Richness and Clumpiness of Forest

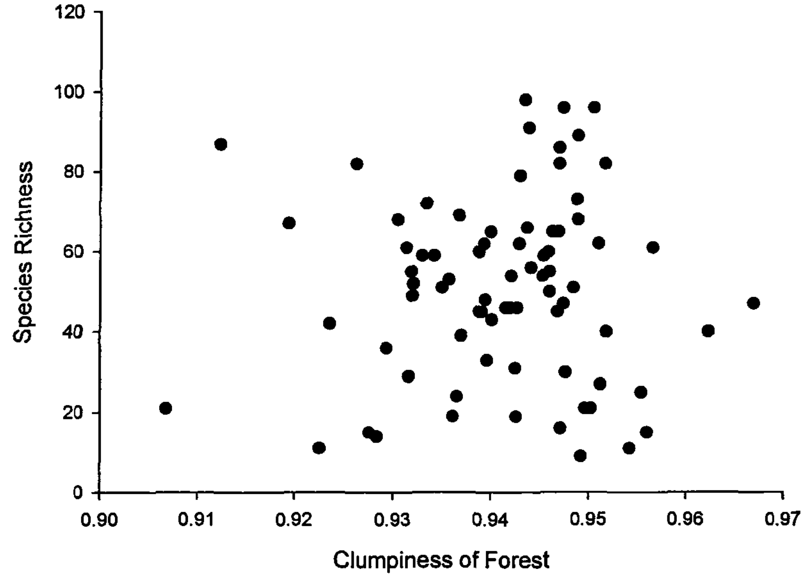


Figure 7.12 Scatterplot of Species Richness and Clumpiness of Human-Influenced Lands

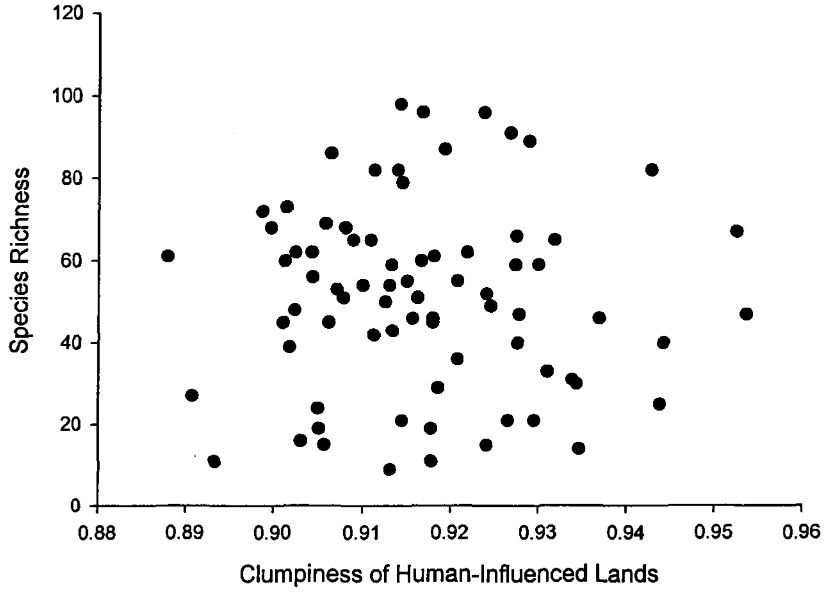


Figure 7.13 Scatterplot of Species Richness and Clumpiness of Roads

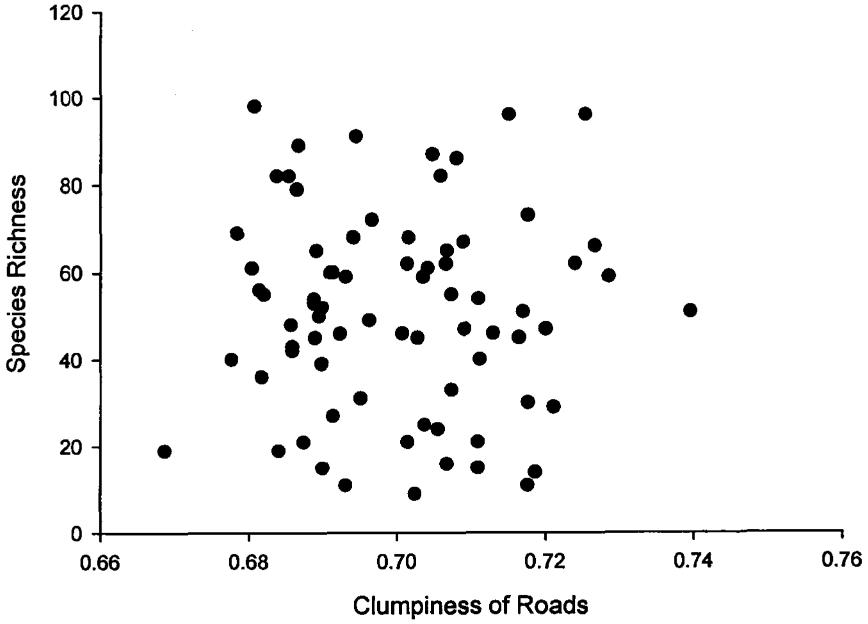
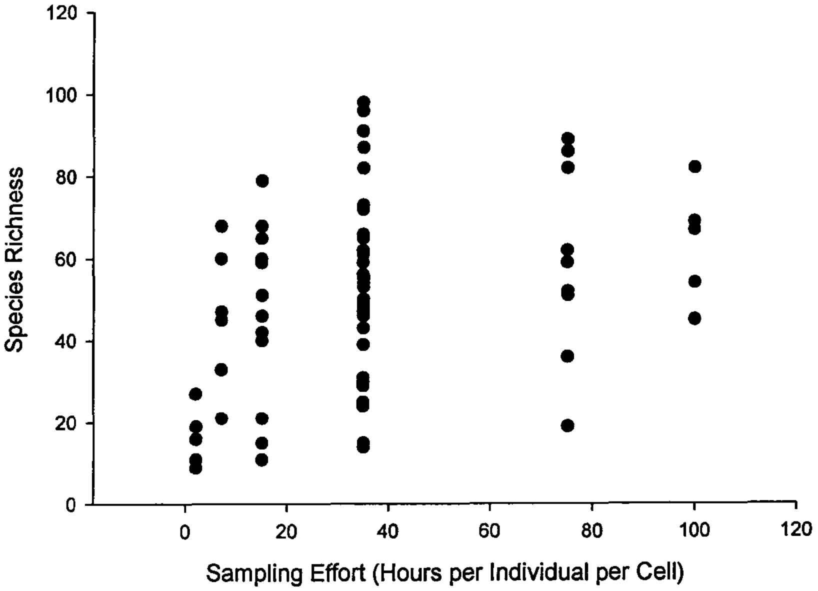


Figure 7.14 Scatterplot of Species Richness and Sampling Hours



Appendix 3. Raw Pearson correlation outputs examining the statistical association of land-cover metrics. Analyses computed using SAS v.8.3. Variables used in correlation analysis: TA = Total Area; AGR_PLAND = Percentage of agricultural land in a cell; AG_PAFRAC = Fractal dimension of agriculture; AGR_CLUMPY = Aggregation of agriculture; FOR_PLAND = Percentage of forest in a cell; FOR_PAFRAC = Fractal dimension of forest; FOR_CLUMPY = Aggregation of forest; INF_PLAND = Proportion of human-used land in cell; INF_PAFRAC = Fractal dimension of human-used land; INF_CLUMPY = Aggregation of human-used land; WET_PLAND = Proportion of wetland in cell; WET_PAFRAC = Fractal dimension of wetland; WET_CLUMPY = Aggregation of wetland; ROAD_PLAND = Proportion of roads in a cell; ROAD_CLUMPY = Aggregation of roads in a cell; Richcell = Species richness of birds in a sampling cell; Longitude = Longitudinal coordinates of primary sampling location in cell; Latitude = Latitudinal coordinates of primary sampling location in cell; Hours = Sampling effort (hours per individual per cell)

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                          Pearson Correlation Coefficients
                             Prob > |r| under H0: Rho=0
                               Number of Observations

                                    AGR_        AGR_                    FOR_        FOR_
                 TA   AGR_PLAND   PAFRAC      CLUMPY   FOR_PLAND      PAFRAC      CLUMPY

TA          1.00000     0.03718  -0.08523     0.16641     0.16068     0.09539     0.21457
                         0.7498    0.4672      0.1508      0.1656      0.4124      0.0627
                 76          76        75          76          76          76          76

AGR_PLAND   0.03718     1.00000   0.22660    -0.76490    -0.89281     0.67498    -0.33447
             0.7498                0.0506      <.0001      <.0001      <.0001      0.0031
                 76          76        75          76          76          76          76

AGR_PAFRAC -0.08523     0.22660   1.00000    -0.15998    -0.20960     0.34308     0.02788
             0.4672      0.0506                0.1704      0.0711      0.0026      0.8123
                 75          75        75          75          75          75          75

AGR_CLUMPY  0.16641    -0.76490  -0.15998     1.00000     0.67395    -0.50313     0.55979
             0.1508      <.0001    0.1704                  <.0001      <.0001      <.0001
                 76          76        75          76          76          76          76

FOR_PLAND   0.16068    -0.89281  -0.20960     0.67395     1.00000    -0.68835     0.41440
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```
                 0.1656       <.0001       0.0711       <.0001                    <.0001       0.0002
                     76           76           75           76           76           76           76

FOR_PAFRAC      0.09539      0.67498      0.34308     -0.50313     -0.68835      1.00000     -0.28040
                 0.4124       <.0001       0.0026       <.0001       <.0001                    0.0142
                     76           76           75           76           76           76           76

FOR_CLUMPY      0.21457     -0.33447      0.02788      0.55979      0.41440     -0.28040      1.00000
                 0.0627       0.0031       0.8123       <.0001       0.0002       0.0142
                     76           76           75           76           76           76           76

INF_PLAND      -0.31797      0.00738     -0.00574      0.06989     -0.39002      0.21003     -0.27091
                 0.0051       0.9495       0.9610       0.5486       0.0005       0.0686       0.0179
                     76           76           75           76           76           76           76

INF_PAFRAC     -0.24346      0.24930      0.15816     -0.29509     -0.25850      0.16053      0.00729
                 0.0353       0.0310       0.1753       0.0102       0.0251       0.1689       0.9505
                     75           75           75           75           75           75           75


                                          The CORR Procedure

                                  Pearson Correlation Coefficients
                                     Prob > |r| under H0: Rho=0
                                       Number of Observations

                                               AGR_         AGR_                      FOR_         FOR_
                     TA    AGR_PLAND         PAFRAC       CLUMPY    FOR_PLAND       PAFRAC       CLUMPY

INF_CLUMPY      0.05307     -0.18554     -0.09467      0.35894      0.01985     -0.18358      0.17011
                 0.6489       0.1086       0.4192       0.0015       0.8649       0.1124       0.1418
                     76           76           75           76           76           76           76

WET_PLAND      -0.40925     -0.26207     -0.01382      0.16880     -0.14714     -0.04539     -0.07439
                 0.0002       0.0222       0.9063       0.1449       0.2047       0.6970       0.5230
                     76           76           75           76           76           76           76

WET_PAFRAC      0.30588      0.11315     -0.10404     -0.12687      0.05800     -0.07453     -0.04517
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                  0.0076       0.3338      0.3744      0.2781       0.6211      0.5251      0.7004
                      75           75          75          75           75          75          75

WET_CLUMPY      -0.15871     -0.19276     0.02104     0.24111     -0.00576    -0.02136     0.22808
                  0.1709       0.0953      0.8578      0.0359       0.9606      0.8547      0.0475
                      76           76          75          76           76          76          76

ROAD_PLAND      -0.18135      0.37942    -0.06141    -0.30242     -0.45623     0.19985    -0.39756
                  0.1169       0.0007      0.6007      0.0079       <.0001      0.0835      0.0004
                      76           76          75          76           76          76          76

ROAD_CLUMPY      0.13271     -0.18015    -0.19710     0.31623      0.09757    -0.30776     0.06497
                  0.2531       0.1194      0.0901      0.0054       0.4017      0.0068      0.5771
                      76           76          75          76           76          76          76

Richcell         0.36417     -0.02035     0.12174     0.06724      0.03081    -0.03580     0.02883
                  0.0012       0.8615      0.2981      0.5638       0.7916      0.7588      0.8047
                      76           76          75          76           76          76          76

Longitude        0.15830     -0.19664     0.02592     0.21737      0.23163    -0.02482    -0.17509
                  0.1720       0.0887      0.8253      0.0593       0.0441      0.8314      0.1303
                      76           76          75          76           76          76          76

Latitude        -0.09452     -0.08633    -0.08657    -0.00396      0.01837     0.00149     0.28293
                  0.4167       0.4584      0.4602      0.9729       0.8748      0.9898      0.0133
                      76           76          75          76           76          76          76

Hours            0.28780      0.20837     0.01629    -0.20619     -0.20839     0.20452    -0.21413
                  0.0117       0.0709      0.8897      0.0739       0.0708      0.0764      0.0632
                      76           76          75          76           76          76          76
```

```
                    The CORR Procedure

                                   Pearson Correlation Coefficients
                                      Prob > |r| under H0: Rho=0
                                        Number of Observations

                                        INF_          INF_                          WET_          WET_          ROAD_
                       INF_PLAND       PAFRAC        CLUMPY     WET_PLAND        PAFRAC        CLUMPY         PLAND

TA                      -0.31797     -0.24346       0.05307     -0.40925       0.30588      -0.15871      -0.18135
                          0.0051       0.0353        0.6489       0.0002        0.0076        0.1709        0.1169
                              76           75            76           76            75            76            76

AGR_PLAND                0.00738      0.24930      -0.18554     -0.26207       0.11315      -0.19276       0.37942
                          0.9495       0.0310        0.1086       0.0222        0.3338        0.0953        0.0007
                              76           75            76           76            75            76            76

AGR_PAFRAC              -0.00574      0.15816      -0.09467     -0.01382      -0.10404       0.02104      -0.06141
                          0.9610       0.1753        0.4192       0.9063        0.3744        0.8578        0.6007
                              75           75            75           75            75            75            75

AGR_CLUMPY               0.06989     -0.29509       0.35894      0.16880      -0.12687       0.24111      -0.30242
                          0.5486       0.0102        0.0015       0.1449        0.2781        0.0359        0.0079
                              76           75            76           76            75            76            76

FOR_PLAND               -0.39002     -0.25850       0.01985     -0.14714       0.05800      -0.00576      -0.45623
                          0.0005       0.0251        0.8649       0.2047        0.6211        0.9606        <.0001
                              76           75            76           76            75            76            76

FOR_PAFRAC               0.21003      0.16053      -0.18358     -0.04539      -0.07453      -0.02136       0.19985
                          0.0686       0.1689        0.1124       0.6970        0.5251        0.8547        0.0835
                              76           75            76           76            75            76            76

FOR_CLUMPY              -0.27091      0.00729       0.17011     -0.07439      -0.04517       0.22808      -0.39756
                          0.0179       0.9505        0.1418       0.5230        0.7004        0.0475        0.0004
```

```
                       76          75          76          76          75          76          76

INF_PLAND         1.00000     0.05024     0.48948     0.47659    -0.24877     0.22927     0.35474
                               0.6686      <.0001      <.0001      0.0314      0.0463      0.0017
                       76          75          76          76          75          76          76

INF_PAFRAC        0.05024     1.00000    -0.35409     0.01738     0.01939    -0.01886     0.18258
                   0.6686                  0.0018      0.8824      0.8688      0.8724      0.1169
                       75          75          75          75          75          75          75

INF_CLUMPY        0.48948    -0.35409     1.00000     0.13900    -0.07785     0.09663     0.03178
                   <.0001      0.0018                  0.2311      0.5068      0.4063      0.7852
                       76          75          76          76          75          76          76

WET_PLAND         0.47659     0.01738     0.13900     1.00000    -0.36339     0.47830    -0.04067
                   <.0001      0.8824      0.2311                  0.0014      <.0001      0.7272
                       76          75          76          76          75          76          76


                                      The CORR Procedure

                               Pearson Correlation Coefficients
                                 Prob > |r| under H0: Rho=0
                                   Number of Observations

                                   INF_        INF_                    WET_        WET_       ROAD_
                INF_PLAND      PAFRAC      CLUMPY   WET_PLAND      PAFRAC      CLUMPY       PLAND

WET_PAFRAC       -0.24877     0.01939    -0.07785    -0.36339     1.00000    -0.71129    -0.00448
                   0.0314      0.8688      0.5068      0.0014                  <.0001      0.9696
                       75          75          75          75          75          75          75

WET_CLUMPY        0.22927    -0.01886     0.09663     0.47830    -0.71129     1.00000    -0.03671
                   0.0463      0.8724      0.4063      <.0001      <.0001                  0.7529
                       76          75          76          76          75          76          76

ROAD_PLAND        0.35474     0.18258     0.03178    -0.04067    -0.00448    -0.03671     1.00000
                   0.0017      0.1169      0.7852      0.7272      0.9696      0.7529
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                     76          75          76          76          75          76          76

ROAD_CLUMPY     0.07922    -0.11607     0.17483     0.18388     0.18113    -0.07618     0.19946
                 0.4964      0.3214      0.1309      0.1118      0.1199      0.5131      0.0841
                     76          75          76          76          75          76          76

Richcell       -0.06654    -0.21655    -0.01147     0.02289     0.13519     0.01211    -0.09597
                 0.5680      0.0620      0.9216      0.8444      0.2475      0.9173      0.4096
                     76          75          76          76          75          76          76

Longitude      -0.10251    -0.28600     0.04799    -0.05793     0.01910    -0.05202    -0.10734
                 0.3782      0.0129      0.6806      0.6191      0.8708      0.6554      0.3560
                     76          75          76          76          75          76          76

Latitude        0.05006     0.15333     0.04643     0.18861    -0.12458     0.20316    -0.06962
                 0.6676      0.1891      0.6904      0.1027      0.2869      0.0784      0.5501
                     76          75          76          76          75          76          76

Hours           0.04504    -0.02834     0.05374    -0.01161     0.17800    -0.13136     0.06043
                 0.6993      0.8093      0.6448      0.9207      0.1265      0.2580      0.6041
                     76          75          76          76          75          76          76
```

```
The CORR Procedure

                          Pearson Correlation Coefficients
                             Prob > |r| under H0: Rho=0
                               Number of Observations

                 ROAD_
                CLUMPY      Richcell     Longitude      Latitude         Hours

TA             0.13271       0.36417       0.15830      -0.09452       0.28780
                0.2531        0.0012        0.1720        0.4167        0.0117
                    76            76            76            76            76

AGR_PLAND     -0.18015      -0.02035      -0.19664      -0.08633       0.20837
                0.1194        0.8615        0.0887        0.4584        0.0709
                    76            76            76            76            76

AGR_PAFRAC    -0.19710       0.12174       0.02592      -0.08657       0.01629
                0.0901        0.2981        0.8253        0.4602        0.8897
                    75            75            75            75            75

AGR_CLUMPY     0.31623       0.06724       0.21737      -0.00396      -0.20619
                0.0054        0.5638        0.0593        0.9729        0.0739
                    76            76            76            76            76

FOR_PLAND      0.09757       0.03081       0.23163       0.01837      -0.20839
                0.4017        0.7916        0.0441        0.8748        0.0708
                    76            76            76            76            76

FOR_PAFRAC    -0.30776      -0.03580      -0.02482       0.00149       0.20452
                0.0068        0.7588        0.8314        0.9898        0.0764
                    76            76            76            76            76

FOR_CLUMPY     0.06497       0.02883      -0.17509       0.28293      -0.21413
                0.5771        0.8047        0.1303        0.0133        0.0632
                    76            76            76            76            76

INF_PLAND      0.07922      -0.06654      -0.10251       0.05006       0.04504
                0.4964        0.5680        0.3782        0.6676        0.6993
                    76            76            76            76            76

INF_PAFRAC    -0.11607      -0.21655      -0.28600       0.15333      -0.02834
                0.3214        0.0620        0.0129        0.1891        0.8093
                    75            75            75            75            75

INF_CLUMPY     0.17483      -0.01147       0.04799       0.04643       0.05374
                0.1309        0.9216        0.6806        0.6904        0.6448
                    76            76            76            76            76

WET_PLAND      0.18388       0.02289      -0.05793       0.18861      -0.01161
                0.1118        0.8444        0.6191        0.1027        0.9207
                    76            76            76            76            76
```

```
The CORR Procedure

                        Pearson Correlation Coefficients
                           Prob > |r| under H0: Rho=0
                             Number of Observations

                     ROAD_
                    CLUMPY      Richcell     Longitude      Latitude         Hours

 WET_PAFRAC        0.18113       0.13519       0.01910      -0.12458       0.17800
                    0.1199        0.2475        0.8708        0.2869        0.1265
                        75            75            75            75            75

 WET_CLUMPY       -0.07618       0.01211      -0.05202       0.20316      -0.13136
                    0.5131        0.9173        0.6554        0.0784        0.2580
                        76            76            76            76            76

 ROAD_PLAND        0.19946      -0.09597      -0.10734      -0.06962       0.06043
                    0.0841        0.4096        0.3560        0.5501        0.6041
                        76            76            76            76            76

 ROAD_CLUMPY       1.00000      -0.01051      -0.00406       0.00294      -0.02676
                                  0.9282        0.9722        0.9799        0.8185
                        76            76            76            76            76

 Richcell         -0.01051       1.00000       0.31549      -0.33265       0.35608
                    0.9282                      0.0055        0.0033        0.0016
                        76            76            76            76            76

 Longitude        -0.00406       0.31549       1.00000      -0.66142       0.16096
                    0.9722        0.0055                      <.0001        0.1648
                        76            76            76            76            76

 Latitude          0.00294      -0.33265      -0.66142       1.00000      -0.23185
                    0.9799        0.0033        <.0001                      0.0439
                        76            76            76            76            76

 Hours            -0.02676       0.35608       0.16096      -0.23185       1.00000
                    0.8185        0.0016        0.1648        0.0439

                        76            76            76            76            76
```