RUFFED GROUSE DISPERSAL: RELATIONSHIPS WITH LANDSCAPE AND CONSEQUENCES FOR SURVIVAL

DISSERTATION

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By

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* * * *

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ABSTRACT

In this study, we explore large-scale movements in ruffed grouse (*Bonasa umbellus*) in Ohio by characterizing juvenile and adult dispersal, investigating the effect of landscape characteristics on movement behavior and examining the relationship between movement and the risk of predation. Defining and measuring dispersal is a critical but difficult task in the study of animal movement, and necessary for a complete understanding of the ecology of most species. Our first objective was to investigate the natal and adult dispersal characteristics of ruffed grouse throughout the entire annual breeding cycle, using a behavioral definition of dispersal. Once dispersal movements could be accurately identified, we explored whether landscape variables measured at coarse-grained scales could help explain general movement characteristics. We used Akaike Information Criterion (AIC) techniques for model selection to explore the relationship between metrics of both landscape composition and configuration and the decision to disperse by adults and juveniles during the fall and spring dispersal periods, their net dispersal distances and rates of movement, and their home range sizes. Dispersing individuals are more likely to move at high rates and into unfamiliar areas than non-dispersers and ecologists often assume that dispersing individuals experience an increase in predation risk due to increased exposure to predators while moving. We tested the hypothesis that predation risk is a function of rate of movement and site familiarity using a Cox's proportional hazards model.

Overall, we found general patterns of dispersal consistent with those expected for birds (e.g., juveniles and females moving the greater distances) but documented a surprisingly high proportion of adults undertaking seasonal dispersal movements and juveniles undergoing dispersal in the spring, particularly compared to grouse studies conducted in the northern portion of its range (Chapter 1). We also found that coarse-grained landscape characteristics affect movement behavior, but effects were complex and varied considerably among specific behaviors and across spatial scales. While large-scale landscape composition (i.e. % forest) and edge density significantly affected dispersal behavior (e.g. birds inhabiting areas containing a low proportion of forest and low edge density were more likely to disperse than birds from highly forested areas or areas with high edge density), little evidence was found for landscape configuration (patch area and radius of gyration) per se affecting movements (Chapter 2). Finally, we found evidence indicating that increased movement rates may increase the risk of predation for adult birds but not juveniles. We also found juvenile and adult birds inhabiting unfamiliar habitat were consistently at a much higher risk of predation (3 – 7.5 times greater) than those in familiar habitat. Our results indicate that moving through unfamiliar habitat results in a much greater increase in risk for ruffed grouse than movement activity per se. This supports the hypothesis that increased predation risk may be an important cost of dispersal for birds (Chapter 3).

DEDICATION

To Kathy, for her love, friendship, and encouragement,

and to Theodore and Tobias for their joy and inspiration.

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PUBLICATIONS

Research Publications

1. Yoder, J. M., E. A. Marschall, and D. A. Swanson. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. Behavioral Ecology. 15: 469-476.
2. Connor, E.F., A. C. Courtney, and J. M. Yoder. 2000. Individuals-area relationships: the relationship between animal population density and area. Ecology. 81: 734-748.

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FIELDS OF STUDY

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3.4 The proportion of juvenile birds (A) and adult birds (B) inhabiting familiar habitat (light bars) and unfamiliar habitat (dark bars) in relation to movement rate (m/day) calculated over the time period t to (t – 14 days). Arrows indicate mean movement rates for birds inhabiting familiar and unfamiliar habitats. 143

INTRODUCTION

Understanding animal movement is fundamental to interpreting spatial and temporal patterns in population dynamics and responses to changing habitats at local and landscape scales. Despite its ecological importance, detailed measurement of dispersal characteristics for many species are still scarce and sorely needed to better understand both the proximate factors affecting dispersal and the ultimate implications of dispersal for management or conservation (Martin 1998, Sutherland *et al.* 2000, Storch 2003). Movement data are costly and difficult to collect, particularly for highly mobile species at large spatial scales. Many studies have been able to define dispersal by movement away from well-defined study sites (Cade and Hoffman 1993), islands (Strong and Bancroft 1994, Altwegg *et al.* 2000), nests, or social groups (Palomares *et al.* 2000, Cooper and Walters 2002, Cale 2003), movement between distinct patches in highly fragmented habitats (Brooker and Brooker 2002), or movement into distinct populations (Martin *et al.* 2000).

However, for many species that do not have well-defined, long-term family or social groups, that inhabit relatively contiguous habitat, and that exhibit high variability in both proportions of individuals undergoing natal or adult dispersal and dispersal distances, defining dispersal remains problematic. One such species is the ruffed grouse (*Bonasa umbellus*), a nonmigratory forest game bird. Despite having been the focus of studies for decades, many details of movement and dispersal are not well known, particularly for adult birds and for juveniles studied throughout the entire year. Because the majority of previous studies of ruffed grouse movements have been conducted at northern latitudes in aspen-dominated habitats (Rusch and Keith 1971, Gullion 1977, Cade and Sousa 1985, Small and Rusch 1989, Small *et al.* 1991, Clark 1996), little is known about the propensity to disperse or the timing and distances moved of dispersing ruffed grouse in the oak-hickory dominated forests common in the southern Appalachian portion of its range.

The ability to accurately identify when dispersal movements are occurring allows a range of additional ecological questions to be explored. Interest in the effects of broad-scale environmental changes has spurred the effort by landscape ecologists to decipher the effects of habitat loss and fragmentation on various ecology processes (Turner et al. 2001), including movement. While previous studies have shown that habitat loss or fragmentation results in changes in dispersal rates (Cooper and Walters 2002) and reduction in dispersal success (Brooker and Brooker 2002, Cale 2003) of birds, empirical studies of movement patterns, especially at large spatial scales, remain scarce (Turchin 1998, Martin 1998). The relationship between landscapes characteristics and movement is particularly important to conservation biologists and managers (King and With 2003, Storch 2003).

Investigating the relationship of landscape characteristics with any ecological process presents a broad range of technical and theoretical challenges. One difficulty is distinguishing the effects of habitat loss (changes in landscape composition) from those of fragmentation per se (McGarigal and Cushman 2002, Fahrig 2003). In addition to habitat loss, changes in landscape configuration, such as amount of edge, number of patches, patch size, patch isolation, and connectivity may affect an individual's movement. In general, attempts to derive broad patterns of responses to fragmentation across communities or taxa have been unsuccessful (Fahrig 2003). Most evidence indicates responses to fragmentation are species-specific and there is a need for empirical studies to clarify effects for individual species (McGarigal and McComb 1995, Martin 1998, Bissonette and Storch 2002).

The species-specific nature of response to habitat change also has important consequences for issues of scale. In landscape ecology in particular there is a growing awareness of the importance of studying ecological responses at organism-relevant temporal and spatial scales (Wiens 1989, Bissonette 1997, Turner et al. 2001, McCargical and Cushman 2002, Storch 2002). In studying animal response to landscape change, two important aspects of spatial scale are extent and grain. While extent can be defined simply as the size of the study area or landscape in which landscape variables and ecological processes are to be measured, its importance is often overlooked in studies of habitat fragmentation. Grain refers to the spatial resolution of the data or the spatial resolution in the habitat at which ecological processes are affected. While grain usually refers to the finest spatial resolution within a data set it also refers to the resolution of habitat at which the ecological processes of interest may be affected (Lawler et al. 2004).

It is well established that a heterogeneous mixture of different forest stands (e.g., varying successional stages) is important to ruffed grouse success (Gullion 1984, Rusch et al. 2000), but we know much less about the effect of landscape composition and fragmentation on ruffed grouse ecology at larger spatial scales (both in terms of landscape extent and habitat resolution). No studies have investigated the impacts of habitat loss or configuration on ruffed grouse movements over large study areas with a relatively high level of overall forest loss. Changes in patterns of dispersal or seasonal movements due to changes in landscape may have important impacts on the distribution and spatial population dynamics of ruffed grouse. For example, if the likelihood, rate, or distance of movement changes with landscape characteristics and the likelihood, rate, or distance of movement affects survival probability, then a change in amount of forest or landscape connectivity may have consequences for long-term population persistence and subsequent management strategies.

There has been widespread speculation by ecologists that dispersers experience higher mortality risk and lower reproductive success than philopatric individuals (e.g. Lidicker 1975, Gaines and McClenaghan 1980, Jones 1988, Anderson 1989). Dispersal-related mortality may be due to predation pressure, aggression, stress, energy depletion, or moving through or settling in unfamiliar areas (Greenwood and Harvey 1982, Van Vuren and Armitage 1994). A common assumption across taxa is that increased activity itself can cause an increase in predation risk, although this is only rarely supported by direct evidence in birds and mammals (see Gaines and McClenaghan 1980, Johnson and Gaines 1990 for review). Individuals undergoing natal or breeding dispersal also move through and inhabit unfamiliar space. They may have little knowledge of where to find food in the area (resulting in low energetic efficiency) or of where to find cover from predators (Clarke et al. 1993, Jacquot and Solomon 1997).

Previous studies have attempted to compare survival rates of philopatric and dispersing individuals, both during transience and after settlement. However, most studies use mark-recapture techniques, which may give misleading estimates of survival for long-range dispersers. Most previous survival analyses (telemetry or mark recapture) are also limited by the fact that each individual must be classified as being either a disperser or philopatric. To understand what is causing dispersal-related mortality and to directly test for effects of each possible factor (activity, habitat familiarity) on mortality it is preferable to obtain a direct estimate of the predation-related survival cost to dispersers, for example, by relating predation events to distance moved or rate of movement without having to determine an individual's dispersal status. Because each possible factor (stress, activity, etc.) varies within dispersers and within non-dispersers, we can use this variation to test for an overall effect, regardless of dispersal status.

In this study, we explore large-scale movements in ruffed grouse (*Bonasa umbellus*) in Ohio by characterizing juvenile and adult dispersal, investigating the effect of landscape characteristics on movement behavior and examining the relationship between movement and the risk of predation. In Chapter 1 we investigated the natal and adult dispersal characteristics of ruffed grouse throughout the entire annual breeding cycle, using a behavioral definition of dispersal that does not rely on ad hoc calendar dates or minimum distances between home ranges. We defined dispersal in ruffed grouse as a statistically significant shift in the distribution of locations by an individual bird. For example, juvenile birds were classified as undergoing natal dispersal if a shift occurred between brood ranges in summer-early fall to winter ranges. Once dispersal movements could be accurately identified, we addressed questions related to the proportion of ruffed grouse that disperse and whether this proportion differed with age and sex. Also, when, how far, and at what rate do ruffed grouse disperse and do these measures differ with age and sex? What is the home range size of ruffed grouse and do seasonal home range sizes of non-dispersing ruffed grouse and pre- and post-dispersal grouse differ with age and sex? And how do dispersal characteristics in ruffed grouse in the southern portion of its range compare to those in northern, aspen-dominated portion?

In Chapter 2 we explored whether landscape variables measured at coarse-grained scales could help explain general movement characteristics. We used Akaike Information Criterion (AIC) techniques for model selection to explore the relationship between metrics measuring both landscape composition and configuration and the decision to disperse by adults and juveniles during the fall and spring dispersal periods, their net dispersal distances and rates of movement, and their home range sizes. Our primary goal was to determine whether these landscape variables measured at coarse-grained scales could help explain movement characteristics. The secondary goal was to distinguish between the importance of landscape composition (amount of forest habitat) and configuration (fragmentation) in explaining movement characteristics.

Finally, in Chapter 3 we tested the hypothesis that predation risk is a function of rate of movement and site familiarity using a method of survival analysis based on the extended Cox's proportional hazards model (White and Garrott 1990, Kleinbaum 1996, Hougaard 2000). We modeled mortality due to predation as a function of an individual's rate of movement prior to predation events and included in the models the effect of inhabiting familiar vs. unfamiliar space at the time of a predation event.

Overall, this study provides much-needed empirical data on movement characteristics and improves our knowledge of how to quantify animal movement, factors affecting animal movement, and the role movement and habitat play in the cost of dispersal. This study will also provides insight into the importance of including multiple spatial scales in studies attempting to determine the impact of landscape-level habitat changes on ecological processes. In terms of grouse ecology, this study provides detailed movement and dispersal data for grouse in the southern Appalachian portion of its range, the same region that is experiencing the greatest decline in grouse populations. Ultimately, if habitat loss and fragmentation affect grouse movements and if movement, in turn, affects survival, these results will improve our understanding of ruffed grouse population trends and allow managers to better predict possible impacts of future environmental change.

CHAPTER 1

USING BEHAVIOR-BASED DEFINITIONS OF DISPERSAL TO CHARACTERIZE RUFFED GROUSE MOVEMENTS

ABSTRACT

While the study of dispersal characteristics is critical for a complete understanding of the ecology of many species, defining and measuring dispersal is difficult and detailed data for most species are scarce. The primary objective of this study is to investigate the natal and adult dispersal characteristics of ruffed grouse in Ohio throughout the entire annual breeding cycle, using a behavioral definition of dispersal that does not rely on ad hoc calendar dates or minimum distances between home ranges. Previous studies in the northern portion of its range attempting to measure movements of ruffed grouse have suffered from low sample sizes or were undertaken on only one age class or during only a portion of the year. While we found patterns of dispersal between ages and sexes that were consistent with those expected for birds (e.g., juveniles disperse at greater rates and farther than adults, and females tend to move greater distances than males), we also found some surprising patterns, e.g., a substantial proportion of adults undertake dispersal movements, and many juveniles undergo a spring dispersal. Our results suggest that dispersal may be more prevalent in the southern

than northern portion of the grouse's range and that this high dispersal rate may influence the long-term population trends for grouse in this region.

1.1 INTRODUCTION

Dispersal movements have important consequences for spatial population dynamics, gene flow (Martin *et al.* 2000, Blundell *et al.* 2002), and distribution of individual species (Greenwood 1980, Johnson & Gaines 1990). Habitat loss and fragmentation have also been shown to affect the likelihood and characteristics of dispersal movements (Johnson *et al.* 1992, Keitt *et al.* 1997, Martin 1998, Sutherland *et al.* 2000). Differences in the propensity and length of dispersal movement between sexes and ages within a species also have important ecological implications. Natal dispersal is generally defined as the movement of juveniles from their birth site to the site of first breeding (Greenwood and Harvey 1982) and, for most dispersing animals, is the largest and maybe only long-distance movement made (Sutherland *et al.* 2000). Natal dispersal is generally viewed as the major source of gene flow between populations (Wiklund 1996). While less common, movements by reproducing adults, whether seasonal dispersal between breeding and nonbreeding areas within a single year, or breeding dispersal between successive breeding sites (Clobert *et al.* 2001), can also have important consequences for the survival and lifetime reproductive success of individuals (Clutton-Brock 1988, Newton 1989, Waser 1996, Danchin and Cam 2002).

Despite their ecological importance, detailed measurements of dispersal characteristics for many species are still scarce and sorely needed to better understand both the proximate factors affecting dispersal and the ultimate implications of dispersal for management or conservation (Martin 1998, Sutherland *et al.* 2000, Storch 2003). Movement data are costly and difficult to collect, particularly for highly mobile species at large spatial scales. In addition, high variability among individuals makes it difficult to characterize dispersal in a given population or species. One difficulty is determining when dispersal movement has taken place. This is often species specific and usually involves some degree of subjectivity, the degree of which remains underreported in many studies (White and Garrot 1990, Kernohan *et al.* 2001). Many studies have been able to define dispersal as movement away from well-defined study sites (Cade and Hoffman 1993), islands (Strong and Bancroft 1994, Altwegg *et al.* 2000), nests, or social groups (Palomares *et al.* 2000, Cooper and Walters 2002, Cale 2003), movement between distinct patches in highly fragmented habitats (Brooker and Brooker 2002), or movement into distinct populations (Martin *et al.* 2000).

However, for many species that do not have well-defined, long-term family or social groups, that inhabit relatively contiguous habitat, and that exhibit high variability in both proportions of individuals undergoing natal or adult dispersal and net dispersal distances, defining dispersal remains problematic. One such species is the ruffed grouse (*Bonasa umbellus*), a nonmigratory forest game bird. While survival, habitat use, and management of ruffed grouse have been the focus of studies for over 70 years (Rusch *et al.* 2000), details concerning movements and dispersal are less well known, particularly for adult birds but also for juveniles after their initial fall dispersal. Because the majority of previous studies of ruffed grouse dispersal have been conducted at northern latitudes in aspen-dominated habitats (Rusch and Keith 1971, Gullion 1977, Cade and Sousa 1985, Small and Rusch 1989, Small *et al.* 1991, Clark 1996), little is known about the propensity to disperse or the timing and distances moved of dispersing ruffed grouse in the oak-hickory dominated forests common in the southern Appalachian portion of its range.

Previous radio telemetry studies attempting to measure movements of ruffed grouse either have suffered from low sample sizes (Godfrey and Marshal 1969, Archibald 1975, Archibald 1976) or, due to high annual mortality, have not included data on birds throughout the entire breeding cycle (Small and Rusch 1989, Small *et al.* 1991, Clark 1996). In general, these studies have concluded that juvenile ruffed grouse undertake significant dispersal movements during the fall between summer brood ranges and winter ranges (Bump *et al.* 1947, Godfrey and Marshal 1969, Small and Rusch 1989, Clark 1996). Limited evidence suggests that a small proportion of juveniles also disperse between winter ranges and spring breeding ranges (Small & Rusch 1989, Small *et al*. 1991, Rusch *et al*. 2000). In addition to focusing only on the fall season, previous studies have concentrated only on the natal dispersal of juveniles and have not investigated the degree to which adults shift locations between seasons or breeding sites.

The primary objective of this study is to investigate the natal and adult dispersal characteristics of ruffed grouse in Ohio throughout the entire breeding cycle, using a behavioral definition of dispersal that does not rely on ad hoc calendar dates or minimum distances between home ranges. We defined dispersal in ruffed grouse as a statistically significant shift in the distribution of locations by an individual bird. Juvenile birds were classified as undergoing natal dispersal if a shift occurred either between brood ranges in summer-early fall to winter ranges or between winter ranges to a breeding range in spring. Adults underwent seasonal dispersal if shifts occurred between non-breeding summer/fall ranges and winter ranges or between winter ranges and spring breeding ranges.

In this study, we addressed the following questions.

1. What proportion of ruffed grouse disperse and does this proportion differ with age and sex? In ruffed grouse, as in birds in general, dispersal is usually found to be more common among juveniles than adults and natal dispersal more common among females than males (Greenwood 1980, Clarke *et al*. 1997).
2. When, how far, and at what rate do ruffed grouse disperse and do these measures differ with age and sex?
3. What is the home range size of ruffed grouse and do seasonal home range sizes of non-dispersing ruffed grouse and pre- and post-dispersal grouse differ with age and sex? Accurately classifying individuals as dispersers or non-dispersers and identifying the timing of dispersal periods allowed us to select appropriate locations to use in estimating and making comparisons of home ranges that do not include long range dispersal movements.
4. How do dispersal characteristics in ruffed grouse in the southern portion of its range compare to those in the northern, aspen-dominated portion?

1.2 METHODS

1.2.1 STUDY SITES

The study was conducted at two sites in southeastern and east central Ohio from 1996 to 1999. The sites were centered on Waterloo Wildlife Area in Athens County and

Woodbury Wildlife Area in Coshocton County. Each study site included the state-owned wildlife area and surrounding private lands within 15 km. The sites were characterized by a mixture of early successional to 40+ year old oak-hickory forest and agricultural fields.

1.2.2 RADIO TELEMETRY

Each fall, from 1 August to 10 October, 35 – 50 birds were trapped at each site using modified lily-pad traps (Dorney and Mattison 1956). Radio transmitters (Advanced Telemetry Systems, Isanti, MN) were attached with a necklace harness (Amstrup 1980) of Teflon-coated woven wire. Mean transmitter weight was 11 grams. Only birds weighing more than 250 g were fitted with transmitters to ensure that the transmitter was no more than 5% of the bird's body weight (Fuller 1987). Expected battery life of transmitters was 320-500 days. Transmitters were distributed as equally among all age-sex categories as possible (approximately 55% adult, 45% juveniles and 57% males, 43% females). In all, a total of 193 birds were tagged and tracked over the course of three years.

Attempts were made to locate all tagged birds at least 3 - 4 times per week from August 1 through May 30 and at least bi-weekly during June and July. Individual locations were calculated using the maximum likelihood estimator method (Lenth 1981) with a minimum of three azimuths taken within a span of 10 minutes. Lenth's method generates a 95% error ellipse of the bird's location. Only locations with 95% error ellipses smaller than 2 ha were used in distance calculations (92% of all locations).

All transmitters were equipped with mortality-mode switches (i.e., when the transmitter remains stationary for 6-8 hours, the pulse rate doubles). This allowed for quick location and recovery of dead birds. After necropsy, all recovered birds were classified as killed by avian, mammalian, or unknown predators, or as dying by other causes (e.g., road kill) (Einarsen 1956, Dumke and Pils 1973). In addition, each bird was equipped with a reward leg band that facilitated the identification of birds harvested during the hunting season (10 Oct – 29 Feb). Over the three-year study, the fate of 13% of tagged birds was unknown, most likely due to transmitter failure. To avoid any effect of short-term stress due to capture and handling or from transmitters, birds that died within 7 days of capture were not included in the analyses.

1.2.3 DEFINING DISPERSAL EVENTS

Dispersal can be statistically defined as a significant shift in the distribution of spatial locations by an individual between two time periods. We determined the dispersal status for birds in our study using a procedure to directly test for a shift in the use of space over time by individual birds. Many studies of species in which dispersal is highly variable in a relatively contiguous habitat have used locations from an a priori period and calculated a mean location or home range estimate and then measured some minimum distance between the mean location or home range centroid or minimum overlap in home range boundaries. Besides difficulties with the arbitrary nature of determining relevant time periods, testing for differences in mean locations or home range centroids (e.g. with a Hotelling's *T*-test) ignores variances and covariance in *x-y* coordinates due to range expansion and contraction (White and Garrot 1990). In addition, most home range estimation methods require assumptions regarding the distribution of locations (e.g., uniform vs. center-weighted) or do not yield a measurement of accuracy (e.g., estimates from non-parametric techniques lack confidence intervals). Thus, it is better to test for shifts in location using the raw data than to make inferences based on locations estimated from a home range model (White and Garrot 1990, Kernohan *et al*. 2001).

A powerful non-parametric method for directly detecting the differences in distribution of spatial locations is based on the multi-response permutation procedure (MRPP) (Mielke & Berry 1982, Biondinai *et al*. 1988, Cade & Richards 2001). This procedure tests whether two or more sets of locations come from a common distribution by comparing the observed intragroup average distances between locations with the average distance that would result from all possible combinations of locations. While this procedure has been proposed as a general alternative to other nonparameteric tests in ecological studies (Biondini *et al*. 1998) and has been used in studies of habitat associations (e.g. May and Guitierez 2002), it has rarely been used to explicitly define dispersal movements (but see Blundell *et al.* 2002).

The first step in the MRPP analysis was to determine pre- and post-dispersal time periods over which sets of locations could be compared to see if significant shift in use of space had occurred. Because initial inspection of the telemetry data showed birds apparently beginning and ending dispersal over broad ranges of dates from late September to December, we wished to avoid making a priori assumptions about exact dates when dispersal was taking place at our study sties. We established general dates for these periods by examining all birds captured before 1 September and surviving past 15 January, conservative dates in which we were confident fall dispersal was unlikely to be occurring. A preliminary MRPP analysis on this subset of birds showed that no bird exhibited a significant shift in space use before 9 September. We defined all locations between July 25 (when we started locating birds at least three times per week) and September 9 as occurring within the summer pre-dispersal period. We chose locations between 15 December and 15 February as occurring within the winter post-dispersal period, based on an examination of dispersal termination dates (see *1.2.4 TIMING AND DURATION OF DISPERSAL PERIODS* below) of these preliminary birds and a similar preliminary MRPP analysis for the onset of spring dispersal movements. The winter period also became the pre-dispersal period for detection of spring dispersal movements.

Our main fall MRPP analysis then included all birds that were located more than five times during the pre-dispersal summer period (before 9 September) and more than five times during the post-dispersal winter period. If the MRPP test between these locations resulted in $p < 0.01$, then the bird was classified as a fall disperser and the net dispersal distance was calculated as the straight-line distance between the centers of the pre-dispersal and post-dispersal locations (Figure 1.1a,b). If a comparison of the locations resulted in $p > 0.05$, then the bird was classified as a non-disperser (Figure 1.1c). To reduce the chance of misclassifying birds whose locations exhibited only a weak shift all birds with $0.01 < p < 0.05$ in the MRPP test were classified as unknown. Any bird that did not survive long enough to be located at least five times within the winter period was not classified and not included in any subsequent analyses.

The MRRP test is extremely powerful in detecting even slight shifts in space use and may detect significant shifts in locations at distances that may not be biologically meaningful (White and Garrot 1990). We assumed a priori that any straight-line distance between pre-dispersal and post-dispersal locations less than 250 m was biologically insignificant, even if the shift in location was statistically significant (i.e. $p < 0.01$) based on the MRPP test. This was based on the accuracy of the telemetry locations (< 2 ha 95% error ellipses) and on previous estimates of ruffed grouse home range sizes.

Many of the birds in the study were first captured after 9 September and, in order to still accurately identify dispersal in as many of these birds as possible, we developed a multi-step approach using rules based on the results of the main MRRP analysis. Late capture increased the likelihood that a bird had already initiated or completed dispersal by its capture date, and thus we could not confidently classify it as a non-disperser, even if we saw no shift in location. However, birds captured late that subsequently made a large shift in location could still be confidently identified as dispersers. In the original MRPP analyses we found that 100% of shifts in locations that were at least 500 m were significant at the $p < 0.01$ level (Figure 1.2). Thus, for those birds for which we did not have enough early locations (i.e., five locations we could confidently assume to be pre-dispersal), we classified as dispersers those individuals that permanently moved at least 500 m from their initial point of capture.

Because birds could have moved less than 500 m but still have undergone a shift in use of space (as did 29% of the birds in the original MRPP analysis), we performed a final iterative MRPP analysis on those birds excluded from the main MRPP analysis due to a late capture date and that did not permanently move 500 m from their capture location. MRPP tests were performed between the winter period locations and subsets of locations consisting of the first 3 to 7 post-capture locations. If a significant shift ($p < 0.01$) was found in any of iterative MRPP tests, then the bird was classified as a disperser (unless the distance was less than 250 m, in which case it was classified as unknown). If no significant *p*-value was found in any of the tests, the bird was also classified as unknown. Using only a small number of early locations (e.g., 3) increased the chance that the null hypothesis of no shift would falsely be accepted; increasing the number of early locations increased the chance that a dispersing bird had already moved to its new location, again increasing the likelihood of falsely accepting the null hypothesis of no shift. Thus, this was a conservative test to classify dispersers.

The determination of dispersal for the birds in our study can be summarized as follows. We first established pre– and post-dispersal periods in which dispersal was not occurring by performing a preliminary analysis of a subset of birds using conservative dates. We then eliminated all birds that did not survive into the winter post-dispersal period from any subsequent analysis. Data from all birds located at least five times within both pre- and post-dispersal periods were then analyzed using the MRRP procedure. These birds were classified as dispersers, non-dispersers, or as unknown based on their MRPP *p*-values and only these birds were used in calculations of proportions of dispersers and non-dispersers in the population. Birds not included in the MRPP analysis due to a late capture date could not be classified as non-dispersers, but could be classified as dispersers based on a permanent move of at least 500 m or subsequent iterative MRPP tests using initial capture locations. Late capture birds not moving 500 m or not classified using the iterative MRPP tests were left as unknowns. Data from all birds classified as dispersers were used to characterize net dispersal distances.

To classify spring dispersal we used the same procedure as outlined for classifying fall dispersers with the substitution of different dates for pre- and post-dispersal locations. All locations between the winter dates of 15 Dec. and 15 Feb. were assumed to be within the spring pre-dispersal period. Due to differences in the timing of breeding activity between the sexes, spring post-dispersal periods were defined differently for males and females, with the male post-dispersal period based on observations of drumming behavior and female post-dispersal periods based on nesting dates. In Ohio most males began drumming by 1 April (D. A. Swanson, personal communication) so the male post-dispersal period was defined as 1 April to 1 June (when birds were no longer tracked multiple times per week). Females in our study began nesting by 15 April (unpublished data), so the female post-dispersal period was defined as 15 April to 1 June. In addition, no iterative MRPP analysis was performed for those spring birds that died before the post-dispersal period.

We tested for differences in the proportion of birds undergoing dispersal between different age/sex categories using *G*-tests for independence (Sokal and Rolf 1995). Individual tests were conducted between adults and juveniles, juvenile male and juvenile females, adult male and adult females, study years, and study sites. To avoid the problem of birds classified as unknowns, when comparing proportions dispersing we used only those birds included in the initial MRPP analysis to perform tests.

1.2.4 TIMING AND DURATION OF DISPERSAL PERIODS

We explored the timing and length of dispersal periods by first defining initiation and termination dates for all birds classified as dispersers. Initiation of fall dispersal was defined as the date a dispersing bird permanently moved at least 500 m from either its mean summer pre-dispersal location or capture location if it was captured after 9 September. The end of the dispersal period was defined as the date at which the bird first moved within 500 m of its mean winter post-dispersal period location. Since we did not locate the birds daily, we used the date midway between the dates of the two relevant locations for the initiation and termination dates. In addition, if there was a significant gap in locations due to a temporary inability to either locate the bird or acquire accurate locations we did not include the bird in the analysis. If a bird had a gap of at least 15 days or two or more gaps of at least 10 days each we did not use the bird in the analysis of dispersal timing or movement rates (see *1.2.6 MOVEMENT RATES* below).

Variation in timing and duration of dispersal movements was high and the use of 500 m aided in accurately measuring only final dispersal movements; however, it also made it impossible to measure the timing of short-range dispersers. If a bird was classified as a disperser by the MRPP analysis but never permanently moved greater than 500 m from its pre-dispersal location or was always within 500 m of its post-dispersal location, then no dispersal dates were estimated. Thus, the birds used in the analysis of the timing and duration of dispersal periods do not contain short-range (i.e. less than 500 m) dispersers.

In addition, our definition for initiation and termination of the dispersal periods meant they did not include either pre- or post-dispersal exploratory movements. Because it was possible for a bird to begin long-range movements and return to its pre-dispersal range, the "initiation" definition reflects the latest date a bird may have started its final dispersal and does not incorporate pre-dispersal exploratory movements. Likewise, a bird may have continued to explore and move additional long distances before settling down in its final winter post-dispersal range, so this “termination” date is actually the earliest possible date a bird may have completed its dispersal and does not incorporate post-dispersal exploratory movements. Thus, we are measuring the timing of the actual shifts in locations resulting from dispersal, rather than the timing of all dispersal-related movement.

We determined the timing and duration of spring dispersal periods using the procedure as outlined for fall dispersal periods but substituting appropriate dates for permanently leaving or entering the spring pre- and post-dispersal periods.

The effects of age, sex, study site, and study year on dispersal initiation dates, termination dates, and duration of dispersal periods was tested using General Linear Models for fall and spring data. To investigate the relationships between dispersal timing and distance moved we also calculated the Pearson correlation coefficient between net dispersal distances and the timing and duration of fall and spring dispersal periods.

1.2.5 NET DISPERSAL DISTANCES

Fall net dispersal distances were defined for all dispersers as the straight-line distance between the mean locations of all summer pre-dispersal period locations and all winter post-dispersal period locations as defined in the MRPP analysis. The capture location was used as the starting point for calculations of distances for dispersers caught after the end of the pre-dispersal period (i.e., 9 September). Since we found evidence for a negative correlation between extremely late capture dates (i.e., after 30 September) and fall net dispersal distances, we excluded any bird that was captured after 30 September from distance analyses. Spring net dispersal distances were defined as the straight-line distance between the mean locations of all winter pre-dispersal period locations and spring post-dispersal period locations. We also calculated yearly net dispersal distances for all birds that survived into the spring post-dispersal period and had dispersed at least once during the year (either during the fall, spring, or both). The yearly net dispersal distance was defined as the straight-line distance between the summer pre-dispersal mean location (or capture location) and the spring post-dispersal period mean location.

The effects of age, sex, study site, and study year on fall, spring, and yearly net dispersal distances were tested using General Linear Models. All distances were transformed using the Box-Cox procedure in Minitab (Minitab 13) to meet assumptions of normality.

1.2.6 MOVEMENT RATES

We used data from all dispersing birds in which accurate dispersal periods could be identified (as described above in 1.3.3 DEFINING DISPERSAL EVENTS*)* to investigate the difference in movement rates between pre-dispersal, dispersal, and post-dispersal periods. We calculated movement rates (meters/day) by summing the distances between successive locations and dividing by the total number of days in the period. We used a repeated measures ANOVA to test for differences in movement rates between the pre-dispersal, dispersal, and post-dispersal periods for both fall and spring dispersers.

1.2.7 HOME RANGE SIZE

We calculated home ranges separately for non-dispersing and dispersing birds using the fixed kernel method with least squares cross validation for the smoothing factor (Worton 1989). While kernel home range estimators tend to bias home range size upward when using a relatively small number of locations (particularly less than 30), we chose the fixed kernel method because it is less biased than the adaptive kernel at smaller sample sizes (Seamons *et al.*1999, Kernohan *et al.* 2001). All home range sizes used in the analyses were based on the 95% contour interval and were calculated using the animal movement extension (Hooge and Eichenlaub 1997) for ArcView 3.1 (ESRI 1999).

Since non-dispersing birds, by definition, did not shift their use of space within a season, we used all locations from date of capture until the end of the winter post dispersal period (i.e. 15 February) to estimate a fall/winter home range for all birds classified as fall non-dispersers. We used all locations between 15 February and the end of the spring post-dispersal period (1 June) to calculate a spring home range for all birds classified as spring non-dispersers. Birds that did not have at least 10 locations within each period were not used in the analysis.

We used locations to estimate pre- and post-dispersal home ranges for dispersing birds based on the dates used in the MRPP analysis for summer pre-dispersal periods (25 July - 9 September) and winter post-dispersal periods (15 December – 15 February). Any bird not having a minimum of 10 locations within these periods was not included in the analyses. While this eliminated any bird captured relatively late in the fall from the analysis of pre-dispersal home range size, it assured that locations during dispersal were not included in the pre-dispersal home range estimates. Spring pre- and post-dispersal home ranges were estimated using locations from periods used in the spring MRPP analysis. Spring pre-dispersal home ranges were estimated using all location from 15 December to 15 February and spring post-dispersal home ranges were estimated using all locations from 1 April to 1 June for males and 15 April to 1 June for females.

The effects of age, sex, study site, and study year on fall and spring non-dispersing, pre-dispersal, and post-dispersal home ranges were tested using General Linear Models. All home range sizes were transformed using the Box-Cox procedure in Minitab (Minitab 13) to meet assumptions of normality.

MRPP tests were performed using Blossom software (Cade and Richards 2001), *G* tests for independence were conducted in MS Excel, and all additional analyses were performed using Minitab (Minitab 13).

1.3 RESULTS

1.3.1 SAMPLE POPULATION

During the three-year study we obtained usable locations on a total of 193 birds (85 juveniles and 108 adults). Of the 84 juveniles alive at the beginning of a fall season, 30 individuals died before they could be located at least 5 times within the winter post-dispersal period and were unable to be classified as dispersing or non-dispersing individuals. Of the 108 adults captured during the fall season, 13 individuals died before they could be located at least 5 times within the winter post-dispersal period and were unable to be classified. In addition, 6 juveniles and 32 adults were unable to be classified due to late capture or indeterminate nature of fall movements (see *1.3.3 DEFINING*

DISPERSAL EVENTS above). Thus, the largest possible number of individuals used in any fall analysis was 48 juveniles and 63 adults. Of 39 juveniles and 78 adults alive at the beginning of a spring period, 10 juveniles and 28 adults died before they could be classified as dispersing or non-dispersing. Thus, the largest possible number of individuals used in the spring analyses was 29 juveniles and 45 adults. A total of 76 birds survived long enough to be classified as dispersers or non-dispersers during both fall and spring of the same study year and were used in the yearly analysis.

1.3.2 DISPERSAL DECISIONS

To investigate trends in the proportion of birds undergoing dispersal in the fall we analyzed a subset of birds consisting of 15 juveniles and 47 adults (out of the 48 juveniles and 63 adults that had survived to the winter period). These were individuals captured early enough in the fall to be classified as dispersing or non-dispersing using the MRPP procedure. Those birds included in the MRPP analysis whose dispersal status was still unknown (i.e. $0.01 < p < 0.05$) were used to calculate the proportion in each movement class illustrated in Figure 3, but were not used in the G-tests for independence used to compare differences in the proportions between age/sex categories.

Overall, approximately one half of all grouse underwent dispersal during the fall (Figure 1.3a); however, there were significant differences between ages and sexes in the proportions undergoing dispersal. Nearly 75% of juveniles underwent dispersal in the fall, significantly greater than the approximately 45% of adults that dispersed ($n = 62$, G-test for independence, $p = 0.018$; Figure 1.3a). A larger proportion of adult females underwent fall dispersal than adult males ($n = 47$, G-test for independence, $p = 0.048$;

Figure 1.3a). The proportion of juvenile males and females undergoing dispersal did not differ (*n* = 15, *G*-test for independence, *p* = 0.112). The proportion of birds dispersing also did not differ between study sites (*p* = 0.38) or years (*p* = 0.26).

In the spring, approximately 45% of all birds underwent dispersal (Figure 1.3b). There were no significant differences in the proportion of birds dispersing between any age or sex categories (Figure 1.3b) or between study sites and years. Comparisons between seasons revealed only a significantly higher proportion of juvenile males that underwent dispersal in the fall than in the spring (*n* = 51, *G*-test for independence, *p* = 0.007) (Figure 1.3a, b).

Overall, 63% of the 76 birds that survived long enough to be classified as dispersers or non-dispersers during both fall and spring of the same study year underwent at least one dispersal event during the year (either in the fall or spring). Juveniles were twice as likely to undergo at least one dispersal event per year as adults (90% versus 45%)(*n* = 76, *G*-test for independence, *p* < 0.001). While 72% of females and 57% of males underwent at least one dispersal event, the difference was not significant (*n* = 76, *G*-test for independence, *p* = 0.11). It was unlikely for a bird (particularly a juvenile) to disperse in the spring if it had not also undergone fall dispersal. Of the "yearly dispersers" (i.e. those birds that dispersed at least once during the year), 44% dispersed in both the fall and spring, 38% dispersed in the fall but not the spring, and only 19% dispersed in the spring and not the fall. In addition, of those birds that dispersed only in the spring, only 12% were juveniles.

1.3.3 TIMING AND LENGTH OF DISPERSAL PERIODS

Dispersal periods were identified for 34 of the birds that were classified as dispersing in the fall and 10 of the spring dispersing birds. The mean date for initiating dispersal in the fall was 10 October and ranged from 11 September to 25 November. The mean date for termination of dispersal was 3 November and ranged from 25 September to 14 January. The mean length of dispersal periods was 21 days and ranged from 2 to 78 days. There were no differences in either the dispersal dates or length of the dispersal period between age, sex, study site, or study years. Fall net dispersal distance was negatively correlated with the date dispersal was initiated (Pearson correlation coefficient = - 0.422, $p = 0.013$) and positively correlated with the dispersal ending date (Pearson correlation coefficient = 0.338, $p = 0.05$). Birds tended to move greater distances the earlier in the fall they initiated dispersal and the later in the year they ended dispersal (Figure 1.4a). Fall net dispersal distances were also positively correlated with the overall length of the dispersal period (Pearson coefficient = 0.637, $p < 0.001$). Birds that moved for longer periods tended to move greater distances (Figure 1.4b).

The mean date for initiation of spring dispersal was 1 March and ranged from 9 February to 2 April. The mean date for termination of spring dispersal was 7 March and ranged from 20 February to 15 April. Dispersal periods tended to be shorter in the spring than in the fall, with the mean length of spring dispersal periods 11.5 days and ranging from 3 to 29 days.

1.3.4 NET DISPERSAL DISTANCE

Net dispersal distances were calculated for all birds classified as dispersing by either the MRPP analysis or because they moved more than 500 m from their initial capture location. The overall mean fall net dispersal distance was 2.4 km (*n* = 67). Juveniles moved significantly farther in the fall than adults (mean distance of 3.7 km versus 0.8 km) (General Linear Model, *F* = 12.18, *p* = 0.001; Table 1.1; Figure 1.5) and juveniles accounted for nearly all long-distance movements, exhibiting 94% of the movements greater than 1.5 km (Figure 1.6a). The general linear model did not indicate significant differences in distances between sexes, age, or sites. Although juvenile females had a mean movement distance of almost 4 km compared to only 2.3 km for males, the difference was not significant. Juvenile males rarely dispersed farther than 3 km, with females accounting for 78% of all juvenile dispersal movements over this distance (Figure 1.6b). No differences in net dispersal distances were found between sites but mean distances did differ between years (General Liner Model, *F* = 6.69, *p* = 0.003; Table 1.1) with birds moving farther in year 2 of the study (year 1 = 2.0 km, year 2 = 3.4 km, and year 3 = 1.4 km). The mean spring net dispersal distances was 0.670 km (*n* = 30), considerably less than in the fall, and no significant differences were found between sites, years, or age/sex categories (Table 1.1; Figure 1.5 & 1.7a, b).

The mean yearly net dispersal distance (i.e. linear distance between the fall pre-dispersal period location midpoint and spring post-dispersal location midpoint) for the birds surviving into the spring post-dispersal period was 1.7 km with the only significant difference in distances between juveniles and adults (mean distance of 2.9 km versus 0.7 km) (*n* = 48, General Linear Model, *F* = 19.83, *p* <0.001) (Table 1.1; Figure 1.8). A comparison of yearly and fall net dispersal distances for spring dispersers illustrates that most movement away from their summer pre-dispersal location occurs in the fall and few birds are moving back great distances towards their pre-dispersal location in the spring (Figure 1.9).

1.3.5 MOVEMENT RATES

Among the birds for which we could identify individual dispersal periods (with dates of dispersal initiation and termination), we found significantly higher movement rates during the dispersal period itself compared to the periods both before and after dispersal occurred ($n = 32$, repeated-measures ANOVA, $F = 19.09$, $p = <0.001$). In the fall, birds moved an average of 219 m/day compared to 97 m/day in the period before dispersal and 114 m/day during the winter after dispersal was completed (Figure 1.10). There was no correlation between the movement rate during dispersal and the final distance moved. Movement rates for spring dispersers were also significantly higher during the dispersal period than during pre- or post- dispersal periods ($n = 10$, $F = 4.09$, $p < 0.037$). Spring dispersing birds moved 157 m/day while dispersing compared to 104 m/day during the winter and 57 m/day after dispersal was completed (Figure 1.10).

1.3.6 HOME RANGE SIZE

There was no difference in overall mean home range sizes between fall and spring non-dispersing birds (Figure 1.11a). However, the age × sex interaction term in the general linear model indicated significant differences among ages and sexes during the fall ($n = 65$, $F = 16.6$, $p < 0.001$; Table 1.2), with juvenile males having larger home ranges than juvenile females or adult birds (Figure 1.11b). Study year also had a significant effect on fall home range sizes, with birds in year 2 of the study having larger home ranges than in years 1 or 3 (*n* = 65, *F* = 8.04, *p* = 0.001; Table 1.2). Among spring non-dispersing birds there appeared to be a trend towards juveniles also having larger home ranges than adults but the effect of age or sex was not significant (Figure 1.11b; Table 1.2). Non-dispersing birds had the largest number of locations included in estimates of home ranges size, with a median number of locations per bird of 41 in the fall and 31 in the spring.

Among fall dispersing birds, pre-dispersal home range sizes were smaller than post-dispersal home range sizes (Figure 1.11a). This appears to be driven by differences in juvenile pre- and post-dispersal home ranges, although the age x period interaction term was not significant (*n* = 40, *F* = 3.95, *p* = 0.054; Table 1.3; Figure 1.11c). The model did not indicate any difference between pre- or post-dispersal home range sizes in the spring, although the number of spring dispersers included in the analysis was small (Figure 1.11c). There was also no effect of sex, year, or site on either pre- or post-dispersal home range sizes during either fall or spring. The median number of locations for fall pre-and post-dispersal home range estimates was 15 and 29 per bird in the fall and 18 and 13 per bird during the spring.

1.4 DISCUSSION

Overall we found that natal dispersal is extremely common in ruffed grouse with 90% of juveniles undergoing shifts in location either during the fall or spring dispersal periods. While this was expected based on previous studies of grouse and birds in general, less expected was the prevalence of seasonal dispersal among adults, with 45% of adults also undergoing significant shifts in location during the fall and spring.

We found that 75% of our juvenile birds underwent dispersal in the fall with no differences in the likelihood of dispersal between males and females. Among juvenile ruffed grouse, inbreeding avoidance is likely a significant ultimate factor driving fall dispersal, as it is for most species that undergo natal dispersal (Greenwood and Harvey 1982). Juvenile ruffed grouse remain with their brood mates and mother throughout the summer and into the fall season. While we captured too few broods to estimate detailed characteristics of brood break-up, previous studies have shown that brood breakup is usually shortly followed by large scale movements (Godfrey and Marshal 1969, Small *et al.* 1991).

Immediate factors also driving fall dispersal in juvenile as well as adult ruffed grouse include 1) the establishment of new breeding territories (i.e. natal dispersal by juveniles or breeding dispersal by adults), 2) differences in seasonal habitat requirements (i.e. seasonal dispersal) or 3) a combination of both. Ruffed grouse have a promiscuous mating system with males establishing territories and attempting to attract females by drumming and displaying (Bump *et al.* 1947, Johnsgard 1989). Females do not defend territories and may visit more than one male in a season (Johnsgard 1989, Rusch *et al.* 2000). The occurrence of male drumming behavior in the fall suggests that at least a portion of males defend their spring breeding territories in the fall (Gullion 1967, Rusch *et al.* 2000) and juvenile males may be attempting to establish new territories in the fall as well.

While 43% of juveniles disperse in the spring, our data indicate that fall is the more significant of the two seasonal dispersal periods. A higher proportion of juveniles dispersed in the fall and while many birds also shifted locations in the spring, it was very rare for a juvenile to disperse only in the spring. Only 2 of 25 birds that dispersed at least once did so in the spring and not the fall. Juvenile net dispersal distances were also shorter in the spring than fall (3.7 km vs. 0.7 km) and it is clear that most of the movement away from the pre-dispersal brood range is done in the fall. That juveniles dispersed in approximately the same proportions and the same distances as adults in the spring also may be evidence of these shifts in location due to differences in seasonal preferences between winter and spring breeding habitats, as opposed to the innate natal dispersal behavior exhibited at brood break up.

In general, the percentage of juveniles that dispersed in our study was higher than that found in northern portions of ruffed grouse range. Clark (1996) reported that 48% of juvenile ruffed grouse underwent fall dispersal movement in a study conducted in central Michigan in which dispersal was defined as permanent movement away from the trapping location during the fall or winter. This should be considered a minimum estimate, however, as birds first captured late in the fall (e.g., first week October) were included in the estimates and dispersal may already have been completed.

In their 6-year study of in Wisconsin, Small *et al.* (1991) acquired daily locations of birds, allowing them to identify distinct "transient" periods using a dispersal index based on a running sum of daily movement rates. Thus, they did not classify dispersal per se, but periods of "transience" when individual movement rates increased. They found similar proportions of juveniles dispersing in the fall, with 66% of juvenile males and

72% of juvenile females undergoing “transient” periods. However, they found only 27% of juveniles undergoing transience in the spring, compared with 43% of juvenile dispersing in our study.

We found that 45% of adults underwent dispersal both in the fall and in the spring, but found significant differences between the sexes only in the fall. Seasonal habitat requirements are likely to play the strongest role in adult dispersal movements with fall dispersal due to different seasonal cover and food requirements as opposed to the establishment of new territories. Adult males rarely change breeding territories once established (Gullion and Marshall 1968, Rusch and Keith 1971) and fall drumming is likely due to males defending territories from dispersing juvenile males. The fall male defense of territories may help explain the significantly smaller percentage of adult males (25%) than females (57%) that dispersed.

We also saw an overall higher proportion of adult birds disperse in our study than in Wisconsin and Michigan. Clark (1996) found approximately 36% of 45 adults underwent fall dispersal and Small et al. (1991) tracked 60 adults during the fall in their study and found that 9% of adult males and 52 % of adult females exhibited transience (Small *et al.* 1991).

The importance of adequate cover and food resources may contribute to the relatively high proportion of birds undergoing seasonal dispersal in our study. For example, grouse may have to shift their ranges during winter to find appropriate understory and coniferous cover. Habitat differences between the northern and southern portion of their range may also account for the overall higher proportion of birds that dispersed in our study compared to those in Wisconsin and Michigan. Optimal winter habitat for ruffed grouse consists of forest with high stem density or dense cover that provides protection from predation. In northern forests, this is provided by young aspen and poplar stands (*Populus spp.*) and deep snow for roosting cover (Gullion 1977). Buds and catkins of nearby mature aspen stands can also provide winter food. Studies of habitat use in the southern portion of its range indicated that in the absence of aspen, grouse prefer areas with dense understudy and low coniferous vegetation in the winter and for roosting (White and Dimmick 1978, Thompson and Fritzell 1988). At our study sites, less than 3.5% of forest was classified as coniferous and most were pines (*Pinus spp*.) with relatively sparse foliage (NLCD data, Ohio Division of Wildlife).

Several studies have also indicated the importance of winter food availability and quality in the absence of aspen dominated forests. Grouse in the Appalachians often undergo prolonged periods of nutritional stress and energy deficiency during winter months (Norman and Kirkpatrick 1984, Hewitt and Kirkpatrick 1997). Hewitt and Kirkpatrick (1996) found that grouse must forage longer on herbaceous plants and fruits to acquire energy equivalent to that from aspen buds and it has been proposed that winter food may be a limiting factor for ruffed grouse in the central and southern Appalachian portions of its range (Servelo and Kirkpatrick 1987).

It is generally expected in most birds that juveniles undergoing natal dispersal move the longest distances within a population (Greenwood 1980, Greenwood and Harvey 1982) and the mean net dispersal distance was significantly greater for juveniles in the fall than adults. While our data did not indicate a significant difference between net dispersal distances for males and females, females did make the majority of long distance (> 3 km) movements in the fall. Longer natal net dispersal distances by females are to be expected under the Greenwood (1980) mating system hypothesis regarding sex bias of dispersal characteristics; males within resource-defense mating systems should remain close to the natal area and thus be less likely to disperse than females. If male ruffed grouse are establishing territories in the fall, then it may be advantageous for them to stay in more familiar areas and for females to assess as many males as possible. There are few empirical data on the degree to which female grouse visit male territories in the fall. However, Small and Rusch (1989) proposed that female selection of potential mates in the fall accounted for greater total and net movement distances and rates in the fall by females than males in their study. Females could be visiting multiple male territories, perhaps in an effort to gauge the quality of males in an area.

The overall mean distances moved by juvenile males (2.3 km) and females (4.0 km) in our study are similar to those found in Wisconsin by Small and Rusch (1989). They reported a mean fall juvenile male distance of 2.1 km (n = 14) and female distance of 4.8 km (n=10). Small and Rusch (1989) also tracked a small number of juveniles in the spring and again found comparable distances to birds in our study; males dispersed a mean distance of 0.86 km (n = 4) and females a mean distance of 0.3 km (n=2). Clark (1996), however, reported overall shorter fall net dispersal distances for birds in Michigan, with adults moving a mean distance of 1.5 km (n = 24) and juveniles 1.2 km (n =13) with no differences found between sexes.

Overall, the largest home ranges were found in birds that were settling after undergoing dispersal. Both juvenile and adult dispersers had home ranges of almost 100 ha after dispersal, while juvenile pre-dispersal home ranges and adult non-disperser home ranges were less than 50 ha. Birds moving into new areas likely are undergoing at least some exploratory movements while searching for adequate cover or food resources. Among non-dispersing birds, fall juveniles alone had comparably sized home ranges to the pre-dispersal home ranges of dispersing birds (approximately 100 ha). These large home range sizes may be due to juveniles that attempted to establish territories but failed. That home range sizes were almost four times as large for these juvenile males than for the pre-dispersal ranges of juveniles that did disperse is consistent with males exploring neighboring areas but then returning to the brood range. Small *et al.* (1991) also reported periods of minor increased movement during the late fall and early winter among juveniles but considered them just slight shifts in winter range. They could correspond to our increase in post-dispersal home range sizes.

In general, previous studies show home ranges of ruffed grouse to be larger in southern than in northern portions of their range (Rusch *et al.* 2000) and, while our estimates of home range size do not necessarily contradict this trend, few previous studies make comparable estimates of age-, sex-, and season-specific home ranges using the same methodology (e.g., using adaptive kernel estimates and separating dispersers from non-dispersers). Our estimates of home range sizes for non-dispersers were comparable to those from studies that specified the inclusion of only non-dispersing birds in their sample. Clark (1996) found fall non-dispersing birds in Michigan to have average home range sizes of 35 to 43 ha at two different sites at two different years using the minimum convex polygon method for calculating home range size. Thompson and Fritzell (1989) found adult territorial males in Missouri to have an average spring home range size of 68 ha in the spring as estimated using the 95% harmonic mean.

In addition to characterizing ruffed grouse movements over a large portion of the year, taking into account age and sex, our definition of dispersal allowed an accurate characterization of the dispersal and movement characteristics of ruffed grouse without the use of a priori minimum distances or home range estimates despite the fact that these birds live in and move through relatively contiguous habitat. Our results were consistent with previously established expectations in birds regarding bias in dispersal characteristics between ages and sexes. In addition, we were able to document the prevalence of seasonal dispersal among adults and spring dispersal among juveniles in the southern portion of it range.

The high proportion of grouse that shifted their locations in the spring as well as the fall may have important implications for grouse population dynamics and distribution. For example, our analysis of the effect of movement rate and inhabiting unfamiliar habitat indicated a significant increase in predation risk for birds traveling at high rates and into new areas (Chapter 3). Birds undergoing dispersal in our study moved at significantly higher rates during dispersal than during both fall and spring pre- and post-dispersal periods. Dispersing birds are also by our definition moving into areas they have not recently inhabited. Thus, dispersing birds are likely to experience higher predation risk than non-dispersers either during dispersal or immediately after settling. Ruffed grouse populations are historically smaller in the southern portion of their range than in the northern portion (Rusch *et al.* 2000, Dessecker and McCauley 2001). The high proportion of birds that undergo dispersal or move great distances in the southern region may contribute to this difference in regional abundance.

1.5 TABLES

Season	Factor	df	SS (adj.)	F	*p*
Fall	Year	2	0.0200	6.69	0.003
	Site	1	0.0018	1.22	0.274
	Age	1	0.0182	12.18	0.001
	Sex	1	0.0028	1.88	0.176
	Year x Site	2	0.0046	1.55	0.223
	Year x Age	2	0.0083	2.79	0.070
	Year x Sex	2	0.0015	0.50	0.611
	Site x Age	1	0.0029	1.94	0.169
	Age x Sex	1	0.0001	0.04	0.833
	Error	53	0.0790		
Spring	Year	2	0.0014	0.89	0.429
	Site	1	0.0000	0.01	0.905
	Age	1	0.0005	0.69	0.418
	Sex	1	0.0000	0.05	0.828
	Year x Site	2	0.0025	1.59	0.231
	Year x Age	2	0.0017	1.07	0.364
	Year x Sex	2	0.0010	1.22	0.284
	Site x Age	1	0.0016	2.03	0.171
	Age x Sex	1	0.0139		
	Error	18			
Yearly	Year	2	0.7639	0.49	0.618
	Site	1	0.0021	0.00	0.959
	Age	1	15.5025	19.83	0.000
	Sex	1	0.0757	0.10	0.757
	Year x Age	2	3.1191	1.99	0.151
	Year x Sex	2	0.4985	0.32	0.729
	Age x Sex	1	0.0301	0.04	0.845
	Error	35	27.3657		

Table 1.1. General linear model explaining distance moved by dispersing birds in the fall (*n* = 67), spring (*n* = 30), and over the entire year (*n* = 46). Year = 1996, 1997, or 1998; Site = Woodbury or Waterloo; Age = juvenile or adult; Sex = male or female.
Year × Site and Site × Age interaction terms were not included in the yearly model due to the lack of birds at both sites during all years and lack of birds of both ages at both sites.

Season	Factor	df	SS (adj.)	F	*p*
Fall	Year	2	0.2781	8.04	0.001
	Site	1	0.0000	1.82	0.183
	Age	1	0.0336	7.71	0.008
	Sex	1	0.0525	13.91	0.000
	Year x Site	2	0.0943	6.03	0.004
	Year x Age	2	0.0223	3.72	0.031
	Year x Sex	2	0.0000	0.70	0.503
	Age x Sex	1	0.2141	16.60	0.000
	Error	52	0.6707		
Spring	Year	2	0.0168	0.48	0.624
	Site	1	0.0019	0.11	0.748
	Age	1	0.0251	1.43	0.241
	Sex	1	0.0131	0.74	0.395
	Year x Age	2	0.0115	0.33	0.723
	Year x Sex	2	0.0050	0.14	0.868
	Age x Sex	1	0.0006	0.03	0.861
	Error	31	0.5443		

Table 1.2. General linear model explaining home range sizes of non-dispersing birds in the fall (n = 65) and spring (n = 42). Year = 1996, 1997, or 1998; Site = Woodbury or Waterloo; Age = juvenile or adult; Sex = male or female. A Year x Site interaction term was not included in the spring model due to the lack of birds at both sites during all years.

Season	Factor	df	SS (adj.)	F	*p*
Fall	Period	1	0.0137	3.49	0.070
	Year	2	0.0087	1.11	0.340
	Site	1	0.0028	0.70	0.407
	Age	1	0.0067	1.70	0.200
	Sex	1	0.0029	0.73	0.399
	Period x Year	2	0.0012	0.15	0.858
	Period x Site	1	0.0000	0.00	0.997
	Period x Age	1	0.0155	3.95	0.054
	Period x Sex	1	0.0009	0.23	0.633
	Age x Sex	1	0.0011	0.27	0.604
	Error	37	0.1448		
Spring	Period	1	0.0036	2.50	0.212
	Year	2	0.0043	1.49	0.356
	Site	1	0.0008	0.54	0.515
	Age	1	0.0009	0.66	0.476
	Sex	1	0.0003	0.23	0.666
	Period x Year	2	0.0005	0.16	0.861
	Period x Site	1	0.0008	0.55	0.514
	Period x Age	1	0.0000	0.00	0.965
	Period x Sex	1	0.0031	2.17	0.237
	Age x Sex	1	0.0021	1.44	0.316
	Error	3	0.0043		

Table 1.3. General linear model explaining home range sizes of dispersing birds in the fall (n = 50) and spring (n = 16). Period = pre-dispersal or post-dispersal; Year = 1996, 1997, or 1998; Site = Woodbury or Waterloo; Age = juvenile or adult; Sex = male or female.

1.6 Figures

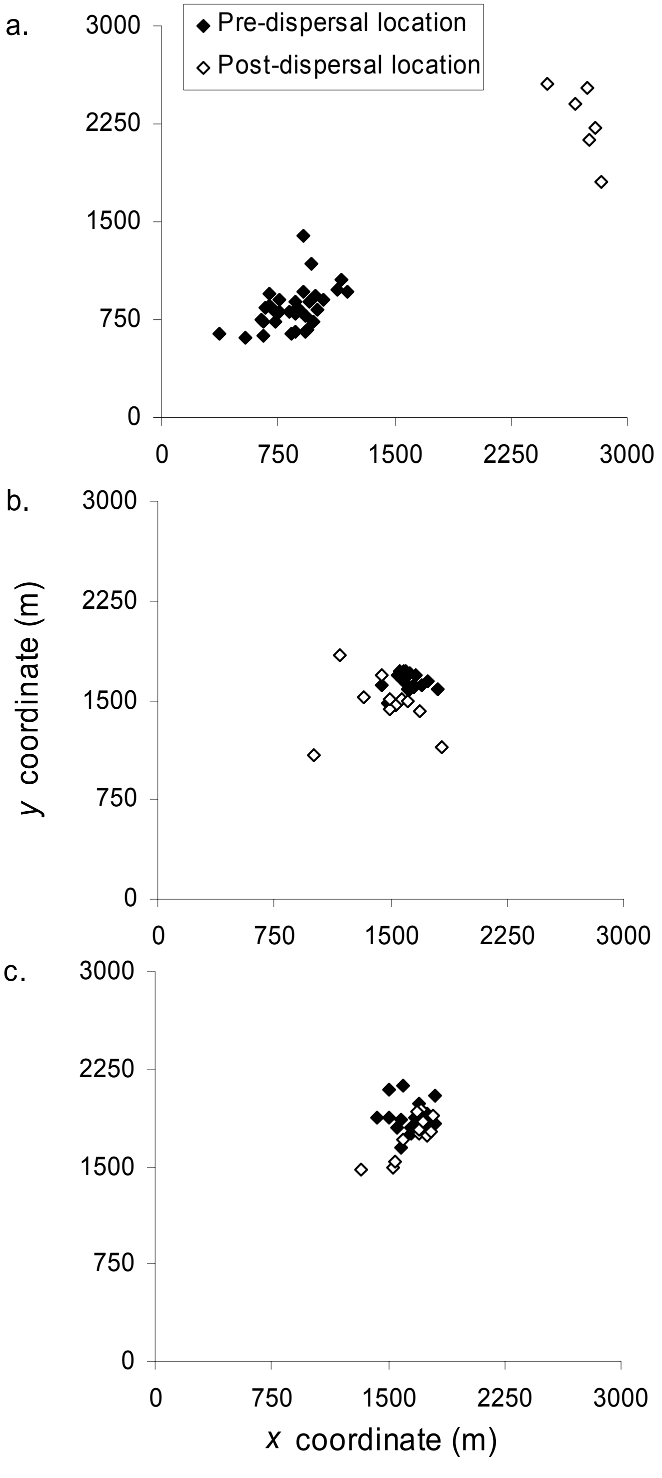

Figure 1.1. Summer pre-dispersal period locations (open diamonds) and winter post-dispersal period locations (filled diamonds) of a (a) long-range dispersing bird ($p < 0.001$, shift distance = 2392 m, (b) short range dispersing bird ($p < 0.001$, shift distance = 325 m) and (c) non-dispersing bird ($p = 0.21$, shift distance = 160 m) as classified by MRPP analysis. Shift distances are linear distances between the mean *x*-*y* coordinates of all pre-dispersal and all post-dispersal locations.

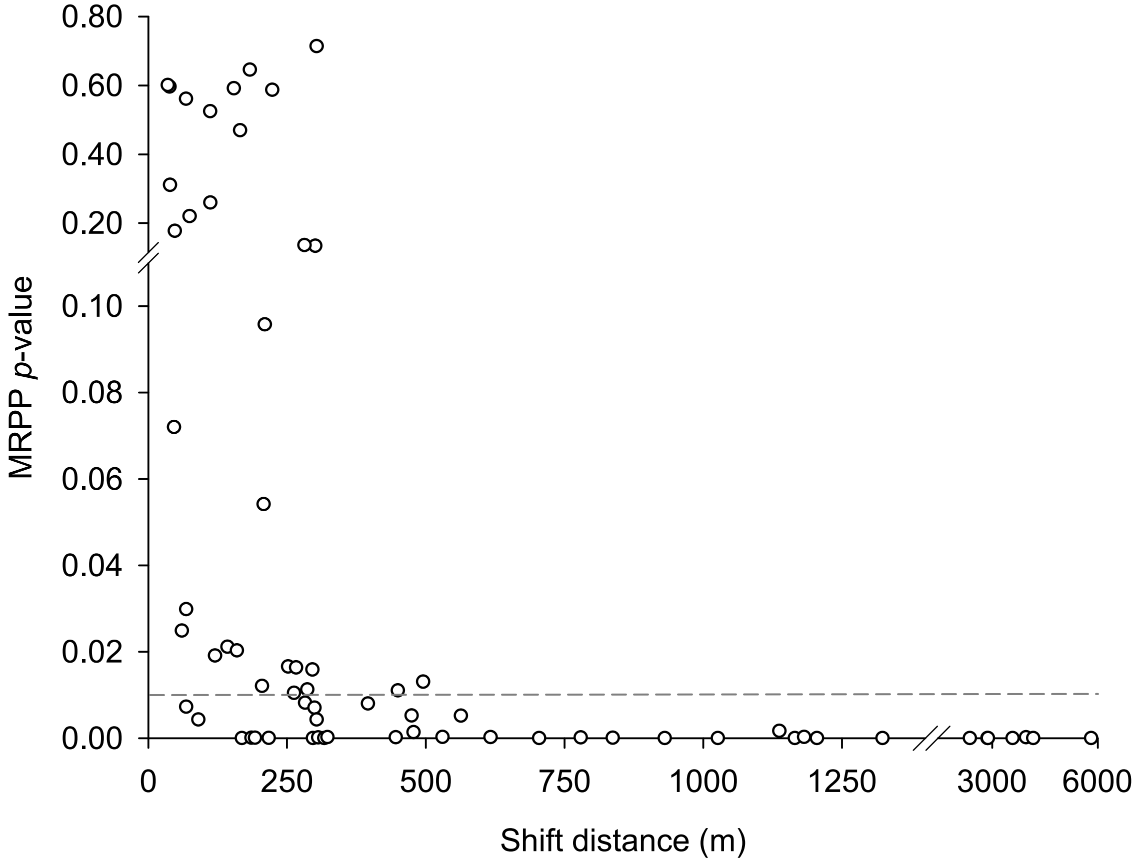

Figure 1.2. The relationship between shift distances and *p*-values from the MRPP analysis comparing the distribution of pre- and post-dispersal locations. Shift distances are straight-line distances between the mean *x*-*y* coordinates of pre-dispersal and post-dispersal locations. Note the change in scales after breaks in both the *x* and *y* scales.

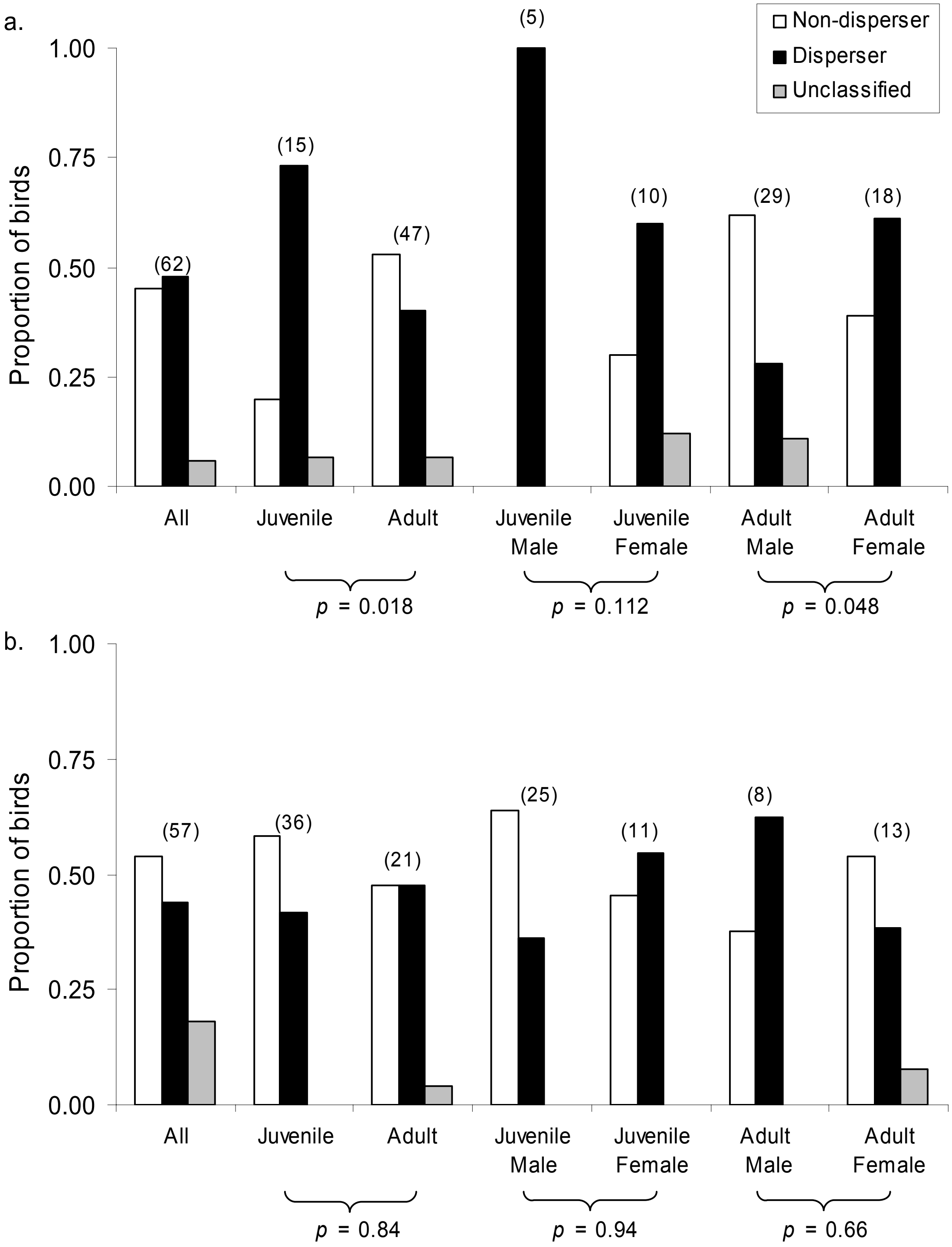

Figure 1.3. The proportion of birds during the (a) fall and (b) spring that did not undergo dispersal (white bars), underwent dispersal (black bars) and were unclassified (gray bars). Sample sizes are indicated in parentheses above each class. *P*-values are from *G*-tests for independence within bracketed age/sex categories. The difference between the proportion of juvenile males dispersing during the fall and the proportion dispersing in the spring is also significant ($n = 30$, $p = 0.007$).

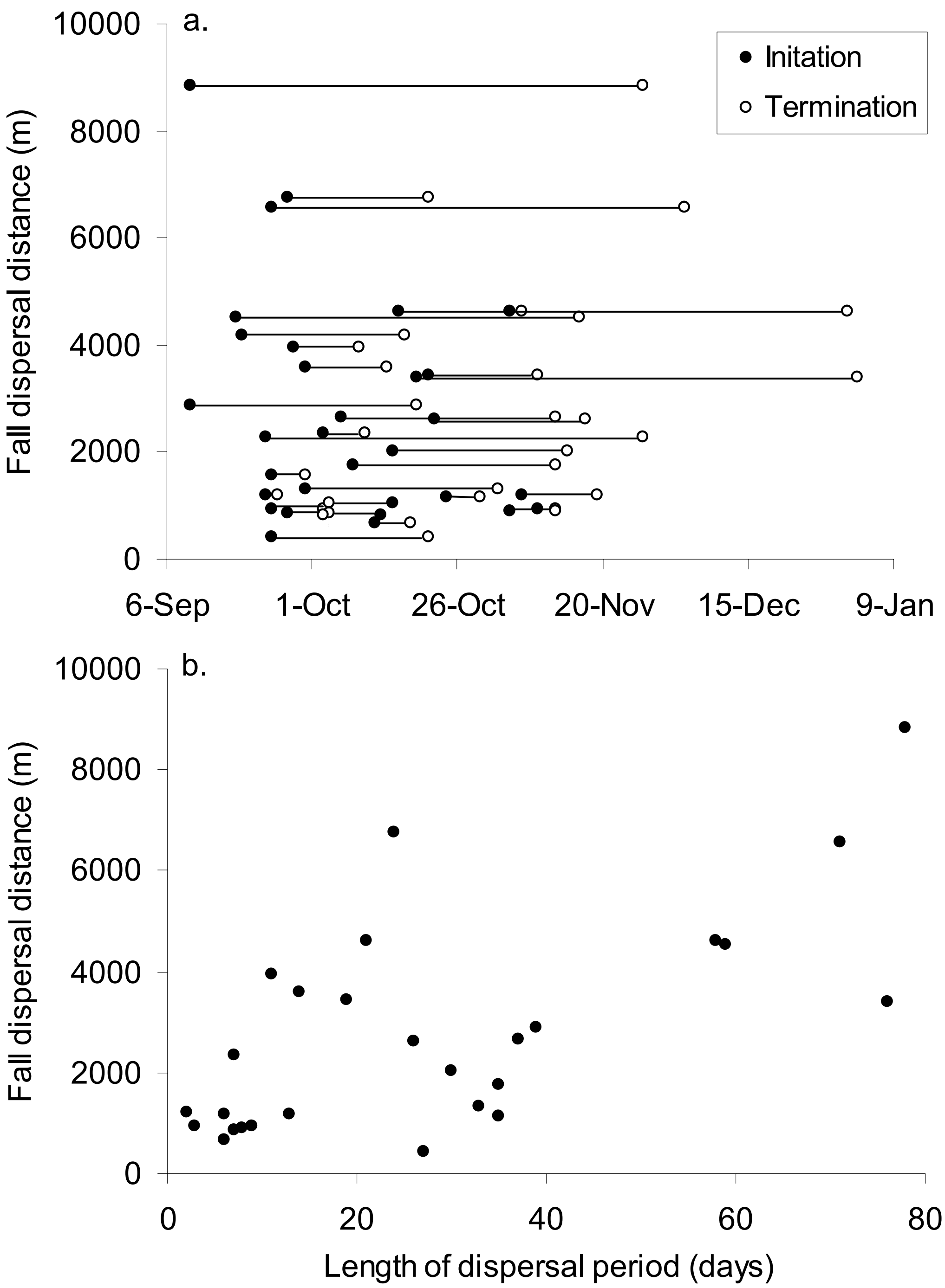

Figure 1.4. The relationship between fall dispersal distance and (a) date of dispersal initiation (dark circles) and termination (open circles) and (b) length of dispersal period (days).

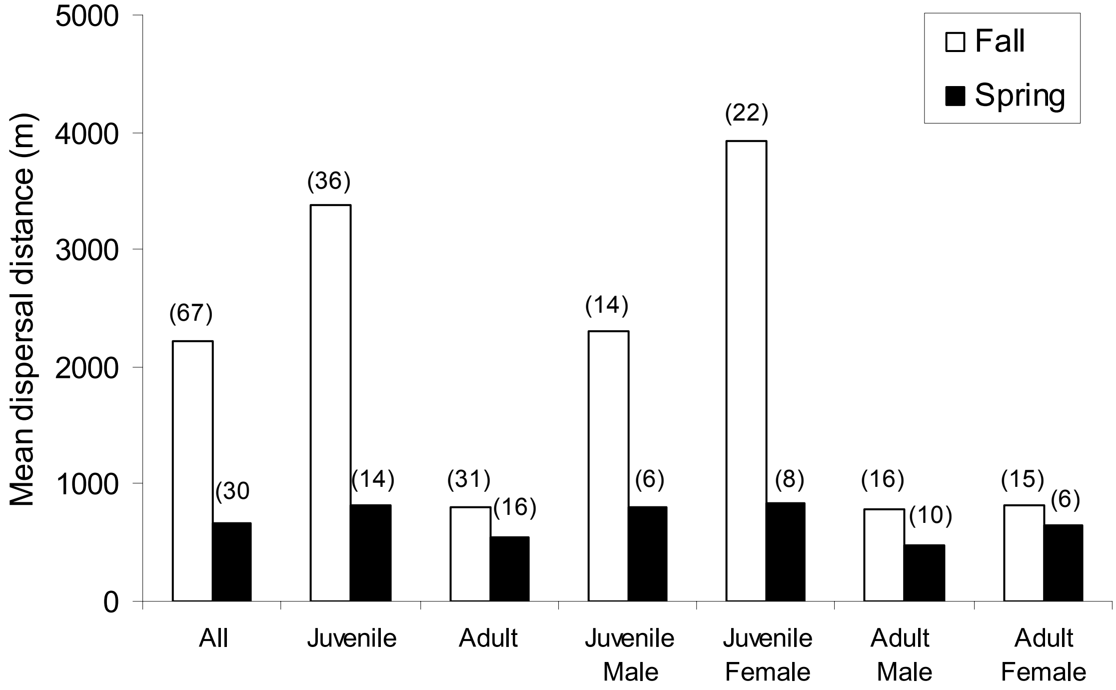

Figure 1.5. Mean dispersal distance of birds during the fall (white bars) and spring (black bars). Sample sizes are indicated in parentheses above each class

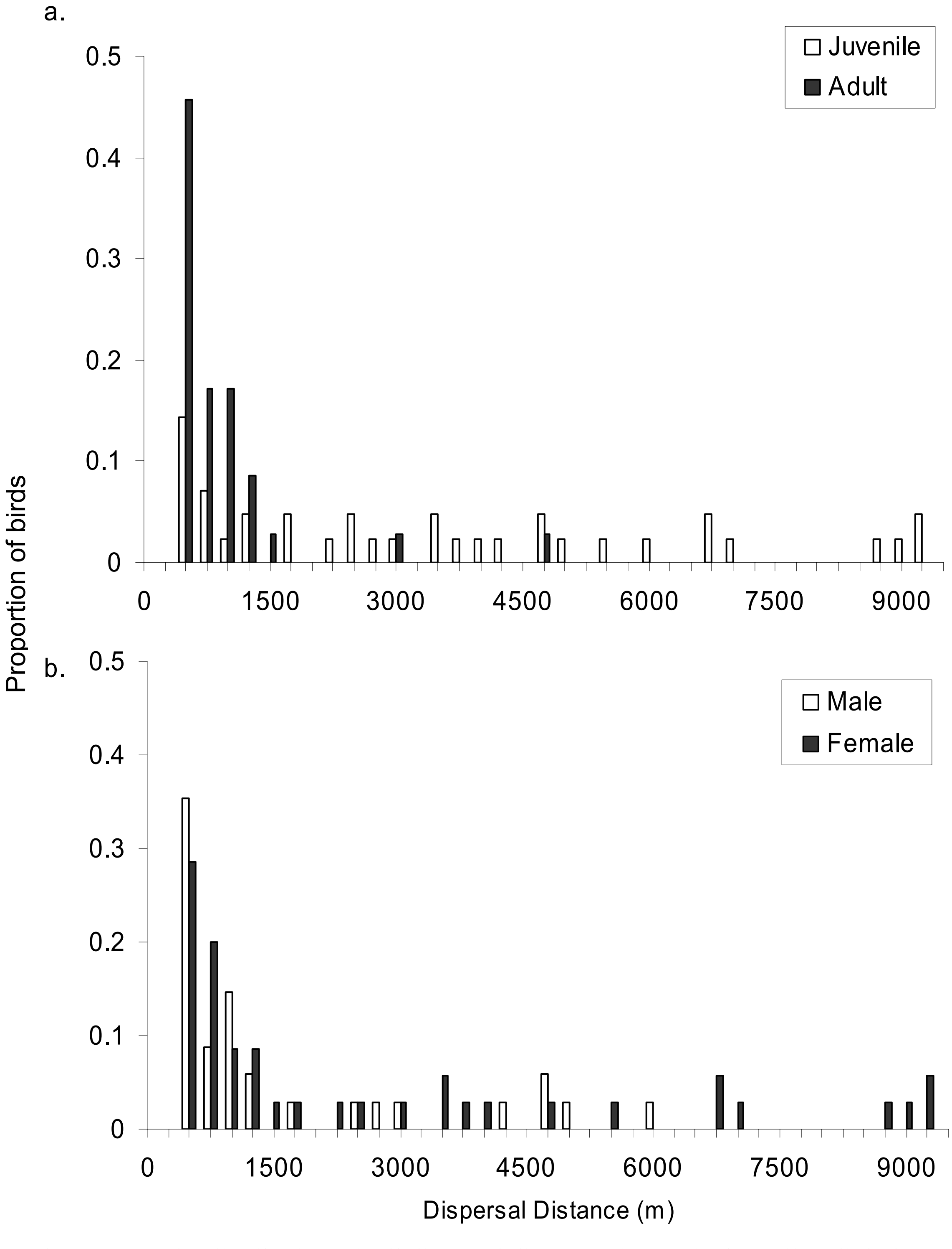

Figure 1.6. The distribution of fall dispersal distances (m) of (a) juveniles (light bars, *n* = 42) and adults (dark bars, *n* = 35) and (b) males (light bars, *n* = 43) and females (dark bars, *n* = 34). Fall dispersal distance is the linear distance between the mean fall pre-dispersal location and mean winter location.

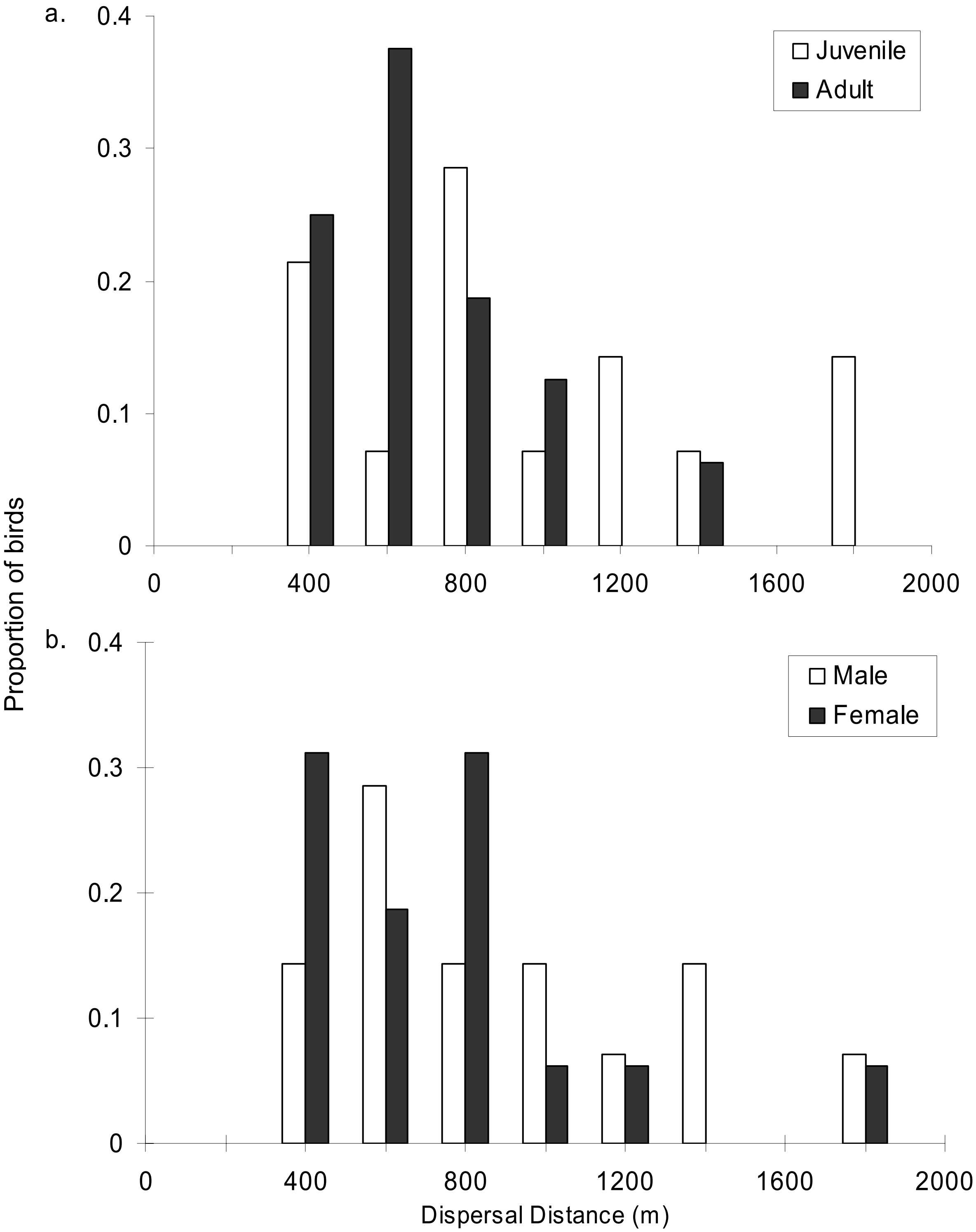

Figure 1.7. The distribution of spring dispersal distances (m) of (a) juveniles (light bars, *n* = 14) and adults (dark bars, *n* = 16) and (b) males (light bars, *n* = 16) and females (dark bars, *n* = 14). Spring dispersal distance is the linear distance between the mean winter location and mean post-dispersal spring location.

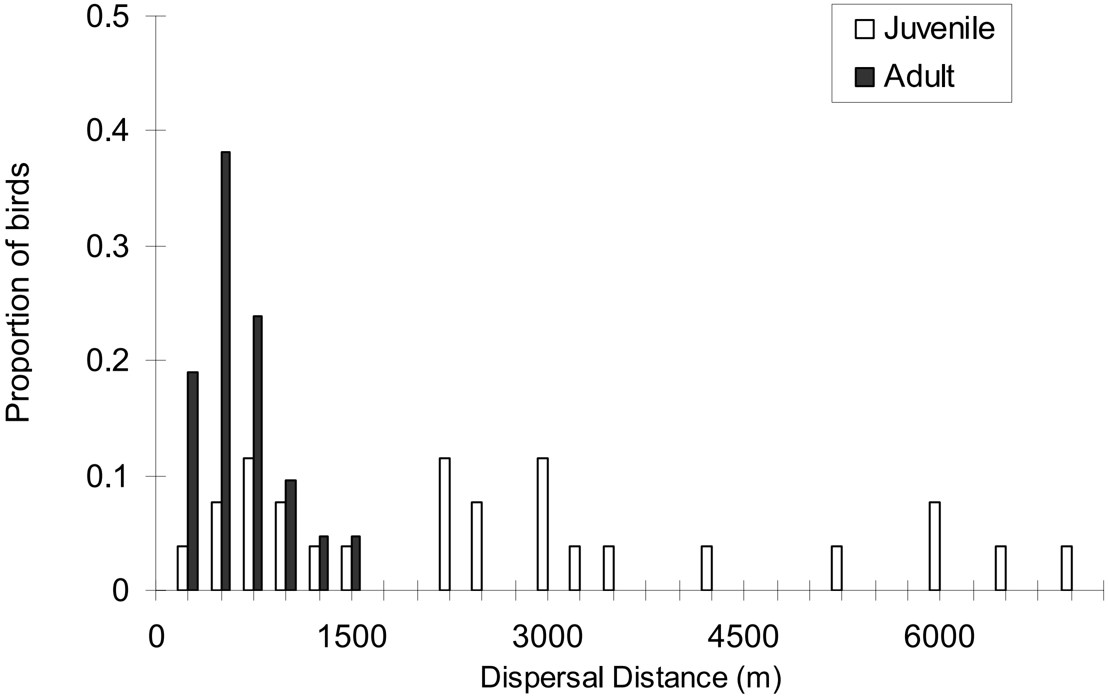

Figure 1.8. The distribution of yearly dispersal distances (m) of juveniles (light bars, *n* = 24) and adults (dark bars, *n* = 21). Yearly distance is the linear distance between the mean fall pre-dispersal location and mean spring post-dispersal location.

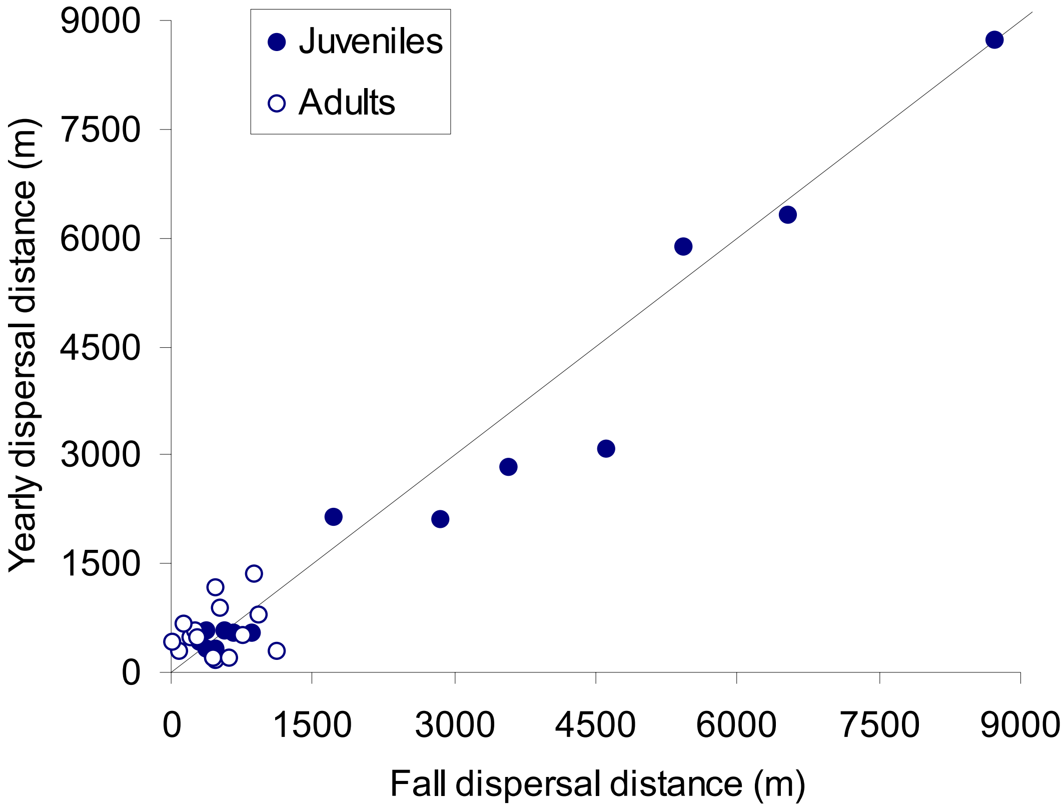

Figure 1.9. The relationship between fall dispersal distance and yearly dispersal distance for juveniles (dark circles) and adults (open circles) also undergoing spring dispersal. Fall dispersal distance is the linear distance between the mean summer pre-dispersal location and mean winter location. Yearly distance is the linear distance between the mean fall pre-dispersal location and mean spring post-dispersal location. Points well below the line would indicate movement back towards the summer pre-dispersal location during spring dispersal. Points well above the line would indicate further movement away from the summer pre-dispersal home range during spring dispersal.

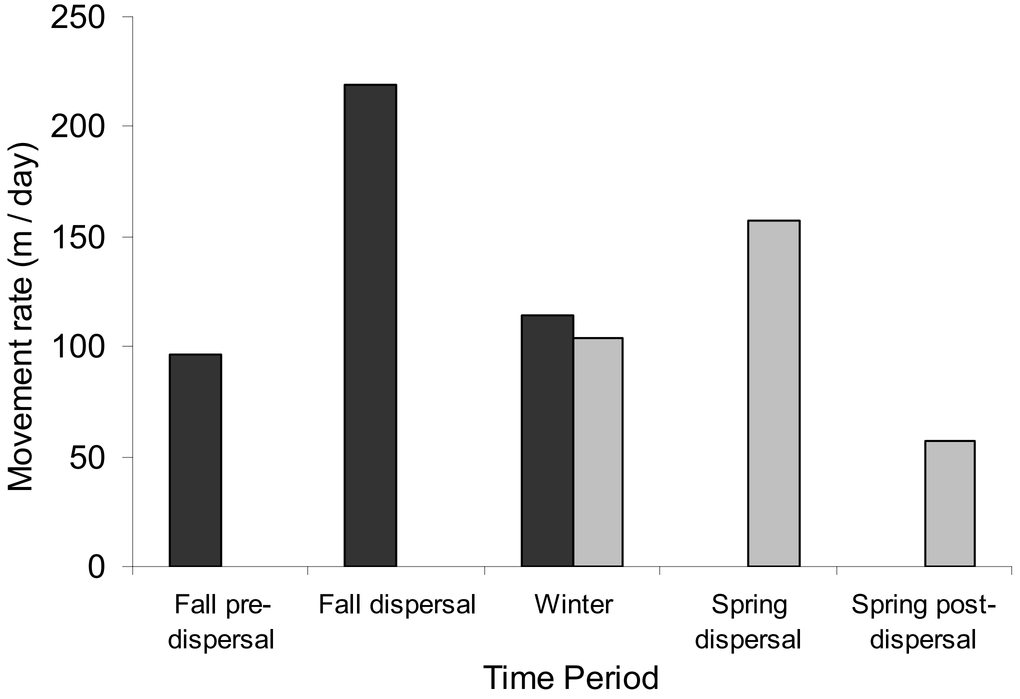

Figure 1.10. The mean movement rates for dispersing birds in the fall (*n* = 32, black bars) and spring (*n* = 10, gray bars) calculated over pre-dispersal, dispersal, and post-dispersal time periods. The winter is the post-dispersal period for fall disperser and the pre-dispersal period for spring dispersers.

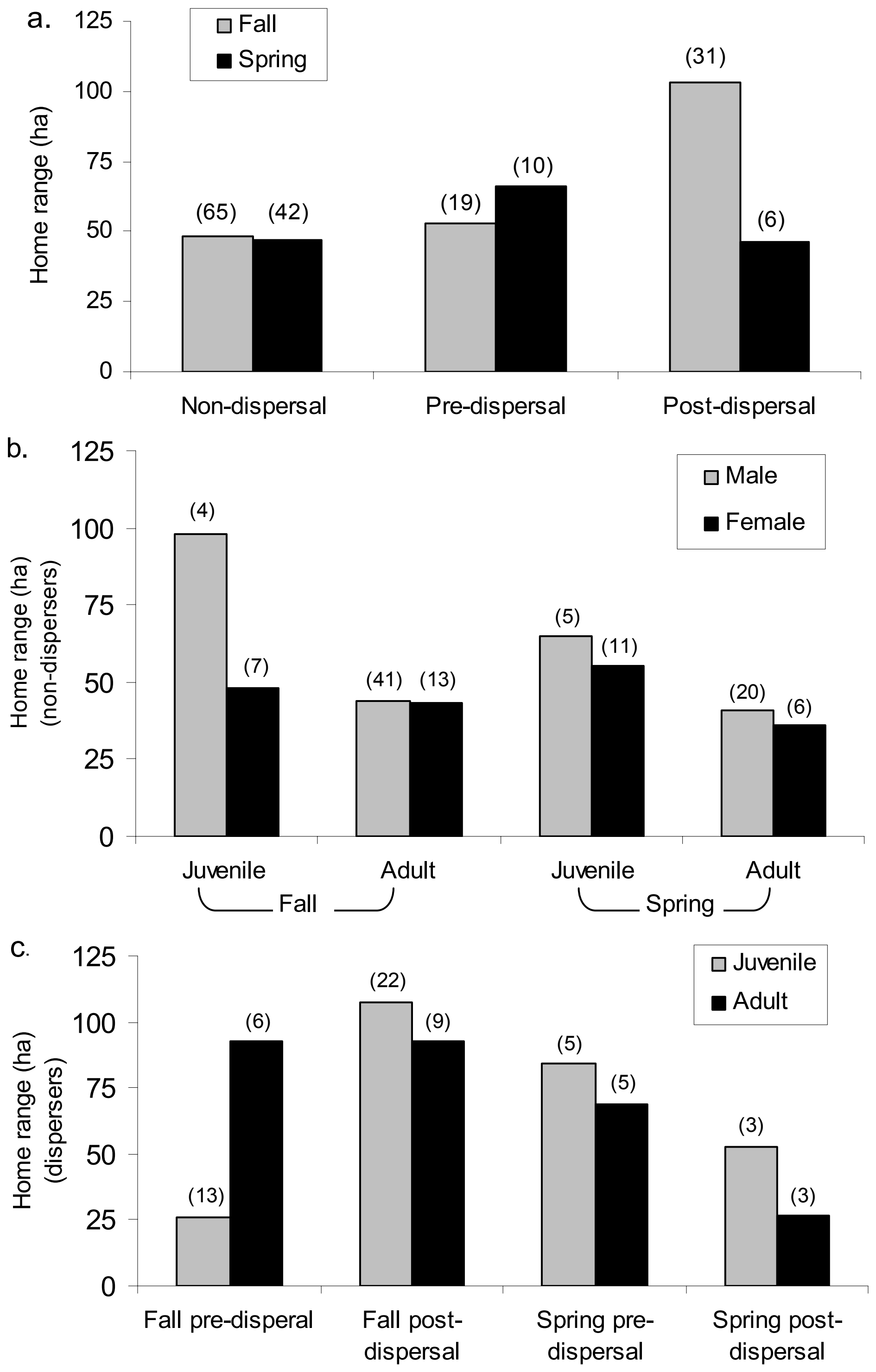

Figure 1.11. The mean home range sizes (ha) for (a) all fall and spring dispersers (pre- and post-dispersal periods) and non-dispersers, (b) fall and spring non-dispersers by age and sex, and (c) fall and spring pre- and post-dispersers by age. Sample sizes are given in parentheses above each set of birds.

CHAPTER 2

THE RELATIONSHIP OF COARSE-GRAINED LANDSCAPE CHARACTERISTICS TO RUFFED GROUSE MOVEMENTS

ABSTRACT

Habitat loss and fragmentation are known to affect many ecological processes; however, few studies have attempted to investigate the effect of landscape characteristics on detailed movement behaviors. The primary goal of this study was to determine whether these landscape variables measured at coarse-grained scales could help explain movement characteristics of ruffed grouse. We measured habitat characteristics in binary landscapes (forest vs. non-forest) at multiple, species-relevant spatial scales. We used Akaike Information Criterion (AIC) techniques for model selection to explore the relationship between a small number of easily interpretable landscape metrics and the decision to disperse by adults and juveniles during the fall and spring dispersal periods, the net dispersal distances and rates of movement, and the home range sizes for ruffed grouse at two sites in southeastern Ohio. Overall, we found coarse-grained landscape characteristics do affect movement behavior, but effects were complex and varied considerably among specific behaviors and spatial scales. While large-scale landscape composition (i.e. % forest) and edge density significantly affected dispersal behavior,

particularly the decision to disperse, little evidence was found for landscape configuration (patch area and radius of gyration) per se affecting movements.

2.1 INTRODUCTION

Interest in the effects of broad-scale environmental changes has spurred the effort by landscape ecologists to decipher the effects of habitat loss and fragmentation on various ecological processes (Turner et al. 2001). An increasing number of studies haves focused on the effects of large scale changes in habitat on biodiversity (Fahrig 2003), species distribution and abundances (Westphal et al 2003, Sallabanks et al 2000), local extinctions (see Fahrig 2002 for review), predation (see Andren 1995 for review, Storaas et al. 1999), reproductive success (Johnson et al. 1992, Kurki et al. 2000), and, to a lesser extent, animal movements. Previous studies have shown that habitat loss or fragmentation results in changes in dispersal rates (Cooper and Walters 2002) and reduction in dispersal success (Brooker and Brooker 2002, Cale 2003) of birds. Detailed study of movement patterns, especially at large spatial scales, remains difficult (Turchin 1998, Martin 1998), but knowledge of the relationship between landscapes characteristics and movement is particularly important to conservation biologists and managers as it is often a key component of spatial population models (King and With 2003) and predictions of the persistence of metapopulations (Storch 2003).

While habitat loss can occur without an increase in fragmentation, the fact that fragmentation always involves some degree of habitat loss has made it difficult to separate their relative effects. In fact most studies do not attempt to differentiate the effects of habitat loss (changes in landscape composition) from those of fragmentation per se (McGarigal and Cushman 2002, Fahrig 2003). In addition to habitat loss, changes in landscape configuration, such as amount of edge, number of patches, patch size, patch isolation, and connectivity may have importance to individual birds.

Critical amounts of habitat for various ecological processes have been proposed as thresholds for when fragmentation effects rather than habitat loss are most important. Empirical studies of birds and mammals have suggested that habitat levels less than 20-30% (i.e., 20-30% of landscape is composed of the necessary habitat) are required before effects of spatial configuration of habitat becomes important to species richness or abundance (Andren 1994, Fahrig 1998). Landscape connectivity, defined as the degree to which a landscape facilitates or impedes movement (Tischendorf & Farhig 2000), is affected by both habitat loss and habitat fragmentation. However, simulations using neutral landscape models and random walks by dispersers predict that landscape connectivity will not be severely affected unless the proportion of necessary habitat falls below 40-60%. At habitat levels above this threshold, the landscape is likely dominated by a small number of large, connected patches and spatial habitat configuration may not be important for predicting dispersal success or movement patterns (King and With 2003).

However, in general, attempts to derive broad patterns of responses to fragmentation across communities or taxa have been unsuccessful (Fahrig 2003). For example, some empirical and simulation studies have indicated that habitat loss may have a greater effect on population extinctions than fragmentation (configuration) and empirical studies of the distribution of forest birds species suggested a similar conclusion (McGarigal and McComb 1995, Fahrig 1997, Trzcinski *et al*. 1999, Fahrig 2002). Other empirical studies have shown that, in some systems, habitat configuration is as important as amount of habitat (Villard *et al*. 1999). In general, most evidence indicates responses to fragmentation are species-specific and there is a need for empirical studies to clarify effects for individual species (McGarigal and McComb 1995, Martin 1998, Jansson and Angelstam 1999, Bissonette and Storch 2002, Keppie and Kierstead 2003).

The species-specific nature of response to habitat change also has important consequences for issues of scale. In landscape ecology in particular there is a growing awareness of the importance of studying ecological responses at organism-relevant temporal and spatial scales (Wiens 1989, Bissonette 1997, Turner et al. 2001, McCargical and Cushman 2002, Storch 2002). In studying animal response to landscape change, two important aspects of spatial scale are grain and extent. Grain refers to the spatial resolution of the data or the spatial resolution in the habitat at which ecological process are affected. While extent can be defined simply as the size of the study area or landscape in which landscape variables and ecological processes are to be measured, its importance is often overlooked in studies of habitat fragmentation.

In their review of fragmentation studies, McGarigal and Cushman (2002) found that only 5% of studies considered fragmentation from an explicit species-relevant scale (e.g., at the scale of a species home range). In addition, they noted that the majority of studies are patch or patch-landscape in nature, in which individual patches are the experimental unit, as opposed to landscape-level studies in which entire landscapes (i.e. patch mosaics) are the experimental unit. While patch-based studies aid in answering many questions, fragmentation is a fundamentally landscape level process and it is problematic to extrapolate findings from patch-level to landscape-level scales (McGarigal and Cushman 2002, Farhig 2003). Finally, many available metrics used to quantify landscape characteristics are severely affected by choices of landscape extents (McGarigal et al. 2001).

While grain usually refers to the finest spatial resolution within a data set (e.g., cell size of a raster image) it may also be used to describe a level of fragmentation (e.g., "coarse grained" if habitat patches are larger than a single territory (Rolstad 1991)) or to refer to the resolution of habitat at which various ecological processes may be affected (Lawler *et al.* 2004). Storch (2002) illustrates this multi-scale habitat concept using data from 15 years of research on capercaillie (*Tetrao urogallus*), a forest grouse species in central Europe. At the spatial scale of forest stands (1 – 100 ha), within-stand vegetation influences daily habitat use in terms of foraging and utilization of cover. The mosaic of forest stands within a forest (100 – 1000 ha) is important to the capercaillie in terms of habitat use over the course of an entire year, with the mixture of different successional stages or classes affecting capercaillie home range size. Finally, the interspersion of forests and open areas at the landscape scale (1000 – 10000 ha) affect the size, spatial structure, and dynamics of populations, with decreased connectivity and dispersal among subpopulations likely playing a role in regional population declines (see Storch 2002 for review).

Although the North American ruffed grouse (*Bonasa umbellus*) has similar patterns of fine-grained habitat use as the capercaillie, we know much less about the effect of landscape composition and fragmentation on ruffed grouse ecology at larger spatial scales (both in terms of landscape extent and habitat resolution). It is well established that a heterogeneous mixture of different forest stands (e.g., varying successional stages) is important to ruffed grouse success (Gullion 1984, Rusch et al. 2000) and small-scale habitat modification has been a key management strategy for decades (Bump et al. 1947, Gullion and Alm 1983, Rusch et al. 2000). However, no studies have investigated the impacts of habitat loss or configuration on ruffed grouse movements over large study areas with a relatively high level of overall forest loss. As seen in capercaillie, changes in patterns of dispersal or seasonal movements due to changes in landscape may have important impacts on the distribution and spatial population dynamics of ruffed grouse. Rate of movement and movement into unfamiliar areas affects predation risk in ruffed grouse (Chapter 3) and a decrease in the likelihood of dispersing due to a loss of landscape connectivity may increase the use of sub-optimal habitats for foraging, cover, or as breeding sites. These, in turn, may have consequences for long-term population persistence and subsequent management strategies. Ruffed grouse populations are experiencing long-term declines in Ohio (Stoll et al. 1999) and throughout the southern and central Appalachian portions of its range (Dessecker and McAuley 2001) and it is unclear at what scale changes in habitat may be contributing to this trend.

The objective of the study is to investigate the relationship of ruffed grouse movement behavior to large scale, landscape-level habitat characteristics. We measured coarse-grained habitat characteristics in binary landscapes (forest vs. non-forest) at multiple, species-relevant spatial scales. Our primary goal was to determine whether these landscape variables measured at coarse-grained scales could help explain movement characteristics. The secondary goal was to distinguish between the importance of landscape composition (amount of forest habitat) and configuration (fragmentation) in explaining movement characteristics. Finally, we hoped to determine a threshold level of forest habitat below which grouse movement is significantly affected. Using Akaike information Criterion (AIC) techniques for model selection, we investigate the relationships between a small number of easily interpretable landscape metrics and the decision to disperse by adults and juveniles during the fall and spring dispersal periods, the net dispersal distances and rates of movement during dispersal, and the home range sizes for ruffed grouse at two sites in southeastern Ohio. Finally, we use a previous statistical model of the effect of movement rate and habitat familiarity on predation risk (Chapter 3) to determine any additional effects of landscape characteristics on predation risk.

2.2 METHODS

2.2.1 STUDY SITES

The study was conducted at two sites in southeastern and east central Ohio from 1996 to 1999. The sites were centered on Waterloo Wildlife Area in Athens County and Woodbury Wildlife Area in Coshocton County. Each study site included the state-owned wildlife area and surrounding private lands within 15 km. The sites were characterized by a mixture of early successional to 40+ year old oak-hickory forest and agricultural fields.

2.2.2 RADIO TELEMETRY

Each fall, from 1 August to 10 October, 35 – 50 birds were trapped at each site using modified lily-pad traps (Dorney and Mattison 1956). Radio transmitters (Advanced

Telemetry Systems, Isanti, MN) were attached with a necklace harness (Amstrup 1980) of teflon-coated woven wire. Mean transmitter weight was 11 g. Only birds weighing greater than 250 g were fitted with transmitters to ensure that the transmitter was not more than 5% of the bird's body weight (Fuller 1987). Expected battery life of transmitters was 320-500 days. Transmitters were distributed as equally among all age-sex categories as possible (approximately 55% adult, 45% juveniles and 57% males, 43% females). In all, a total of 193 birds were tagged and tracked over the course of three years.

Attempts were made to locate all tagged birds at least 3 - 4 times per week from August 1 through May 15 and at least bi-weekly during June and July. Individual locations were calculated using the maximum likelihood estimator method (Lenth 1981) with a minimum of three azimuths taken within a span of 10 minutes. Lenth's method generates a 95% error ellipse of the bird's location. Only locations with 95% error ellipses smaller than 2 ha were used in distance calculations (92% of all locations).

All transmitters were equipped with mortality-mode switches (i.e., when the transmitter remained stationary for 6-8 hours, the pulse rate doubled). This allowed for quick location and recovery of dead birds. After necropsy, all recovered birds were classified as killed by avian, mammalian, or unknown predators, or as dying by other causes (e.g., road kill) (Einarsen 1956, Dumke and Pils 1973). In addition, each bird was equipped with a reward leg band that facilitated the identification of birds harvested during the hunting season (10 Oct – 29 Feb). Over the three-year study, the fate of 13% of tagged birds was unknown, most likely due to transmitter failure. To avoid any effect of short-term stress due to capture and handling or from transmitters, birds that died within 7 days of capture were not included in the analyses.

2.2.3 MOVEMENT DATA

In order to investigate the effects of landscape characteristics on Ruffed grouse movements we used individual bird dispersal classification, timing of pre-, post- and dispersal periods, dispersal distance, rate of movement, and home ranges size calculated in Chapter 1. In general, ruffed grouse undertake significant shifts in their use of space during fall and spring dispersal periods (Bump et al. 1947, Small et al. 1991, Chapter 1). In the analysis for Chapter 1, we determined the dispersal status for birds using a procedure to directly test for a shift in area by individual birds during the fall and spring seasons. We first established pre– and post-dispersal periods within each season in which dispersal was not occurring by performing a preliminary analysis of a subset of birds using conservative dates. We then eliminated all birds that did not survive into the winter post-dispersal period from any subsequent analysis. Data from all birds located at least five times within both pre- and post-dispersal periods were then analyzed using the multi-response permutation procedure (MRPP) (Cade & Richards 2001). These birds were classified as dispersers or non-dispersers based on their MRPP *p*-values. Birds not included in the MRPP analysis due to a late capture date could not be classified as non-dispersers, but could be classified as dispersers based on a permanent move of at least 500 m or subsequent iterative MRPP tests using initial capture locations (see section 1.2.3 DEFINING DISPERSAL EVENTS for details of the classification procedure and movement period dates).

During the fall, we found that approximately 90% of juveniles undergo natal dispersal and 45% of the adult population undertakes a seasonal shift between fall and over-wintering areas. The proportion of the juveniles dispersing in the fall was significantly greater than adults but approximately 45% of both ages dispersed during the spring. No difference was found between juvenile males or females in the proportion dispersing in the fall, but a significantly higher proportion of adult females dispersed than adult males. No difference in proportions dispersing between sexes was found in the spring and there was no difference in proportions dispersing between study sites or years during either season (Chapter 1).

Seasonal dispersal distances were defined for all dispersers as the straight-line distance between the mean locations of all summer pre-dispersal period locations and all winter post-dispersal period locations as defined in the MRPP analysis. During the fall, juvenile mean dispersal distances were significantly greater than those for adults (3.7 km vs. 0.8 km). No differences in dispersal distances were detected between the sexes or study sites but fall distances were greater during year 2 of the study than in the other years. Spring dispersal distances were shorter (mean = 0.7 km) than fall distances and did not differ between ages, sexes, study sites, or years (Chapter 1).

We calculated movement rates (meters/day) by summing the distances between successive locations and dividing by the total number of days in the period for dispersing birds in which accurate dispersal periods could be identified (as described above in 1.3.3 DEFINING DISPERSAL EVENTS*)*. Mean movement rates during dispersal periods were approximately 220 m/day and averaged 90 – 110 m/day during non-dispersal periods (Chapter 1).

We calculated home ranges separately for non-dispersing and dispersing birds using 95% contour interval from the fixed kernel method with least squares cross validation for the smoothing factor (Worton 1989, Kernohan *et al.* 2001). We calculated home ranges during the seasonal periods (fall/winter and winter/spring) for non-dispersers and pre- and post-dispersal home ranges for fall and spring dispersing birds (see 1.2.7 HOME RANGE SIZE for specific period dates). We included only data for non-dispersing birds in the analysis investigating the effect of landscape characteristics on home range size. Among non-dispersers, juvenile males had significantly larger home range sizes (≈ 100 ha) than juvenile females or adults in the fall (≈ 45 ha). Overall fall home range sizes were also larger in year 2 of the study than in other years. No difference in home range size was found between ages, sexes, study sites, or study years among spring non-dispersers (Chapter 1).

2.2.4 LANDSCAPE DATA

Land cover maps of study areas derived from a 1994 LANDSAT-TM image (resolution 25 m) were obtained from the Ohio Division of Wildlife and analyzed using ArcView 3.3 (ESRI Inc. 2002). The landscape data were initially classified as forest, agriculture, development, open water, wetland, barren (primarily abandoned strip mines) or shrub. Since forest and agricultural classes accounted for greater than 98% of total area and grouse were unlikely to use any of the additional classes, we considered a binary landscape consisting of grouse habitat (forest) and non-habitat (primarily agriculture).

We created individual "minilandscapes" of different extents for all birds that could be classified as dispersers or non-dispersers during each season. To investigate landscape effects on dispersal decisions and home range sizes we buffered a single point (the center) of a specified set of locations. Many landscape measurements are functions of area of landscape considered, and this method ensured landscapes of equal total area were created for each individual. Buffering the mean location of all usable locations during an entire season was done to create non-disperser landscapes. Pre-dispersal and post-dispersal landscapes for dispersing birds were created by buffering the harmonic center of all usable locations during pre-dispersal or post-dispersal periods within a season. We created landscapes of varying extents for each bird by using buffers of 500 and 3000 m (Figure 2.1). A buffer distance of 500 m was based on mean 95% adaptive kernel home range sizes for grouse in our study (during non-dispersing periods) of 44 ha (adults) and 66 ha (juveniles), which correspond to circular areas with radii of 375 and 460 m. Therefore, we believe a buffer distance of 500 will ensure a landscape that includes all of the immediate area around the bird that is likely to affect movement decisions on a short-term basis. The larger 3000 m landscape incorporates habitat available to birds during dispersal (mean dispersal distances were 0.8 km for adults and 3.3 km for juveniles (Chapter 1) or over longer time scales.

2.2.5 METRIC SELECTON

We quantified landscape composition and configuration using four landscape metrics (Table 1) computed using FRAGSTATS 3.0 (McGarigal et al. 2002). While a multitude of metrics and indices that quantify spatial characteristics are available (more than 40 can be calculated with FRAGSTATS alone), inadequate understanding of the behavior of many of them results in difficulty with interpretation (particularly when using real-world landscapes and response variables) (Davidson 1998, Tischendorf 2001, McGarigal et al. 2002, Bogaert 2003, Li & Wu 2004). Many metrics are also of questionable biological relevance to the species of interest and suffer from biases in calculation and lack of independence (Gustafesen 1998, Turner et al. 2001, Li & Wu 2004). When selecting metrics, we attempted to maximize ecological relevance based on a priori knowledge of grouse movement and ease of interpretation while also minimizing correlations between metrics and bias that may occur due to methodology used in selecting the individual landscapes (e.g., the effect of boundary at different landscape extents). We also wished to avoid "data dredging" for significant responses to a large number of metrics (Turner et al 2001, McGarigal et al. 2002).

A large number of metrics were eliminated from consideration because we were exploring a binary landscape and, thus, metrics measuring landscape habitat diversity and structure were inappropriate. The need to measure the responses at multiple scales (extents) also limited the number of suitable metrics. For example, many isolation metrics, such as nearest neighbor distances, are greatly affected by the artificial truncation of patches that extend beyond the landscape boundaries and thus inappropriate for extents that are not at least 2 – 5 times greater than the largest patch (O'Neil 1996). However we wished to measure landscape characteristics at relatively small extents and large patch sizes.

We attempted to choose a relatively small number of metrics, which would reduce the risk of overparameterizing regression models as well as facilitate interpretation. As the coarsest and simplest measure of landscape composition, we used the percentage of landscape area classified as forest (FRAGSTAT metric PLAND). Metrics can be broadly categorized according to aspects of landscape configuration they most directly measure (McGarigal et al. 2002, Turner et al. 2001). We sought to use the minimum number of metrics that allowed us to measure all of four categories thought most likely to affect movement decisions in a binary forested landscape. These categories included 1) amount of forest edge, 2) patch size, 3) contagion, and 4) structural connectivity. While patch isolation is often investigated in studies of dispersal success and fragmentation, metrics measuring isolation are unlikely to be important in landscapes that are 60 to 100 % forested as ours were, because the landscapes have a higher percentage of habitat than the fragmentation threshold predicted by percolation theory (With and King 1999, Turner 2001).

The final set of metrics included edge density (FRAGSTAT metric ED), the total amount of forest patch edge divided by the total landscape area, to quantify edge effects. Edge density is also highly negatively correlated with indices of contagion, thus we did not use an additional measure of contagion in our analysis. We chose area-weighted mean patch area (FRAGSTAT metric AREA) as a measure of patch size. Area-weighted mean patch area is the mean of all forest patch areas as a proportion of total forest area. Given that a bird is in forested habitat, area-weighted mean patch area gives the expected size of that forest patch. When comparing binary landscapes of equal size, mean patch area is one of the simplest indices of fragmentation.

Finally, we chose the area-weighted mean radius of gyration (FRAGSTAT metric GYRATE) as a measurement of structural connectivity. The radius of gyration is the mean distance between each cell in a patch and the patch centroid and reflects the spread of a habitat type across a given landscape, affected by both patch size and patch shape

(McGarigal et al. 2002). It is also referred to as correlation length and is interpreted as the average distance an organism could traverse from a random starting point in a random direction and not encounter a patch edge (Keitt et al.1997). Many measurements of connectivity require knowledge of a minimum distance between patches that reflects gap crossing ability of the study organism; radius of gyration does not. We know of no study that has quantitatively investigated the gap crossing ability or the use of an agriculture matrix by ruffed grouse, but believe a reasonable assumption is that a high risk of predation deters grouse from using areas with little or no cover.

Summary statistics for the four metrics used in the analysis at each study site are provided in Table 2.1 and detailed formulas for the computation of all metrics can be found in the appendices of the FRAGSTATS documentation (McGarigal et al. 2002).

2.2.6 STATISTICAL ANALYSIS

We used the Akaike Information Criteria (AIC) model selection procedure (Burnham & Anderson 2002) to investigate the effects of landscape composition and configuration on ruffed grouse decisions to disperse, home range sizes, dispersal distances and rates of movement. AIC analysis is an information-theoretic approach in which AIC values, based on maximum likelihood estimates, are calculated for each model in an a priori set of models. Models with the lowest AIC values are determined to best represent the data. Thus we could evaluate the fit and explanatory power of multiple logistic or least-square regression models incorporating the four landscape metrics as independent variables.

Any model with an AIC value within 2 AIC units of the best model (ΔAIC <2) is commonly thought to provide similar "substantial" explanation of the data while ΔAIC values ranging from 4 - 7 units indicate "considerably less" explanatory power (Burnham and Anderson 2002). Due to relatively small sample sizes compared to number of parameters, corrected values (AICc) were used in all analyses (Burnham & Anderson 2002). Overdispersion of the data was also evaluated using the global (fully parameterized) model in each model set and an additionally corrected AIC value (QAICc) used if overdispersion was detected (Burnham and Anderson 2002).

We also used Akaike model weights (w_i), which can be interpreted as the probability that model *i* is the best model in the set being considered (Burnham and Anderson 2002), to distinguish between models. In cases in which there was considerable model uncertainty (e.g., many models with low ΔAIC_c values), Akaike parameter weights can be used to quantify the relative importance of individual variables (Burnham and Anderson 2002). We calculated parameter weights by adding together the model weight for each model that contained the parameter. While it is important to calculate parameter weights using the entire model set (Burnham and Anderson 2002), it is also important to use the same number of models for each parameter. In cases in which variables were not used in the same number of models, we summed the weights from only the number of models equal to the number of models containing the least used variable. For example, if AREA was the least used variable and included in only 8 of 12 models in the entire model set, parameter weights for every variable were calculated by summing the model weights for the best 8 models in which each appeared.

Selecting the plausible candidate models (i.e., the a priori set of models) to be included in AIC analysis is a critical component of this type of information-theoretic approach to data analysis. Prior knowledge of the study organism needs to be taken into account to avoid the data dredging that results from including all possible combinations of variables. Burnham and Anderson (2002) also recommend that the global model contain no more than $n/10$ parameters (n = number of observations). Thus, we chose to include variables such as age and sex of birds and study year only if we had evidence of significant differences in movements within these categories from previous analyses (Chapter 1). Differences between our study sites were represented by the landscape metric variables themselves, so study site was not included as a separate parameter. We also included a null model that included no individual parameters, in all candidate model sets. If effects of landscape composition or configuration play a role in movement decisions by ruffed grouse, models that incorporate landscape metric parameters should better describe grouse responses than a null model including no individual parameters. A null model containing no landscape metrics having a $\Delta AIC_c < 4$ is highly unlikely if landscape characteristics are important in influencing movements. Thus, in our analysis when $\Delta AIC_c < 4$ for null models, we concluded that landscape effects were not important.

In addition to the null and global models, we included all possible combinations of the amount of forested landscape (PLAND), edge density (ED), and age, sex, or study year if appropriate. Since mean patch size (AREA) and radius of gyration (GYRATE) were correlated with PLAND ($p > 0.8$), we added AREA and GYRATE only to models already including PLAND. A primary objective of the analysis was to investigate the effects of landscape composition and it was highly unlikely that AREA or GYRATE would have an effect independent of PLAND. Interaction terms were not included in the models since patterns were unlikely to emerge due to correlations between metrics and in an effort to limit the number of overall parameters.

As an indication of general preference in landscape composition by ruffed grouse, we compared the local landscapes actually used by individual birds with landscapes of larger regions containing the local landscapes. The percentage of forest (PLAND) in landscapes buffered at 5000 m was used to characterize regional landscapes. The percentage of forest in landscapes buffered at 500 m was used to represent local landscapes actually used by grouse within the larger 5000 m area. Paired *T*-tests were used to test for differences in PLAND between local and regional landscapes of all birds in both the fall and spring season. All locations during a season were buffered for non-dispersing birds and only locations during the pre-dispersal period were buffered for dispersing birds. As an additional indication of preference in landscape composition and configuration by dispersing birds, we compared pre-dispersal landscapes to post-dispersal landscapes. We used Wilcoxon signed rank tests to make separate comparisons of landscape metrics for adults and juveniles, at 500 and 3000 m buffers, and for spring and fall dispersal.

The effect of landscape on dispersal decisions was analyzed using logistic regression with whether a bird ultimately dispersed or not as the binary response variable. We considered brood break-up and natal dispersal of juvenile birds during fall to be a fundamentally different biological process than fall movements undertaken by adults and spring movements by both adults and juveniles. Thus, we ran separate sets of logistic regression models for juvenile and adult fall dispersal. Because individuals may respond differently to landscape characteristics in the fall than in the spring, we ran separate models for each season. Landscape metrics were calculated from pre-dispersal landscapes of dispersers and non-dispersers buffered at 500 and 3000 m. In all, 20 candidate models were fitted to the dispersal decision data (Appendix A). Previous analyses indicated significant differences in the proportion of males and females dispersing in the fall but not the spring (Chapter 1), so the variable SEX (male or female) was included in the fall model sets only. We analyzed only one set of models for both juveniles and adults in the spring but included AGE (juvenile or adult) as a possible factor.

A similar approach was used to investigate landscape effects on home range sizes. We used a similar set of candidate models but used multiple least squares regression as a measure of maximum likelihood in calculations of AIC. Home range sizes of fall adult non-dispersers and spring juvenile and adult non-dispersers were used as the response variables. There were insufficient numbers of fall juvenile non-dispersers to perform AIC analysis. Previous analysis indicated no significant differences in home ranges sizes between sexes or study years so they were not included as parameters in the models. Landscape metrics were calculated from the non-disperser landscapes buffered at 500 and 3000 m.

Dispersal distance and movement rates were investigated using a smaller set of models that differed by the removal of all models containing patch area and radius of gyration. Because landscape metrics for these model sets were calculated from landscapes derived from dispersal routes (by buffering all locations during a dispersal period), total landscape areas varied with dispersal distance even within landscapes buffered at the same distances along the route. Since mean patch area and radius of gyration are strongly positively correlated with total landscape area, they are inappropriate to use when studying dispersal distances or movement rates. Dispersal route landscapes were buffered at distances of 250 m and 2000 m, based on the range of daily movement rates for dispersing birds in the study (Chapter 1). Dispersal distances and movement rates were not normally distributed and were transformed using the box-cox transformation procedure in Minitab (Minitab 13).

The effect of landscape composition and configuration on the risk of predation for ruffed grouse was explored by the addition of the landscape metrics PLAND and ED to the Cox proportional hazards model used in Chapter 3. The model estimates the hazard (i.e., the effect on survival time) for an individual due to one or more explanatory covariates and was originally used to test for the effects of movement rate and habitat familiarity on the risk of predation (*see* Chapter 3 *for model details*). The new Cox model was run with all the original covariates plus PLAND and ED metrics calculated from landscapes constructed by buffering all bird locations from capture date to death date for each bird at distances of 250 and 3000 m.

All statistical analyses were performed using SAS (SAS 8.1) and Minitab (Minitab 13).

2.3 RESULTS

2.3.1 SAMPLE POPULATION

During the three-year study we obtained usable locations on a total of 193 birds (85 juveniles and 108 adults). Of the 84 juveniles alive at the beginning of a fall season, 30 individuals died before the end of a season and were unable to be classified as dispersing or non-dispersing individuals. Of the 108 adults captured during the fall season, 13 individuals died before the end of a season and were unable to be classified. In addition, 6 juveniles and 32 adults were unable to be classified due to late capture or indeterminate nature of fall movements (see 2.3.3 MOVEMENT DATA). Thus, the total number of individuals used in fall analyses was 48 juveniles and 63 adults. Of 39 juveniles and 78 adults alive at the beginning of a spring period, 10 juveniles and 28 adults died before they could be classified as dispersing or non-dispersing. Thus, the total number of individuals used in the spring analyses was 29 juveniles and 45 adults.

2.3.2 FOREST PREFERENCE

Local landscapes (i.e., buffer distance of 500 m) inhabited by adult birds in the fall were more forested than regional landscapes (i.e., buffer distance of 5000 m) ($n = 95$, paired T-test, $p < 0.001$; Figure 2.2a). Among juveniles in the fall, there was no difference between 500 m and 5000 m landscapes ($n = 54$, paired T-test, $p = 0.214$; Figure 2.2a). However, there was less variation in the percentage of forested habitat in regional landscapes inhabited by juveniles than in landscapes inhabited by adults, with no juvenile inhabiting regional landscapes with less than 75% forest habitat (Figure 2.2a). In the spring, the percentage of forested habitat was significantly higher in individual 500 m landscapes than in 5000 m landscapes for both adults ($n = 45$, paired T-test, $p = 0.043$) and juveniles ($n = 29$, paired T-test, $p <0.001$) (Figure 2.2b).

2.3.3 FALL DISPERSAL DECISIONS

AIC analysis of logistic regression models showed that landscape characteristics differed between landscapes inhabited by juveniles that ultimately dispersed in the fall and landscapes inhabited by those that did not. The AIC analysis did not clearly identify a single "best" model. For landscapes buffered at 500 m, the decision to disperse was best explained by four models containing the variables PLAND, ED, GYRATE, and SEX with $\Delta AIC_c < 2$ (Table 2.2), with the top-ranking model (PLAND, ED, and SEX) having an Akaike model weight (w_i) of 0.212, indicating only a 21.2% chance of being the best model in the set. Although it is impossible to clearly distinguish the most important variables based on the model weights alone, the low explanatory power of the null model ($\Delta AIC_c = 4.8$, $w_i = 0.019$; Table 2.2) indicates that the decision to disperse in the fall by juveniles is being affected by landscape characteristics.

Akaike parameter weights (w_j) measure the probability that a given parameter will occur in the best model of the set and in this analysis indicates that the proportion of forest habitat ($w_j = 0.685$; Table 2.2) and edge density ($w_j = 0.681$; Table 2.2) are the most important landscape characteristics affecting dispersal decisions. While the overall probability of a juvenile dispersing in the fall was extremely high, those juveniles that did not disperse were more likely to inhabit more forested landscapes than those that did disperse (Figure 2.3a). Juveniles inhabiting landscapes with high edge densities were also less likely to disperse than those inhabiting landscapes containing less edge (Figure 2.3b). The parameter SEX was also among the top-ranked models and had a parameter weight of 0.64. While the overall proportion of juveniles undergoing dispersal was high for both sexes, all of the juveniles that did not disperse during the fall were females

(Figure 2.3a,b). Although radius of gyration was among the models with a $\Delta AIC_c < 2$, its relatively low parameter weight ($w_j = 0.354$; Table 2.2) does not indicate any additional explanatory power when added to the models already containing the proportion of forest habitat in the landscape.

At a buffer size of 3000 m the decision to disperse was best explained by the global model containing all 5 possible model parameters, although its model weight indicated only a 27% chance of it being the best model in the set (Table 2.2). The null model was among the lowest ranking in the set ($\Delta AIC_c = 9.6$, $w_i = 0.002$), again indicating an overall effect of landscape characteristics on the decision to disperse. SEX was again a relatively important parameter ($w_j = 0.761$; Table 2.2) due to all juvenile males dispersing. Parameter weights clearly indicated that edge density ($w_j = 0.903$; Table 2.2) and the percentage of the landscape that was forested were also the most important landscape parameters at this buffer distance. However, the direction of the effect of the landscape variables was opposite of that found at the smaller buffer distances. Juvenile females inhabiting landscapes with high edge densities and a high percentage of forested habitat were more likely to disperse than individuals in less forested areas with lower edge density (Figure 2.4). Thus, even for birds inhabiting less forested areas, the expected likelihood of dispersing was greater in areas also having high edge densities than in areas with low edge densities (Figure 2.4).

The decision to disperse in the fall by adult birds in 500 m buffered landscapes was best explained by the model containing proportion of forest habitat, edge density, and radius of gyration (Table 2.2), although models containing the additional variables sex and mean patch area also had $\Delta AIC_c < 2$. Again, the model weight for the top-ranked model was relatively low ($w_i = 0.287$) but the null model ranked considerably lower ($\Delta AIC_c = 9.6$, $w_i = 0.002$; Table 2.2). Individual parameter weights indicate that edge density ($w_j = 0.919$; Table 2.2) and the percentage of forest habitat ($w_j = 0.831$; Table 2.2) have the greatest explanatory power. Overall, the effects were similar to juveniles in landscapes of this buffer distance, with adults inhabiting less forested areas more likely to disperse than those inhabiting more forested areas and birds inhabiting landscapes with low edge densities more likely to disperse than those inhabiting landscape with high edge density (Figure 2.5). Thus, even in landscapes with a high percentage of forested habitat, birds were more likely to disperse if edge density was relatively low (Figure 2.5).

When buffering adult pre-dispersal landscapes by 3000 m, the best model was the null model (Table 2.2), indicating little likelihood of any effect of landscape characteristics on adult dispersal decisions when measured at this scale.

2.3.4 SPRING DISPERSAL DECISIONS

AIC analysis of spring dispersal decisions indicated only a minor effect of landscape characteristics and only at the larger spatial scale. When spring landscapes were buffered at 3000 m, models including only edge density and edge density plus age were among the best models ($\Delta AIC_c < 2.0$) while the null model had less explanatory power ($\Delta AIC_c = 6.7$, $w_i = 0.010$; Table 2.3). Parameter weight clearly indicated that edge density had the greatest explanatory power ($w_j = 0.763$; Table 2.3), with birds inhabiting landscapes with high edge density less likely to undergo spring dispersal than birds inhabiting landscapes with less edge (Figure 2.6). Although age was also among the lowest rank models, the relatively low parameter estimate for age ($w_j = 0.321$; Table 2.3) indicated little difference in the effects of edge density between adults and juveniles.

The analysis of landscapes buffered at 500 m resulted in a null model with marginal explanatory power ($\Delta AIC_c = 3.1$, $w_i = 0.074$; Table 2.3), indicating no overall effect of landscape variables measured as the smaller spatial scale on the decision to disperse in the spring.

2.3.5 DISPERSAL DISTANCES

AIC analyses of multiple least-squares regression models comparing fall and spring dispersal distances and movement rates included measurements only of percentage of forest habitat and edge density along with study year and sex. We found no models containing landscape variables that were substantially better at describing the dispersal distances than the null models except in the case of distances moved by dispersing adults in the fall when landscapes were buffered at 250 m (Tables 2.4 & 2.5). For dispersing adults in the fall, the percentage of forest habitat and edge density along with study year were among the best models in the set ($\Delta AICc < 2.0$; Table 2.4), with the null model having a ΔAICc of 4.6. Adults who moved through landscapes with a low proportion of forest habitat and high edge densities tended to disperse longer distances than those moving through more forested areas with less edge (Figure 2.7a,b); however, these effects are obvious only in year three of the study (Figure 2.7a,b).

2.3.6 MOVEMENT RATES

Landscape characteristics affected juvenile fall movement rates. The AIC analysis clearly identified the model including the amount of forest habitat and study year as best explaining the rates when landscapes were buffered at 250 m ($w_i < 0.571$; Table 2.6). The parameter weight for amount of forest habitat ($w_j = 0.837$; Table 2.6) and study year ($w_j = 0.656$; Table 2.6) further indicated they were the most important predictors of movement rates. Juvenile birds moving through 250 m buffered landscapes with a higher percentage of forest habitat tended to move at lower rates than birds in less forested habitat (Figure 2.8).

When fall juvenile landscapes were buffered at 2000 m, the four top-ranking models ($\Delta AIC_c < 2.0$;Table 2.6) all contained edge density. While the amount of forest habitat, study year, and sex of birds were also included in these models, a parameter weight of 0.884 clearly indicates edge density has the greatest explanatory power in 2000 m buffered landscapes. Juvenile birds moving through landscapes with high edge densities move at higher rates than birds in areas containing less edge (Figure 2.9).

There was no evidence for an effect of landscape characteristics on fall adult rates or spring movement rates for either sex in landscapes measured at either buffer distance. The null model ΔAIC_c values were less than 2 in all cases (Tables 2.6 & 2.7) and no distinct differences were seen in individual parameter weights (Table 2.6 & 2.7), indicating little additional explanatory power for landscape variables. Sample size in the spring analyses was very low ($n = 8$).

2.3.7 DIFFERENCE IN PRE-DISPERSAL AND POST-DISPERSAL LANDSCAPES

Pre-dispersal landscape characteristics differed from post-dispersal landscapes for juveniles in the fall and adult birds in the spring. During the fall, juvenile 500 m buffered pre-dispersal landscapes were composed of smaller patches ($n = 42$, Wilcoxon signed-ranks test, $p = 0.002$; Figure 2.10a) and had lower mean radius of gyration ($n = 42$, Wilcoxon signed-ranks test, $p = 0.002$; Figure 2.10b) than post-dispersal landscapes. When landscapes were buffered at 3000 m, pre-dispersal landscapes were significantly more forested than post-dispersal landscapes ($n = 42$, Wilcoxon signed-ranks test, $p = 0.006$; Figure 2.11). No differences were found between 500m or 3000 m buffered fall adult pre- and post-dispersal landscapes.

Differences in spring adult 500 m buffered pre- and post-dispersal landscapes included a significantly higher percentage of forested habitat in post-dispersal landscapes ($n = 316$, Wilcoxon signed-ranks test, $p = 0.011$; Figure 2.12). No significant differences in pre- and post-dispersal landscapes were found among adults in 3000 m buffered landscapes or juveniles at either buffer distance in the spring.

2.3.8 HOME RANGE SIZES

AIC analysis of multiple least-squares regression models comparing home range sizes of fall and spring non-dispersers provided little evidence of any effects of large-scale landscape characteristics on home range size. AIC analysis of juvenile fall home ranges could not be conducted due to the small number of juveniles that did not disperse ($n = 6$). Adult fall home ranges sizes in landscapes buffered at 500 m were explained best by the model that included the proportion of forested habitat (Table 2.8). However, the low model weight of the best model ($w_i = 0.300$) and the null model $\Delta\mathrm{AIC_c}$ of 2.0 indicated little explanatory power by any of the landscape variables (Table 2.8).

There was even less evidence for an effect of landscape characteristics measured at a buffer scale of 3000 m on fall home range sizes. The null model explained the data almost as well as the best model ($\Delta\mathrm{AIC_c} = 1.3$, $w_i < 0.110$; Table 2.8). AIC analysis of spring home range sizes also provided little evidence for an effect of landscape characteristics on home range size. At both buffer sizes, the null model $\Delta\mathrm{AIC_c}$ values were less than 2 (Table 2.8), and no parameter weight indicated any additional explanatory power by the landscape variables (Table 2.8).

2.3.9 RISK OF PREDATION

The addition of parameters measuring percentage of forest habitat and edge density to the Cox proportion hazard model (Chapter 3) did not change the direction or significance of the effects of movement rate and habitat familiarity from the original model run. Among juveniles, only the percentage of forested habitat within 250 m of locations had a significant effect on predation risk, with an increase in predation risk occurring with an increase in percentage of forested habitat within the buffered landscapes. No significant effect of the amount of forest habitat or edge density within a landscape buffered at 3000 m was found on predation risk of juveniles and no effect of either metric at either scale was found on adult predation risk

2.4 DISCUSSION

Overall, we found that coarse-grained landscape characteristics do affect movement behavior of ruffed grouse, but effects were complex and varied considerably among specific behaviors and spatial scales. Among the behavioral responses included in our analysis, the decision to undergo fall dispersal was most consistently affected by landscape characteristics while, in contrast, we could detect no effect of coarse-grained landscape characteristics on home range size. Dispersal distances and movement rates exhibited the most highly age, season, or scale specific responses to landscape characteristics. While other factors not targeted in our study, such as intra-specific social interactions and fine-scale habitat characteristics, undeniably affect movement behavior in ruffed grouse, our results suggest that large scale changes in landscape composition (i.e. habitat loss) and edge density also can significantly affect dispersal behavior. Ruffed grouse exhibited an overall preference for heavily forested landscapes and landscape composition (i.e., the amount of forested habitat) had the most consistent impact on movements. Edge density also affected many behaviors, although what was driving these patterns remains unclear and will be explored below. We found no evidence that the other measurements of landscape configuration per se, patch size and radius of gyration, affected the decision to disperse or home range size.

The amount of forest habitat and forest/non-forest edge within local landscapes (i.e., those buffered at 500 m) affected the decision to disperse in the fall by juvenile females and adults in a similar pattern. Those birds inhabiting areas containing a low proportion of forest and low edge density were more likely to disperse than birds from highly forested areas or areas with high edge density. This pattern of results is surprising considering the negative correlation between the amount of forest habitat and edge in our study areas. While the amount of edge is generally expected to decrease with decreasing amount of target habitat (forest, in this case) in binary landscapes with less than 50 % target habitat, ruffed grouse in this study rarely inhabited local landscapes (i.e. buffered at 500 m) that were so sparsely forested. Thus, we expected the direction of the individual effects of forest amount and edge to be negatively correlated (e.g., likelihood of dispersal negatively related to amount of forest and positively related to edge density).

Adult ruffed grouse in our study exhibited a clear preference for local areas with a higher percentage of forested habitat than the surrounding landscapes. While we could not detect a similar selection of more heavily forested areas by juvenile grouse, juvenile pre-dispersal landscapes were rarely less than 75% forested even at the regional (i.e. 5000 m buffer) scale, making further selection for forest unnecessary. Pre-dispersal landscapes that already contain a relatively high percentage of forested habitat are more likely to contain the fine-scale habitat requirements (e.g., habitat with good year-round foraging and cover) than less forested areas, thus accounting for the lower likelihood of dispersal by birds in more forested areas, regardless of any additional effect of edge density.

While birds that inhabit pre-dispersal landscapes with a relevantly low percentage of forest habitat are more likely to disperse overall, there are two possible roles of edge density in these dispersal decisions. The negative effect of edge density on the likelihood of dispersal may be the result of edges acting as barriers to dispersal or edges indicating good grouse habitat. High densities of forest/non-forest edges may limit usable movement routes, making dispersal risky. Or, at the local scale, edge is an indicator of relatively desirable grouse habitat, even in areas with less overall forest making dispersal unnecessary. Previous research on ruffed grouse provides little evidence for which of these scenarios is most likely. Traditionally, edge has been thought to benefit many wildlife species (Leopold 1933) by increasing heterogeneity of habitat types at local levels. It is well established that heterogeneous mixtures of forest types, particularly with substantial early successional areas are important to meet foraging and cover requirements for ruffed grouse (Gullion 1984, Rusch et al. 2000, Dessecker and McAuley 2001). It is unclear, however, to what degree the forest/non-forest edge as measured in our study reflects the amount of desirable ruffed grouse habitat. While stands of early successional forest (e.g., created as a regeneration cut as part of grouse management plan) may have similar microhabitat characteristics as a forest/agricultural edge in terms of stem density and amount of understory, this similarity would exist only in a narrow corridor along a forest/agriculture edge. Indeed, Gullion (1989) states that while it is was common to include ruffed grouse among those species that benefit from edges, ruffed grouse actually avoid “high contrast” edges and use of such areas is a sign of poor quality habitat throughout the rest of their range. Gullion suspected that grouse are more vulnerable to predation when inhabiting hard edges, and it has been shown that nest predators may concentrate hunting behavior along hard edges (*see* Chalfoun *et al*. 2002 *for review*).

There have been no studies that have explicitly documented the degree of use of an agricultural matrix or the gap crossing ability of ruffed grouse and the precision of our telemetry locations prevents us from distinguishing the use of the non-forest matrix from forest edges. Given that grouse move predominately by walking, with flights of only short distances, and are under relatively high predation pressure, it is reasonable to assume that they would be reluctant to cross edges, thus limiting movement routes in areas with high edge densities. But the nature of forest/non-forest edges could just as well facilitate movement by providing cover during movement.

We also measured characteristics of landscapes buffered at 3000 m, a scale more reflective of landscape composition and configuration of a region that grouse may encounter during dispersal movements as opposed to daily movements within a home range. Our results indicated an effect of these regional landscape characteristics on the dispersal decision only of juvenile grouse in the fall. The lack of any detectable effect of landscape at this scale on adult dispersal distances may reflect the much shorter dispersal distances moved by adults (0.8 km) versus that of juveniles (3.7 km). Juveniles birds were more likely to disperse if inhabiting regions containing a higher percent of forest and high edge density, effects opposite in direction of those found at smaller buffer distances, and again unexpected in light of the expected negative correlation between amount of forest and edge density.

The large majority of juveniles undergo dispersal in the fall and previous analysis of juvenile fall dispersal distances indicated that long distance movements associated with natal dispersal occur predominantly in the fall rather than the spring (Chapter 1). Natal dispersal is likely an innate behavior and the few juveniles in our study that did not disperse in the fall may have begun exploratory dispersal movements but then returned to their brood areas. Our analysis indicates that these juvenile non-dispersers were more likely to inhabit sparsely forested regions than dispersers. Juveniles in these sparsely forested regions are less likely to encounter suitably forested areas and have a greater likelihood of encountering large areas of non-forested matrix than juveniles in more forested areas, which may discourage attempts to move out of their brood range. While we were unable to explicitly quantify exploratory movements by non-dispersing birds, we did see anecdotal evidence of birds changing directions or returning to previously visited areas when encountering large gaps in forested habitat. Åberg et al. (1995) found evidence that hazel grouse (*Bonasa bonasia*), a European forest grouse species exhibiting similar movement and habitat preferences as ruffed grouse, were reluctant to disperse through even relatively small gaps in forest habitat. In their study of patch occupancy rates in a landscape consisting of forest patches with intervening agricultural matrix, hazel grouse were not found in forest patches more than 100 m from a continuous expanse of forest.

While juveniles inhabiting sparsely forested pre-dispersal regions were less likely to disperse overall than juveniles in heavily forested areas, there are again two possible roles of edge density in these natal dispersal decisions. The positive effect of edge density on the likelihood of juvenile dispersal may be the result of edges facilitating movement or edges may simply be indicating undesirable grouse habitat. High densities of forest/non-forest edges may facilitate movement by providing corridors of heavier cover utilized during the long natal dispersal movement of juveniles. Or, at the regional scale, edge is an indicator of relatively poor grouse habitat, thus encouraging dispersal, even in areas with more overall forest. Again, previous research on ruffed grouse provides little evidence for which of these scenarios is most likely. However, if we assume most juveniles at least attempt to undergo natal dispersal in the fall, regardless of the “quality” of their brood habitat, it seems more probable that the lack of forest habitat at the regional scale is discouraging dispersal and high edge densities facilitate movement out of even sparsely forested regions.

Among juvenile dispersers, we also found that pre-dispersal landscapes were more heavily forested than post-dispersal regions. This is likely due to brood habitat being located in regions already heavily forested and dispersing juveniles are unlikely to find regions as heavily forested while undergoing dispersal. There was no difference in the percentage of forest within pre- and post-dispersal landscape at the local scale, so although juveniles were not necessarily able to find large regions of heavily forested habitat, they were able to select the heavily forested local areas within their larger regions.

While the decision to disperse was consistently affected by the amount of forest habitat and edge density, fall dispersal distances and movement rates of specific ages were also affected by the amount of forest and edge within landscapes defined by buffering the routes of dispersing birds. While adults moved much shorter distances in the fall than juveniles, the adults that moved the greatest distances were moving through landscapes with relatively high edge densities and a low percentage of forest habitat. The effect was evident only in landscapes buffered at 250 m, reflective of a bird’s immediate surrounding habitat while dispersing and it may indicate a reluctance by adults to settle in sparsely forested areas with high edge densities. However, our analysis also indicated that the observed trend was likely driven by a very small number of adults that moved exceptionally long distances during a single year of the study and thus may be an effect of an unmeasured factor and not indicative of a true effect of landscape characteristics on dispersal distances.

The dispersing juveniles in the fall that exhibited the highest rates of movement tended to move through landscapes less forested than landscapes traversed by more slowly moving juveniles when their route was buffered at 250 m. In landscapes buffered at 2000 m, those dispersing juveniles moving at the highest rates tended to be moving through landscapes with higher edge densities than landscapes traversed by more slowly moving juveniles. High rates of movement by dispersing juveniles moving through sparsely forested areas may be due to having to move relatively great distances before encountering suitable habitat, (e.g. traversing gaps in forest habitat or forested areas with inadequate cover or other resources).

In a previous analysis we found birds that move at higher rates of movement experience a significantly greater risk of predation than birds moving at lower rates (Chapter 3). If birds move quickly through an area due to low amounts of forest habitat, habitat loss may indirectly be contributing to an increase in predation mortality as well. Although birds moving through sparsely forested areas tend to move at higher rates than birds in more forested areas, which may lead to increased predation risk, we also found an additional effect of the amount of forest on the risk of predation. Birds that inhabited landscapes buffered at 250 m with a high percentage of forest were more likely to be killed by a predator than birds in less heavily forested areas, independent of any increase in risk due to moving at higher rates or being in unfamiliar territory. The sample of birds used in the Cox proportional hazard model in Chapter 3 included all birds alive at the time of each predation event, and thus included both dispersing and non-dispersing birds. The increase in predation risk due to the amount of forest indicated by the model may be due in part to differences in landscapes between dispersing and non-dispersing birds.

The use of a binary landscape limited our ability to detect the effects of fine scale landscape characteristics on movement decisions. For example, our inability to detect any affect of landscape characteristics on home range size may have been due to issues relating to habitat resolution. It is possible that home range sizes could be affected soley by the amount of forest habitat in an area. For example, capercaillie home range sizes were found to be negatively affected by low abundance of a seasonally preferred habitat, with birds compensating for a low proportion of this single type of habitat in local areas by using larger home ranges (Gjerde and Wegger 1989). However, for ruffed grouse the distribution of stands of different ages and types that provide a variety of foraging and cover resources are more likely to affect home range sizes than amount of forest per se. Fearer and Stauffer (2003) investigated the effects of landscape characteristics measured at a fine resolution on home range size of grouse in Virginia. While their study was conducted in a contiguously forested landscape, they used landscape data consisting of 12 habitat classes consisting of combinations of deciduous or coniferous stands at different soil moisture and understory levels as well as early successional regeneration cuts. They found home range sizes were positively related to the number of different habitat types, amount of core area within habitat patches, mean shape index of habitat patches, and negatively related to the amount of high contrast edge within the home range.

The importance of habitat resolution in detecting ecological process has recently received much attention. Lawler *et al*. (2004) compared the effects of habitat classified at two different resolutions on avian diversity and distributions. They used data sets based on 14 “coarsely” resolved land-cover variables and 160 “finely” resolved land-cover variables and found great variability in explanatory power between the levels of resolution among species, ecological phenomena, and geographic regions. Thus, effects found at one habitat resolution in one area may be absent or significantly different in another region.

Future studies of ruffed grouse dispersal behavior that combine detailed movement data and landscape characteristics measured at multiple-resolutions are needed to fully understand how grouse respond to habitat loss and fragmentation. For example, while we found high densities of forest/non-forest edge in an area increased the likelihood of dispersal and the rate of movement for some birds, knowledge of fine-scale habitat differences between the forest interiors, edges, and the non-forest matrix in a given area would aid in clarifying whether edges are facilitating movement or indicators of unsuitable habitat in a region. In addition, studies investigating landscape effects need to be conducted in the northern portion of ruffed grouse range. Response to habitat loss and/or fragmentation may differ with latitude due to the prevalence of aspen (*Populus spp*.) in northern but not southern forests. Aspen is an important year-round source of food and cover for grouse and likely the main factor in the greater population densities found in northern versus southern regions (Rusch et al. 2001, Dessecker and McCauley 2001).

Ruffed grouse populations are experiencing long-term declines in Ohio (Stoll et al. 1999) and throughout the southern and central Appalachian portions of its range (Dessecker and McAuley 2001). Habitat loss and degradation are thought to be the most important factors affecting this decline (Thomspson and Dessecker 1997, Rusch et al. 2001), particularly through their effect on recruitment (Dessecker and McCauley 2001). While overall amount of forest is declining due to agricultural and urban development, the remaining forests throughout this region are also maturing (Trani *et al*. 2001). Changing management techniques and attitudes towards harvest by public officials and private landowners as well as increased fire suppression have resulted in a decline in early successional forests (Trani *et al*. 2001).

While we did not measure landscape characteristics at a fine enough resolution to incorporate the amount of early successional forest in our analysis, our results did indicate that movement behaviors in ruffed grouse are likely to be affected by changes in the amount of overall forest and edge. While we found no evidence for the spatial configuration of forest (beyond the amount of edge) affecting movement behaviors, some of the effects on behavior we did observe may be contributing to the decline in grouse population seen in portions of its range. Birds inhabiting areas with declining amounts of forest may be more likely to undergo dispersal and move at higher rates during dispersal than birds in more forested areas, both of which increase their risk of predation. The effect of forest/non-forest edges in our study are harder to interpret, and the variation in the direction of edge effects on movement is further evidence of the importance of investigating landscape effects on ecological process at multiple scales. Acquiring detailed movement and landscape data at multiples scales remains difficult, but is the key to understanding the nature of a species' response to habitat loss and fragmentation.

2.5 TABLES

		Woodbury				Waterloo			
Metric[†]	units	mean	SD	min.	max.	mean	SD	min.	max.
PLAND	%	59.9	11.8	40.0	83.0	86.4	9.3	69.3	98.4
ED	m/ha	73.4	6.4	58.3	85.4	54.8	26.4	13.6	94.2
AREA	ha	1329	583	264	2324	2385	328	1401	2768
GYRATE	m	1617	317	785	1993	1959	62	1619	1997

Table 2.1: Summary statistics of landscape composition and configuration metrics for Woodbury and Waterloo study areas. Statistics are calculated from all pre-dispersal and non-disperser 3000 m buffered landscapes.

[†] PLAND = percentage of the landscape consisting of forest habitat, ED = edge density, AREA = area-weighted mean area of all forest patches in the landscape, GYRATE = area weighted mean radius of gyration.

Response	Buffer size (m)	K	AIC_c	ΔAIC_c	w_i	Parameter Estimates[†]				
						PLAND	ED	AREA	GYRATE	SEX
Fall juvenile dispersal decision	500	5	35.6	0.0	0.212	-0.218	-0.075	-	-	-20.0
		4	37.2	1.6	0.096	-0.255	-0.080	-	-	-
		6	37.3	1.7	0.091	-0.170	-0.060	-	-0.093	-20.0
		3	37.4	1.8	0.088	-	-	-	-	-21.0
		2	40.4	4.8	0.019	*null*				
					w_j =	0.685	0.681	0.250	0.354	0.640
	3000	7	30.8	0.0	0.270	3.550	0.344	-0.103	0.062	-26
		5	31.6	0.8	0.180	0.095	0.136	-	-	-20
		4	32.1	1.3	0.140	-	0.066	-	-	-20
		2	40.4	9.6	0.002	*null*				
					w_j =	0.733	0.903	0.437	0.396	0.761
Fall adult dispersal decision[††]	500	6	74.1	0.0	0.287	-0.136	-0.058	-	0.048	-
		7	74.9	0.8	0.190	-0.143	-0.063	-	0.048	0.857
		6	76.1	2.0	0.107	-0.281	-0.043	0.250	-	-
		3	83.7	9.6	0.002	*null*				
					w_j =	0.830	0.919	0.315	0.618	0.390
	3000	3	85.1	0.0	0.230	*null*				
		4	85.1	0.0	0.227	-	-	-	-	0.690
		4	86.5	1.4	0.112	-	0.011	-	-	-
					w_j =	0.279	0.304	0.087	0.096	0.436

Table 2.2. Ranked logistic regression models explaining fall dispersal decisions for juvenile ($n = 48$) and adult ($n = 63$) birds in landscapes buffered at 500 and 3000 meters. K is the total number of parameters (intercept, variance, and individual independent variables). AIC_c values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC_c is the difference in AIC_c values from the lowest AIC_c value. AIC model weight (w_i) is the probability that model i is the best model in the set. All models with $\Delta\text{AIC}_c < 2$ are included in the table. The null model includes the intercept and variance but no additional parameters and is included for comparison regardless of ΔAIC_c. A complete list of AIC values for all models and analyses is located in Appendix A. Akaike parameter weights (w_j) are the sum of Akaike model weights of all models that include that parameter and equal the probability that a given parameter is included in the best model.

[†] PLAND = percentage of the landscape consisting of forest habitat, ED = edge density (m/ha), AREA = area-weighted mean area of all forest patches in the landscape, GYRATE = area-weighted mean radius of gyration, SEX = male or female.

[††] Listed AIC_c and ΔAIC_c values for the fall adult dispersal decision analysis are QAIC_c and ΔQAIC_c values, AIC values that are corrected for small sample size and overdispersion of data.

Response	Buffer size (m)	K	AIC_c	ΔAIC_c	w_i	Parameter Estimates†				
						PLAND	ED	AREA	GYRATE	AGE
Spring dispersal decision	500	3	100.1	0.0	0.357	-	-0.018	-	-	-
		4	102.0	1.6	0.138	-	-0.018	-	-	-0.368
		2	103.2	3.1	0.074			*null*		
					w_j =	0.326	0.760	0.100	0.098	0.281
	3000	3	96.5	0.0	0.284	-	-0.032	-	-	-
		4	97.9	1.4	0.140	-	-0.033	-	-	-0.469
		2	103.2	6.7	0.010			*null*		
					w_j =	0.425	0.763	0.246	0.207	0.321

Table 2.3. Ranked logistic regression models explaining spring dispersal decisions for birds ($n = 74$) in landscapes buffered at 500 and 3000 meters. K is the total number of parameters (intercept, variance, and individual independent variables). AIC_c values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC_c is the difference in AIC_c values from the lowest AIC_c value. AIC model weight (w_i) is the probability that model i is the best model in the set. All models with $\Delta\text{AIC}_c < 2$ are included in the table. The null model includes the intercept and variance but no additional parameters and is included for comparison regardless of ΔAIC_c. A complete list of AIC values for all models and analyses is located in Appendix A. Akaike parameter weights (w_j) are the sum of all Akaike model weights of all models that include that parameter and equal the probability that a given parameter is included in the best model.

† PLAND = percentage of the landscape consisting of forest habitat, ED = edge density (m/ha), AREA = area-weighted mean area of all forest patches in the landscape, GYRATE = area-weighted mean radius of gyration, AGE = juvenile or adult.

Response	Buffer size (m)	K	AICc	ΔAIC$_c$	w_i	Parameter Estimates[†]			
						PLAND	ED	YEAR	SEX
Fall juvenile dispersal distance	250	3	10.1	0.0	0.195	-	-	0.362	-
		2	10.5	0.4	0.166		*null*		
		3	11.3	1.2	0.110	0.021	-	-	-
		4	11.7	1.6	0.092	0.018	-	0.335	-
					w_j =	0.355	0.256	0.475	0.252
	2000	3	10.1	0.0	0.231	-	-	-0.362	-
		2	10.5	0.4	0.197		*null*		
					w_j =	0.254	0.238	0.516	0.256
Fall adult dispersal distance	250	3	-267.1	0.0	0.202	-0.001	-	-	-
		4	-266.6	0.5	0.161	-0.001	-	-0.006	-
		3	-266.0	1.1	0.121	-	0.0003	-	-
		4	-265.9	1.2	0.113	-	0.0003	-0.007	-
		2	-262.5	4.6	0.020		*null*		
					w_j =	0.657	0.489	0.419	0.256
	2000	3	-263.6	0.0	0.193	-	0.0002	-	-
		2	-262.5	1.1	0.111		*null*		
		4	-262.4	1.2	0.105	-	0.0003	0.006	-
		3	-261.9	1.7	0.081	-0.0002	-	-	-
		4	-261.8	1.8	0.077	-0.0002	0.0003	-	0.004
					w_j =	0.346	0.574	0.305	0.319

Table 2.4. Ranked linear regression models explaining fall dispersal distances for juvenile (n = 34) and adult (n = 35) birds in landscapes buffered at 250 and 2000 meters. K is the total number of parameters (intercept, variance, and individual independent variables). AIC$_c$ values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC$_c$ is the difference in AIC$_c$ values from the lowest AIC$_c$ value. AIC model weight (w_i) is the probability that model i is the best model in the set. All models with ΔAIC$_c$ < 2 are included in the table. The null model includes the intercept and variance but no additional parameters and is included for comparison regardless of ΔAIC$_c$. A complete list of AIC values for all models and analyses is located in Appendix A. Akaike parameter weights (w_j) are the sum of all Akaike model weights of all models that include that parameter and equal the probability that a given parameter is included in the best model.

[†] PLAND = percentage of the landscape consisting of forest habitat, ED = edge density (m/ha), YEAR = 1996, 1997, or 1998, SEX = male or female.

						Parameter Estimates†			
Response	Buffer size (m)	K	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	w_i	PLAND	ED	YEAR	AGE
Spring dispersal distance	250	3	-214.0	0.0	0.302	-	-	-	0.018
		2	-212.0	2.0	0.113		*null*		
					w_j =	0.277	0.277	0.211	0.668
	2000	3	-214.0	0.0	0.211	-	-	-	0.018
		4	-213.8	0.2	0.187	0.0003	0.0004	-	0.017
		4	-213.0	1.0	0.128	-	0.0002	-	0.018
		2	-212.0	2.0	0.079		*null*		
					w_j =	0.359	0.490	0.191	0.701

Table 2.5. Ranked linear regression models explaining spring dispersal distances for birds ($n = 30$) in landscapes buffered at 250 and 2000 meters. K is the total number of parameters (intercept, variance, and individual independent variables). $\mathrm{AIC_c}$ values are Akaike Information Criteria values corrected for small sample sizes and $\Delta\mathrm{AIC_c}$ is the difference in $\mathrm{AIC_c}$ values from the lowest $\mathrm{AIC_c}$ value. AIC model weight (w_i) is the probability that model i is the best model in the set. All models with $\Delta\mathrm{AIC_c} < 2$ are included in the table. The null model includes the intercept and variance but no additional parameters and is included for comparison regardless of $\Delta\mathrm{AIC_c}$. A complete list of AIC values for all models and analyses is located in Appendix A. Akaike parameter weights (w_j) are the sum of all Akaike model weights of all models that include that parameter and equal the probability that a given parameter is included in the best model.

† PLAND = percentage of the landscape consisting of forest habitat, ED = edge density (m/ha), YEAR = 1996, 1997, or 1998, AGE = juvenile or adult.

						Parameter Estimates†			
Response	Buffer size (m)	K	AIC$_c$	ΔAIC$_c$	w_i	PLAND	ED	YEAR	SEX
Fall juvenile movement rate	250	4	152.3	0.0	0.573	-4.618	-	-67.89	-
		2	164.0	11.7	0.002	*null*			
					w_j =	0.837	0.212	0.896	0.173
	2000	3	152.8	0.0	0.322	-	5.343	-	-
		4	154.1	1.3	0.169	-	3.994	-39.24	-
		4	154.4	1.6	0.144	-1.724	4.077	-	-22.48
		4	154.8	2.0	0.117	-1.623	4.323	-	-
		2	164.0	11.2	0.001	*null*			
					w_j =	0.375	0.884	0.335	0.261
Fall adult movement rate	250	2	65.9	0.0	0.706	*null*			
					w_j =	0.052	0.068	0.048	0.135
	2000	2	65.9	0.0	0.694	*null*			
					w_j =	0.064	0.068	0.068	0.133

Table 2.6. Ranked linear regression models explaining fall movement rates for juvenile (*n* = 17) and adult (*n* = 8) birds in landscapes buffered at 250 and 2000 meters. *K* is the total number of parameters (intercept, variance, and individual independent variables). AIC$_c$ values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC$_c$ is the difference in AIC$_c$ values from the lowest AIC$_c$ value. AIC model weight (w_i) is the probability that model *i* is the best model in the set. All models with ΔAIC$_c$ < 2 are included in the table. The null model includes the intercept and variance but no additional parameters and is included for comparison regardless of ΔAIC$_c$. A complete list of AIC values for all models and analyses is located in Appendix A. Akaike parameter weights (w_j) are the sum of all Akaike model weights of all models that include that parameter and equal the probability that a given parameter is included in the best model.

† PLAND = percentage of the landscape consisting of forest habitat, ED = edge density (m/ha), YEAR = 1996, 1997, or 1998, SEX = male or female.

						Parameter Estimates†			
Response	Buffer size (m)	K	AIC_c	ΔAIC_c	w_i	PLAND	ED	YEAR	AGE
Spring movement rates	250	2	75.8	0.0	0.737	*null*			
					w_j =	0.109	0.068	0.049	0.047
	2000	2	75.8	0.0	0.621	*null*			
					w_j =	0.090	0.218	0.041	0.043

Table 2.7. Ranked linear regression models explaining spring movement rates for birds (n = 8) in landscapes buffered at 250 and 2000 meters. K is the total number of parameters (intercept, variance, and individual independent variables). AIC_c values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC_c is the difference in AIC_c values from the lowest AIC_c value. AIC model weight (w_i) is the probability that model i is the best model in the set. All models with $\Delta AIC_c < 2$ are included in the table. The null model includes the intercept and variance but no additional parameters and is included for comparison regardless of ΔAIC_c. A complete list of AIC values for all models and analyses is located in Appendix A. Akaike parameter weights (w_j) are the sum of all Akaike model weights of all models that include that parameter and equal the probability that a given parameter is included in the best model.

† PLAND = percentage of the landscape consisting of forest habitat, ED = edge density (m/ha), YEAR = 1996, 1997, or 1998, AGE = juvenile or adult.

						Parameter Estimates†				
Response	Buffer size (m)	*K*	AIC$_c$	ΔAIC$_c$	w_i	PLAND	ED	AREA	GYRATE	AGE
Fall home range size	500	3	394.7	0.0	0.300	0.615	-	-	-	
		3	395.7	1.0	0.182	-	-0.308	-	-	
		2	396.7	2.0	0.110			*null*		
		4	396.7	2.0	0.107	0.465	-0.120	-	-	
					w_j =	0.656	0.459	0.297	0.168	
	3000	3	395.5	0.0	0.318	-	-0.377	-	-	
		3	396.6	1.1	0.188	0.467	-	-	-	
		2	396.7	1.2	0.168			*null*		
					w_j =	0.534	0.556	0.233	0.147	
Spring home range size	500	3	-18.1	0.0	0.224	-	-	-	-	-0.429
		4	-17.0	1.1	0.128	0.008	-	-	-	-0.449
		2	-16.3	1.8	0.089			*null*		
		4	-16.1	2.0	0.082	-	-0.003	-	-	-0.435
					w_j =	0.456	0.375	0.278	0.197	0.638
	3000	3	-18.1	0.0	0.201	-	-	-	-	-0.429
		4	-17.6	0.5	0.158	-	0.008	-	-	-0.406
		3	-17.1	1.0	0.123	-	0.009	-	-	-
		3	-16.3	1.8	0.080	-0.009	-	-	-	-
		2	-16.3	1.8	0.080			*null*		
					w_j =	0.361	0.510	0.197	0.176	0.552

Table 2.8. Ranked linear regression models explaining home range sizes for fall (n = 54) and spring (n = 41) birds in landscapes buffered at 500 and 3000 meters. *K* is the total number of parameters (intercept, variance, and individual independent variables). AIC$_c$ values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC$_c$ is the difference in AIC$_c$ values from the lowest AIC$_c$ value. AIC model weight (w_i) is the probability that model *i* is the best model in the set. All models with ΔAIC$_c$ < 2 are included in the table. The null model includes the intercept and variance but no additional parameters and is included for comparison regardless of ΔAIC$_c$. A complete list of AIC values for all models and analyses is located in Appendix A. Akaike parameter weights (w_j) are the sum of all Akaike model weights of all models that include that parameter and equal the probability that a given parameter is included in the best model.

† PLAND = percentage of the landscape consisting of forest habitat, ED = edge density (m/ha), AREA = area-weighted mean area of all forest patches in the landscape, GYRATE = area-weighted mean radius of gyration, AGE = juvenile or adult.

2.6 Figures

Figure 2.1. Pre- and post-dispersal locations and landscape boundaries (blue) and dispersal locations and landscape boundaries (red) for a single dispersing bird during the fall of 1996. Boundaries for pre- and post-dispersal landscapes were created by buffering the mean pre- and post dispersal locations at 500 m and 3000 m (labeled). The bird dispersed a net distance of 6.8 km over 23 days. Dispersal landscape boundaries were created by buffering all locations during dispersing period at 250 m and 2000 m (labeled). Black arrows illustrate the dispersal route. Habitat was classified as forest (green) and non-forest (yellow). Example landscape metric values for the 3000 m pre-dispersal landscape are: PLAND = 50.1%, ED = 15.3 m / ha , AREA = 2761 ha, GYRATE = 1994 m.

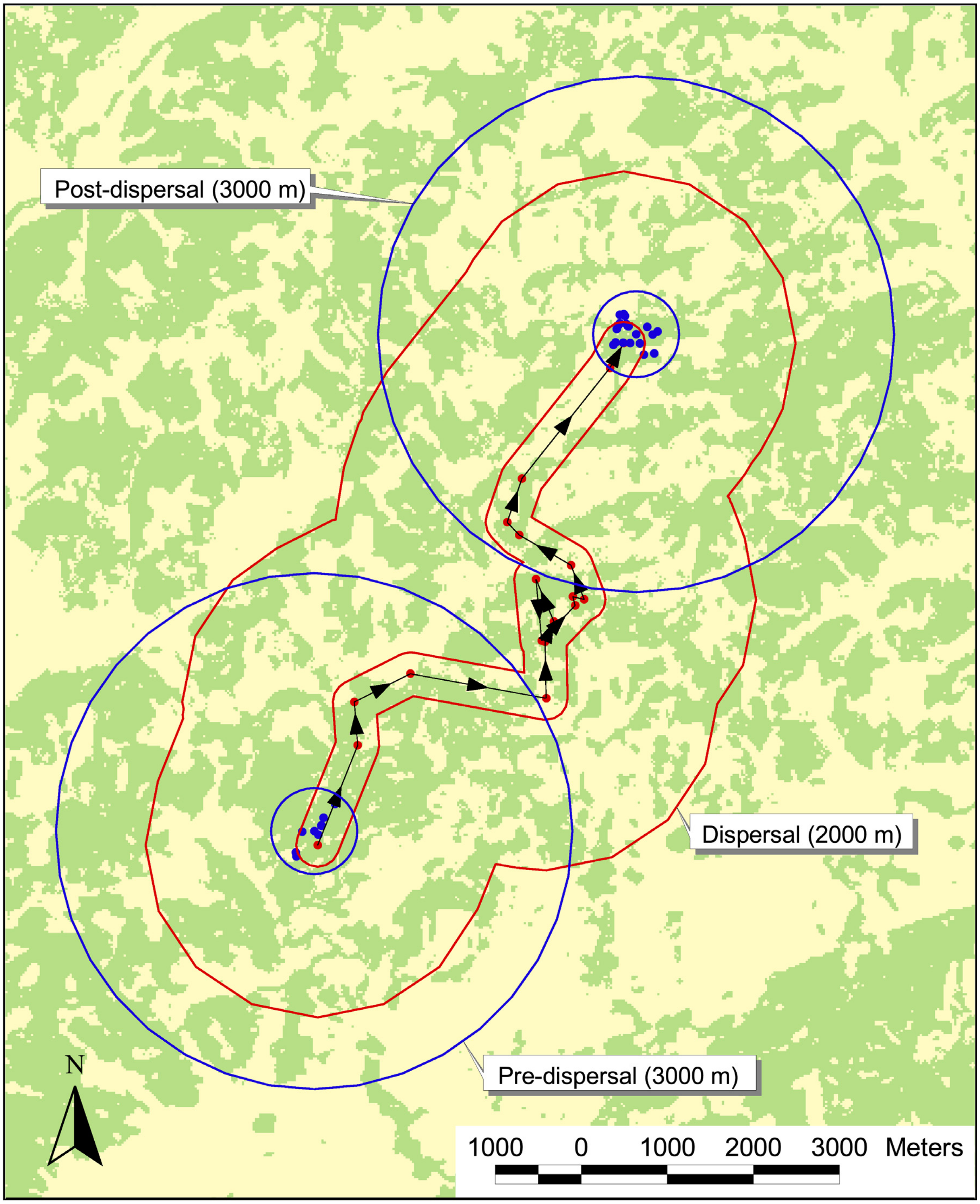
Post-dispersal (3000 m)
Dispersal (2000 m)
Pre-dispersal (3000 m)
N
1000
0
1000
2000
3000
Meters

Figure 2.1

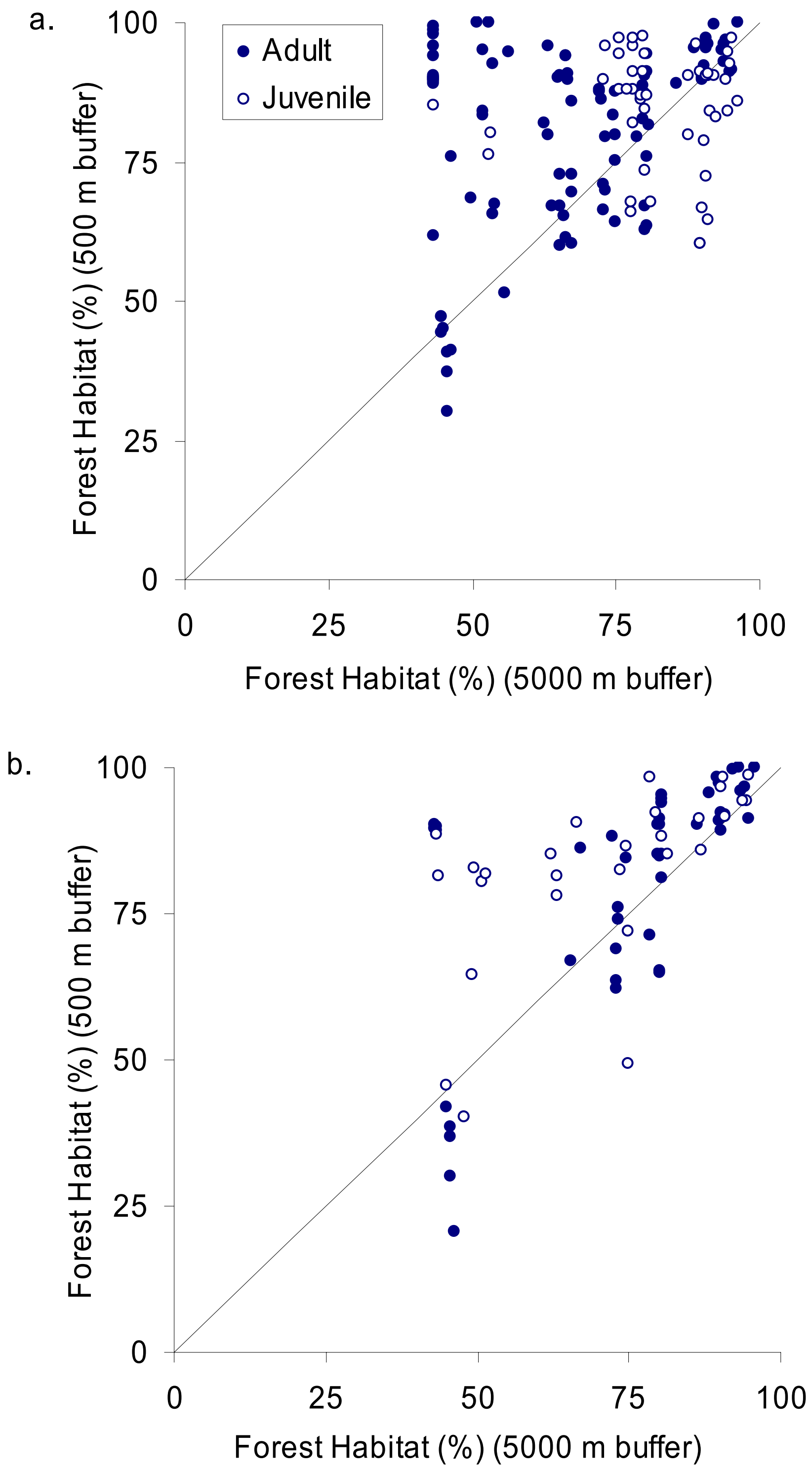

Figure 2.2. The relationship between percentages of forest habitat at landscapes buffered at 500 m and 5000 m for adults (filled circles) and juveniles (open circles) during the (a) fall and (b) spring seasons. Points above the 45° line indicate that local landscapes were more highly forested than regional landscapes.

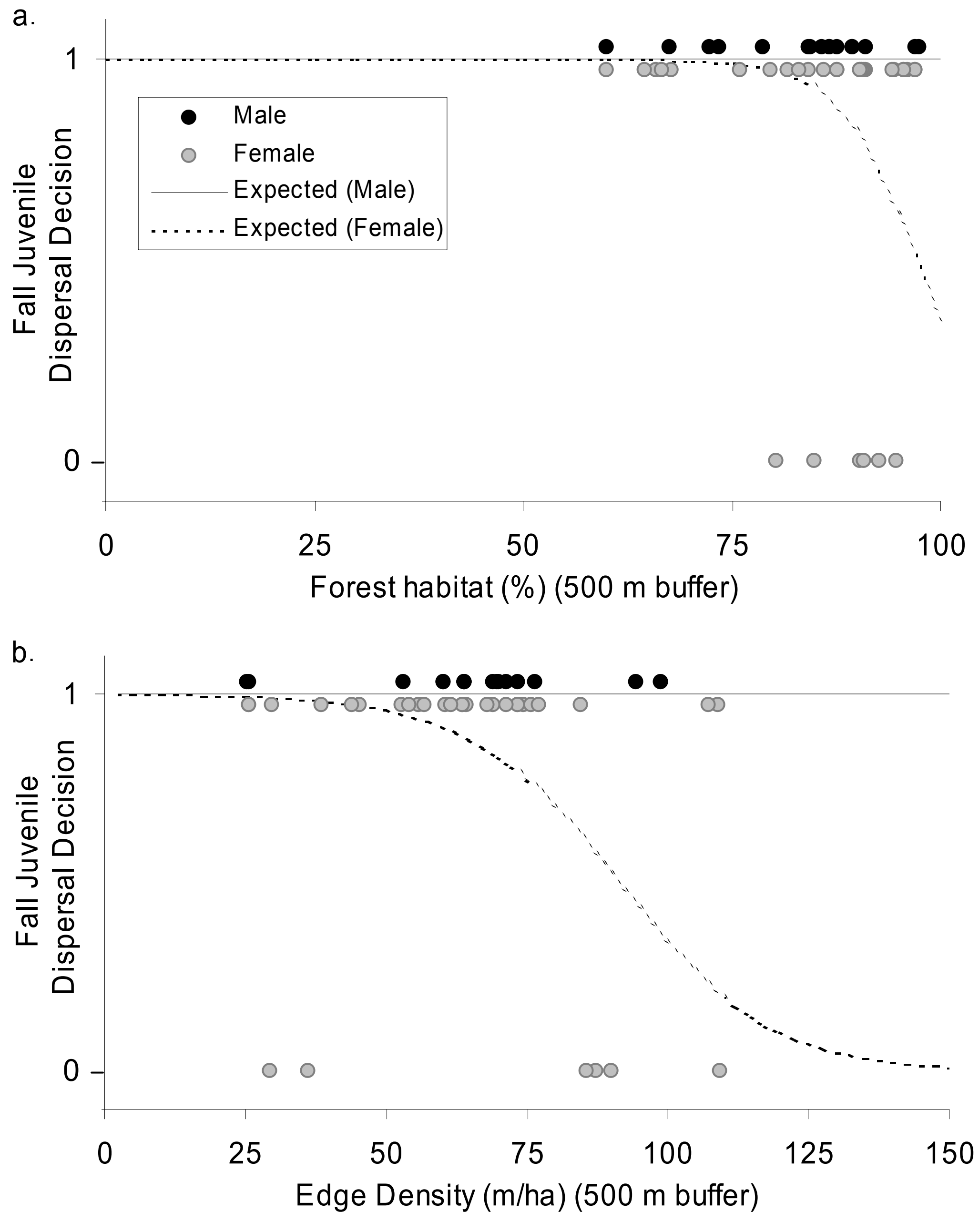

Figure 2.3. The relationship of (a) amount of forest habitat (%) and (b) edge density (m/ha) with fall dispersal decision (non-dispersers = 0 and dispersers = 1) of juveniles in 500 m buffered landscapes. Data points are vertically offset to illustrate differences between sexes (male = black circles and females = gray circles). Expected values for male (solid line) and females (dashed line) were calculated using parameter estimates and median variable values from the logistic regression model with the lowest ΔAIC value.

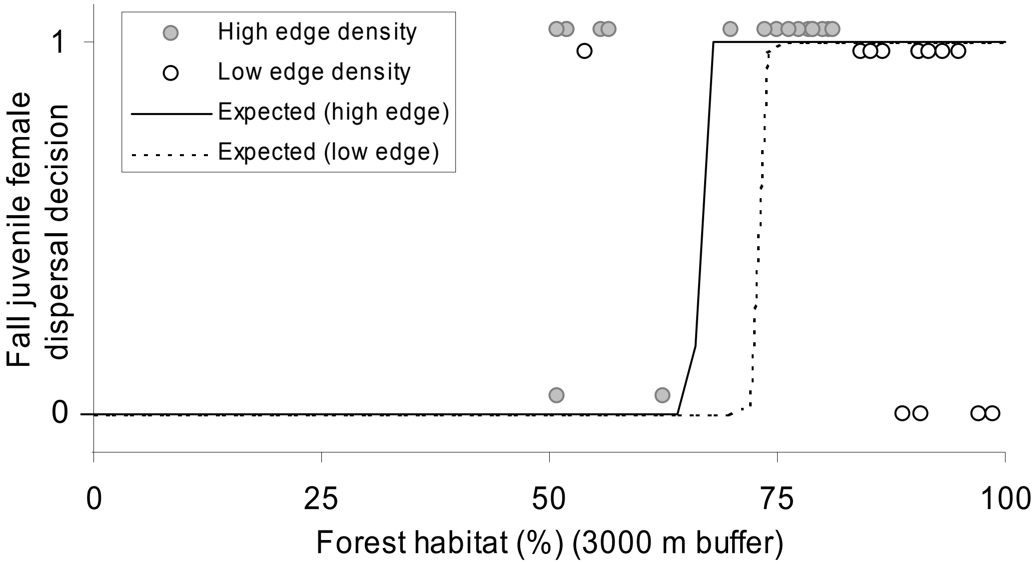

Figure 2.4. The relationship of percentage of forest habitat with the fall dispersal decision of juvenile females in landscapes with low levels of edge density (open circles) and high levels of edge density (gray circles) buffered at 3000 m. Expected values were calculated using parameter estimates from the logistic regression model with the lowest ΔAIC value. An edge density value of 100 m/ha was used to calculate the expected curve at high edge density (solid line) and 50 m/ha to calculate the expected curve at low edge density (dashed line). The median values of the radius of gyration and mean patch area variables were used in the calculation of both expected curves.

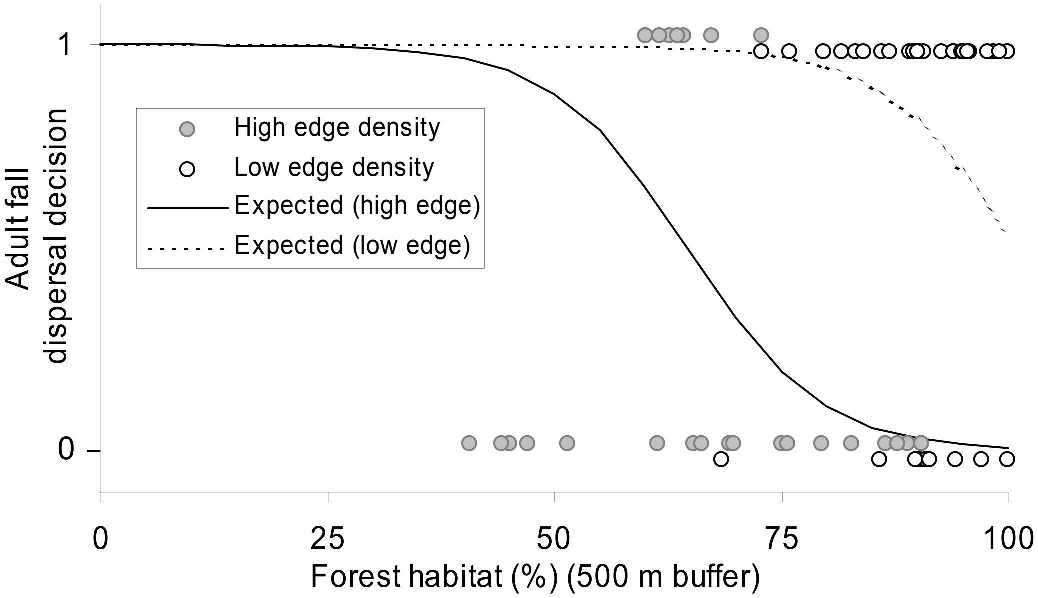

Figure 2.5. The relationship of percentage of forest habitat with the fall dispersal decision of adults in landscapes with low levels of edge density (open circles) and high levels of edge density (gray circles) buffered at 500 m. Expected values were calculated using parameter estimates from the logistic regression model with the lowest ΔAIC value. An edge density value of 100 m/ha was used to calculate the expected curve at high edge density (solid line) and 50 m/ha to calculate the expected curve at low edge density (dashed line). The median value of the radius of gyration variable was used in the calculation of both expected curves.

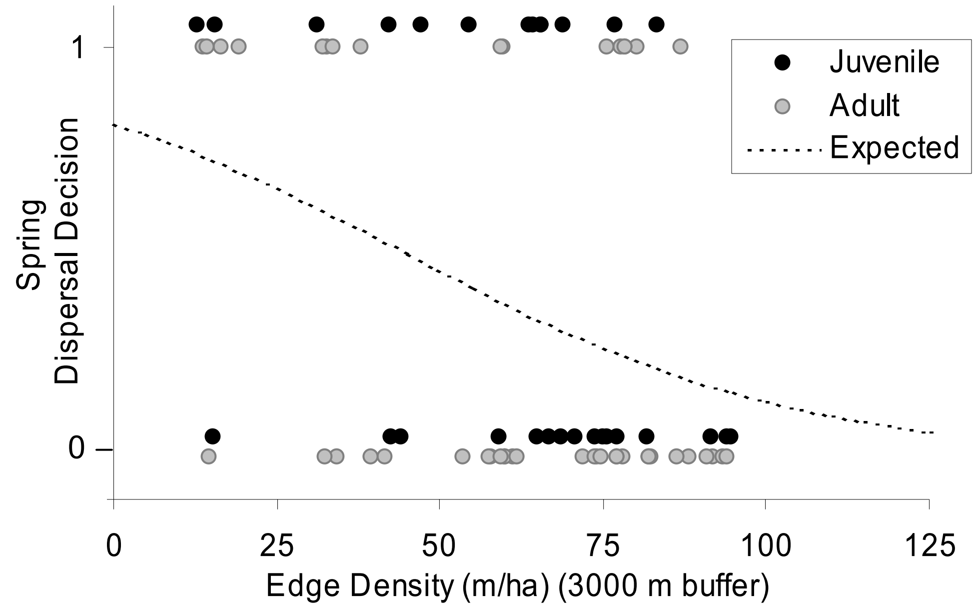

Figure 2.6. The relationship of edge density (m/ha) with the spring dispersal decision (non-dispersers = 0 and dispersers = 1) of birds in 3000 m buffered landscapes. Data points are vertically offset to illustrate differences between ages (juvenile = black circles and adult = gray circles). Expected values (dashed lines) were calculated using parameter estimates and median variable values from the logistic regression model with the lowest ΔAIC value.

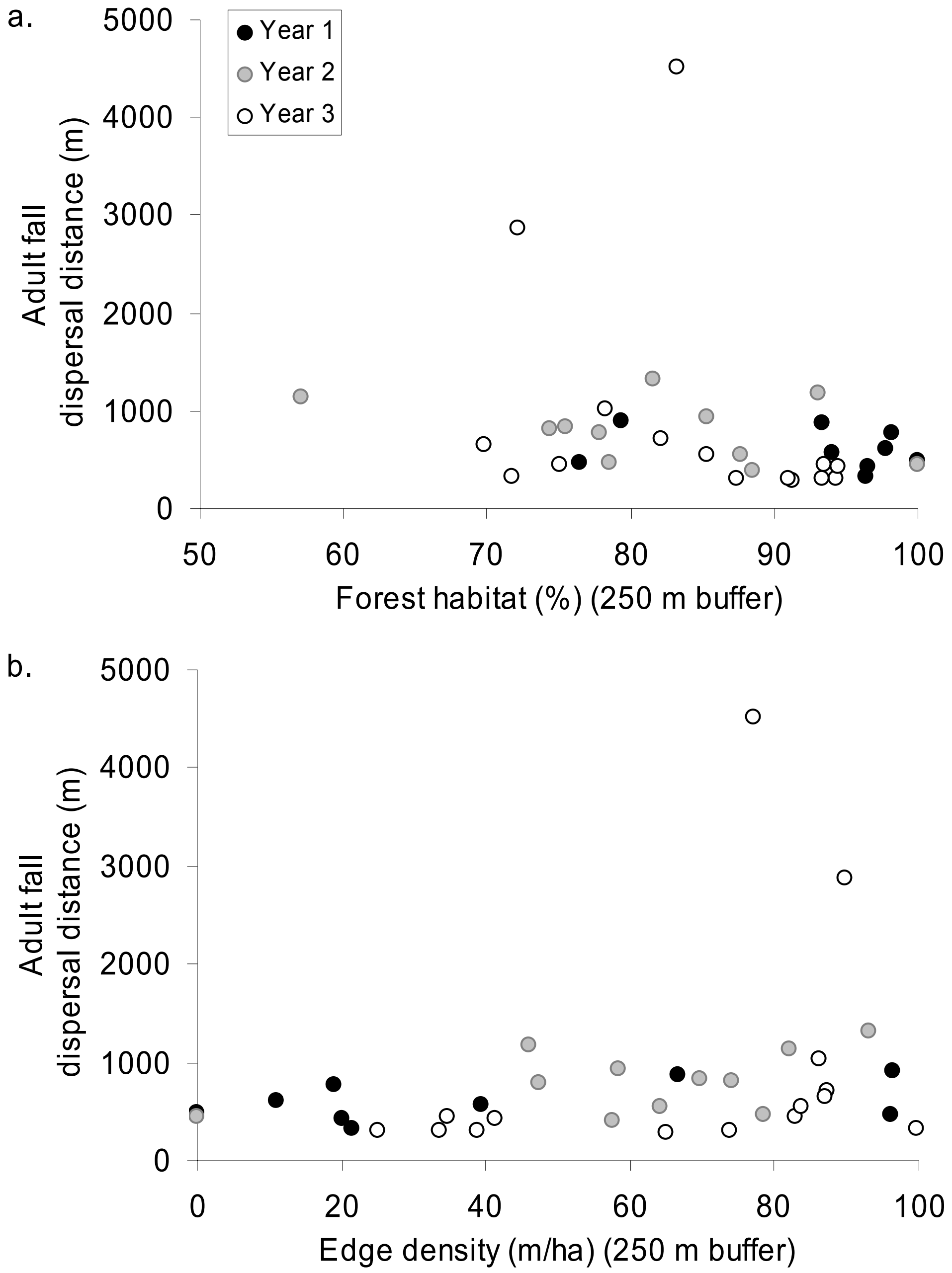

Figure 2.7. The relationship of (a) amount of forest habitat (%) and (b) edge density (m/ha) with fall adult dispersal distances in 250 m buffered landscapes. Study years are indicated by circle color (year 1 = black circles, year 2 = gray circles and year 3 = open circles).

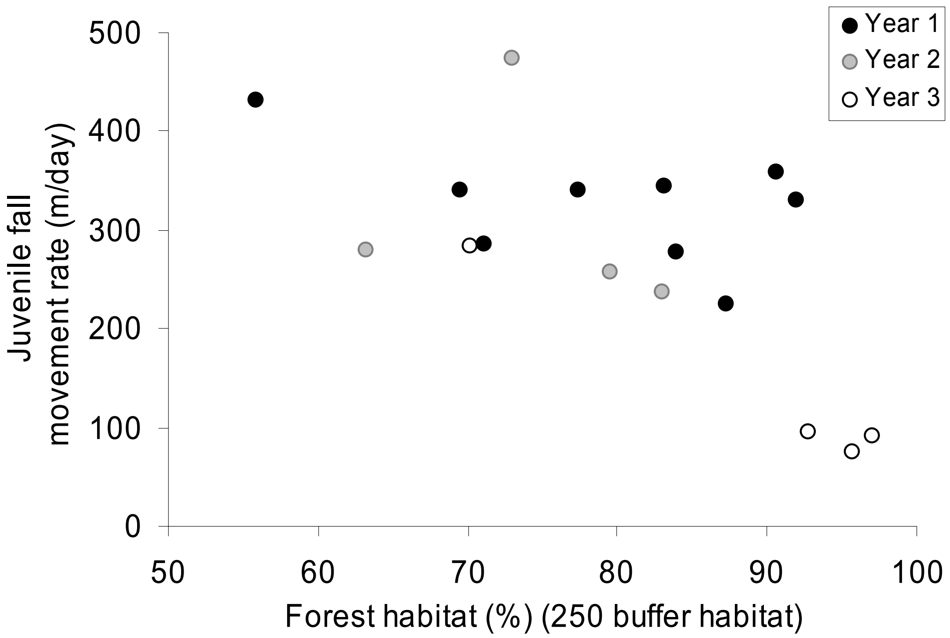

Figure 2.8. The relationship amount of forest habitat (%) with fall juvenile movement rates in 250 m buffered landscapes. Study years are indicated by circle color (year 1 = black circles, year 2 = gray circles and year 3 = open circles).

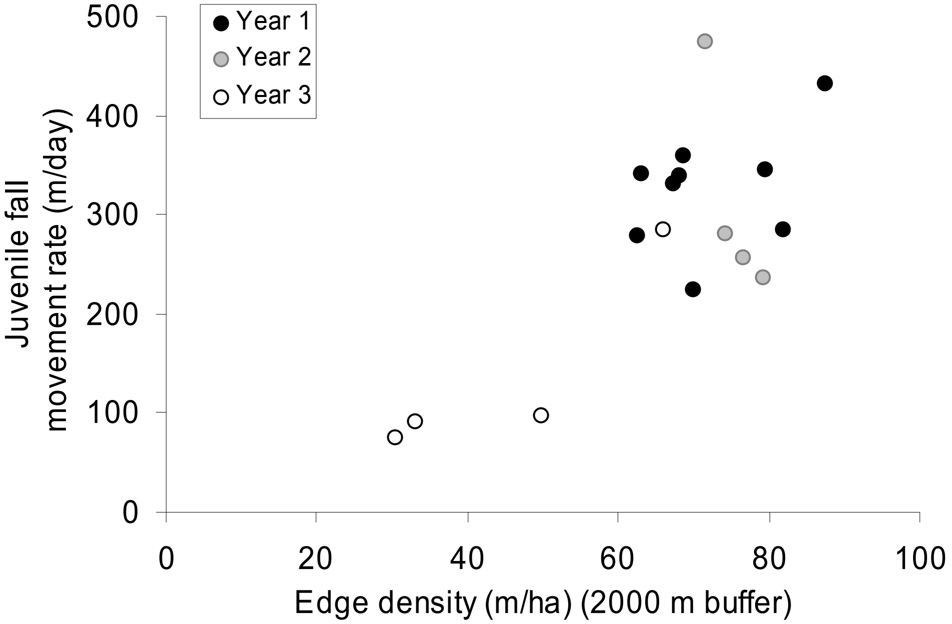

Figure 2.9. The relationship amount of edge density (m/ha) with fall juvenile movement rates in 2000 m buffered landscapes. Study years are indicated by circle color (year 1 = black circles, year 2 = gray circles and year 3 = open circles.)

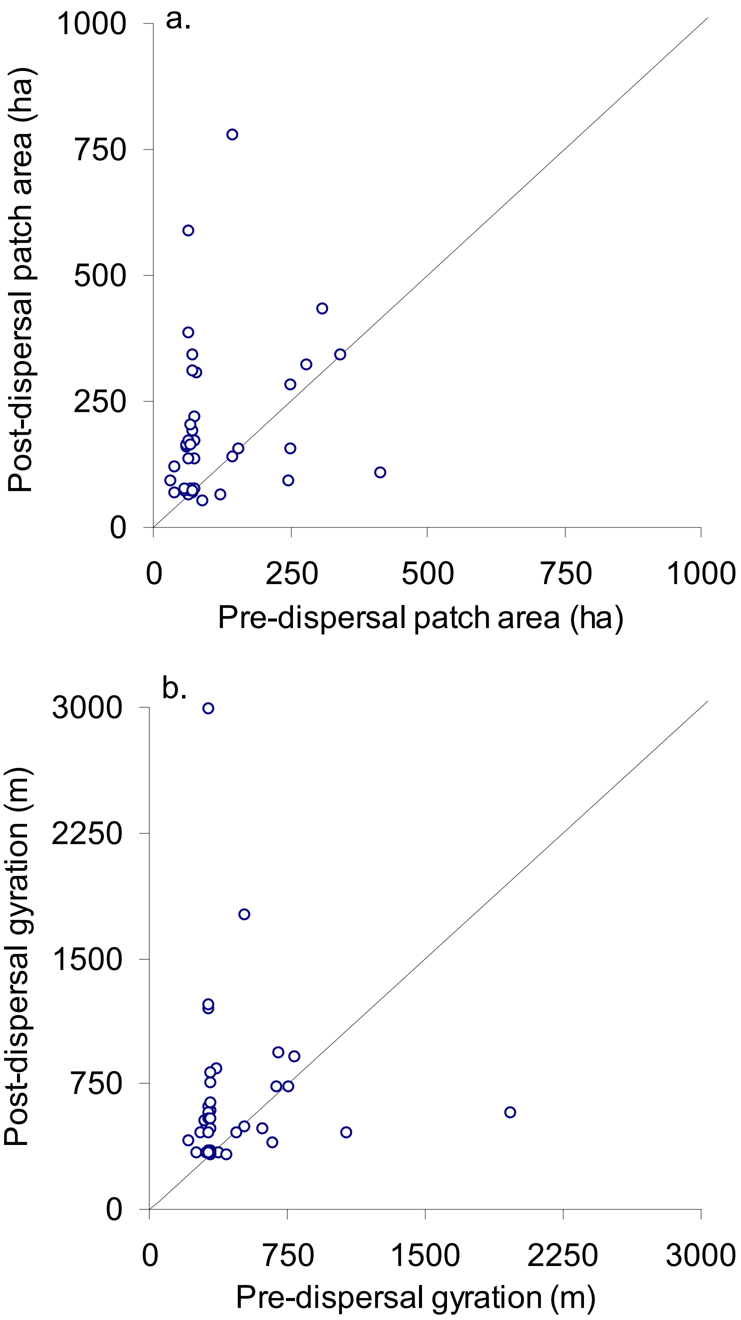

Figure 2.10. The relationship between a) mean patch area (ha) and b) radius of gyration (m) of fall juvenile pre-dispersal and post-dispersal 500 m buffered landscapes.

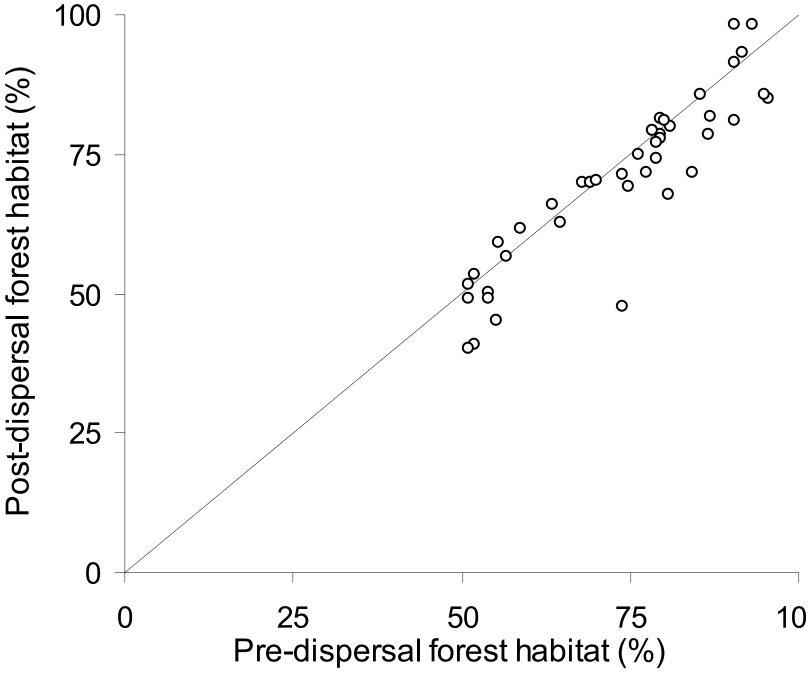

Figure 2.11. The relationship between amount of forest habitat within fall juvenile pre-dispersal and post-dispersal 3000 m buffered landscapes.

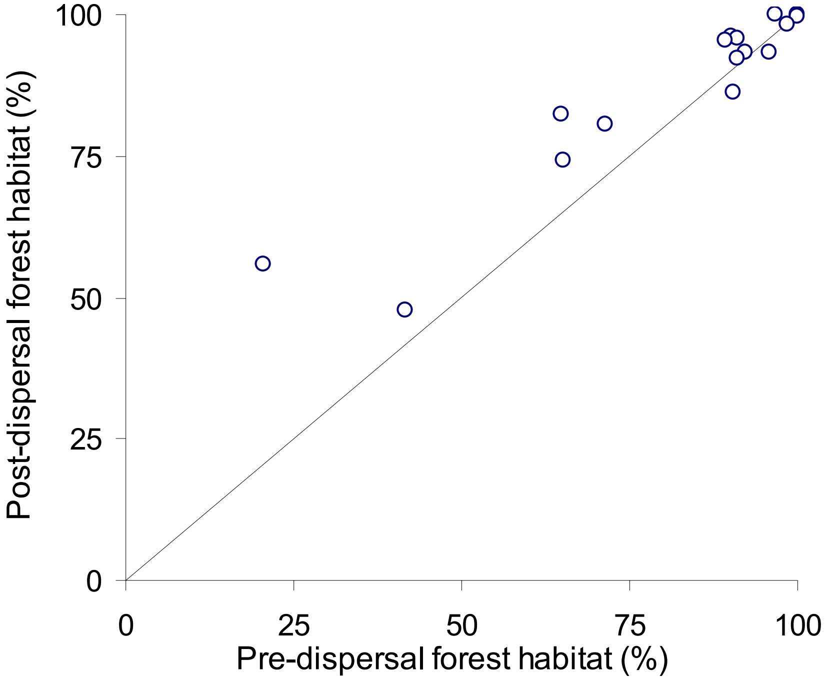

Figure 2.12. The relationship between amount of forest habitat within adult spring pre-dispersal and post-dispersal 500 m buffered landscapes.

CHAPTER 3

THE COST OF DISPERSAL: PREDATION AS A FUNCTION OF MOVEMENT AND SITE FAMILIARITY IN RUFFED GROUSE†

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ABSTRACT

Ecologists often assume that dispersing individuals experience increased predation risk due to increased exposure to predators while moving. To test the hypothesis that predation risk is a function of movement distance or rate of movement we used radio-telemetry data collected from 193 ruffed grouse (*Bonasa umbellus*) during 1996-99 in southeastern Ohio. Cox's proportional hazards model was used to examine whether the risk of predation was affected by the rate of movement and site familiarity. We found evidence indicating that increased movement rates may increase the risk of predation for adult birds but not juveniles. We also found juvenile and adult birds inhabiting unfamiliar space were consistently at a much higher risk of predation (3 – 7.5 times greater) than those in familiar space. Our results indicate that while movement itself may have some effect on the risk of being preyed upon, moving through unfamiliar

space has a much greater effect on risk for ruffed grouse. This supports the hypothesis that increased predation risk may be an important cost of dispersal for birds.

3.1 INTRODUCTION

Determining the costs of dispersal is crucial to understanding the evolutionary causes of dispersal (Johnson and Gaines 1990) and their demographic consequences (Bélichon et. al 1996). There has been widespread speculation by ecologists that dispersers experience higher mortality risk and lower reproductive success than philopatric individuals (e.g. Lidicker 1975, Gaines and McClenaghan 1980, Jones 1988, Anderson 1989). Dispersal-related mortality may be due to increased predation pressure, aggression, stress, energy depletion, or moving through or settling in unfamiliar areas (Greenwood and Harvey 1982, Van Vuren and Armitage 1994). Dispersers may also incur costs associated with investments in morphology necessary for successful dispersal (Dieckmann et al. 1999), such as trade-offs between flight capability and reproduction in many wing-polymorphic insect species (Langellotto et. al 2000).

Predation is often assumed to be the cause of differences in survival between dispersers and philopatric individuals (Gaines and McClenaghan 1980). Predation risk may be greater for dispersers than non-dispersers because of 1) greater activity rates, 2) lower familiarity with new habitats, or 3) use of lower quality habitat by dispersers. Movement of dispersing individuals may attract the attention of predators. The energetic demands of movement may also affect a disperser's ability to avoid or deter predators or may cause a disperser to forage at risky times. It is well established that an increase in the threat of predation can result in a decrease in prey activity such as daily foraging, or nest or den building (Lima and Dill 1990, Lima 1998). A common assumption across taxa is that increased activity itself can cause an increase in predation risk, although this is only rarely supported by direct evidence (*see* Gaines and McClenaghan 1980, Johnson and Gaines 1990 *for review*). Higher predation rates of more active individuals have been found in kangaroo rats (Daly et al. 1990), field and sibling voles (Norrdahl and Korpimaki 1998), wood frogs (Skelly 1994), and various fish and invertebrates (*see* Lima 1998 *for references*).

Individuals undergoing natal or breeding dispersal move through and inhabit unfamiliar space. They may have little knowledge of where to find food in the area (resulting in low energetic efficiency) or of where to find cover from predators (Clarke et al. 1993, Jacquot and Solomon 1997). Whereas the effects of high activity rate would be important only during the actual movement phase of dispersal (transience), the effects of unfamiliar space may be important both during transience and after settlement in a new territory. The effects of energy depletion from increased activity or from foraging inefficiency in an unfamiliar area may be important both during dispersal and after settlement.

Previous studies have attempted to compare survival rates of philopatric and dispersing individuals, both during transience and after settlement. A review of 10 studies of birds (2 studies) and mammals (8 studies) comparing disperser survival during transience to survival during the same period for philopatric individuals showed dispersers to have lower survival (Bélichon et al. 1996). However, these studies were biased towards the use of mark-recapture techniques, which may give misleading estimates of survival for long-range dispersers, (*see Discussion*). In a review of 19 studies comparing survival after settlement, there was no consistent difference in survival between dispersers and philopatric individuals (Bélichon et al. 1996). Studies comparing survival after settlement have limited ability to address the question of whether an increase in mortality due to predation is at least partially due to movement per se (i.e., activity itself making dispersers vulnerable to predators). Many of these studies compare survival rates of individuals born on a particular site with survival of those thought to have immigrated to that site and, thus, these studies fail to measure predation during the transient phase. Because comparisons are made after dispersal is completed, differences in survival between dispersers and non-dispersers can be due to the effects of unfamiliar space or energy depletion from the dispersal period, but will not be due to activity itself making dispersers vulnerable to predators.

Most previous survival analyses (telemetry or mark recapture) are also limited by the fact that each individual must be classified as being either a disperser or philopatric. Because there are almost as many different ways of defining a disperser as there are studies and species, comparisons between studies are difficult. Almost all methods include some arbitrary decisions about minimum distance moved when defining dispersal and these may bias the analysis. Bias is most likely to occur when classifying individuals that have died at the beginning of the transient phase. Because it is impossible to determine how far an individual would have moved if it had not been killed, some individuals are never classified as having dispersed but may have still been killed due to the effects of high activity rates.

Relating predation events to distance moved or rate of movement would provide direct estimates of the predation-related survival cost to dispersers and could be calculated during both transience and settlement phases. The use of such a quantitative measure would also avoid some of the methodological concerns in the analysis of survival estimates.

The objective of our study was to use measurements of radio-collared ruffed grouse (*Bonasa umbellus*) to test the hypothesis that predation risk increases with rate of movement. We also attempted to differentiate the effects of movement per se and residing in unfamiliar space on predation risk. We modeled mortality due to predation as a function of an individual's rate of movement prior to predation events and included in the models the effect of inhabiting familiar vs. unfamiliar space at the time of a predation event. We also separately modeled the effect of rate of movement and site familiarity on the mortality risk due exclusively to avian predators, mammalian predators, and hunting.

3.2 METHODS

3.2.1 STUDY SPECIES

The ruffed grouse is a nonmigratory, forest game bird. In general it undertakes significant dispersal movements during the fall (Bump et al. 1947, Small and Rusch 1991) and primarily between 15 September and 1 November in Ohio (Chapter 1). Approximately 75% of juvenile birds undertake some form of natal dispersal after brood break-up in mid-September. Some adult birds (approximately 45%) also undergo large-scale movements during this time as they move between spring/summer and winter ranges (Chapter 1). Daily movement distances can range from less than 100 m to over 2 km while net seasonal distances can range from a few hundred meters to over 14 km

(Chapter 1). The mean length of a dispersal, or transient, period for an individual bird is approximately 22 days (Chapter 1).

3.2.2 STUDY SITES

The study was conducted at two sites in southeastern and east central Ohio from 1996 to 1999. The sites were centered on Waterloo Wildlife Area in Athens County and Woodbury Wildlife Area in Coshocton County. Each study site included the state-owned wildlife area and surrounding private lands within 15 km. The sites were characterized by a mixture of early successional to 40+ year old oak-hickory forest and agricultural fields.

Each fall, from 1 August to 10 October, 35 – 50 birds were trapped at each site using modified lily-pad traps (Dorney and Mattison 1956). Radio transmitters (Advanced Telemetry Systems, Isanti, MN) were attached with a necklace harness (Amstrup 1980) of teflon-coated woven wire. Mean transmitter weight was 11 g. Only birds weighing >250 g were fitted with transmitters to ensure that the transmitter was ≤5% of the bird's body weight (Fuller 1987). Expected battery life of transmitters was 320-500 days. Transmitters were distributed as equally among all age-sex categories as possible (approximately 55% adult, 45% juveniles and 57% males, 43% females). In all, a total of 193 birds were tagged and tracked over the course of three years.

3.2.3 MOVEMENT DATA

Attempts were made to locate all tagged birds at least 3 - 4 times per week from August 1 through May 15 and at least bi-weekly during June and July. Individual locations were calculated using the maximum likelihood estimator method (Lenth 1981) with a minimum of three azimuths taken within a span of 10 minutes. Lenth's method generates a 95% error ellipse of the bird's location. Only locations with 95% error ellipses smaller than 2 ha were used in distance calculations (92% of all locations). To calculate average daily rate of movement, we used the total distance moved during a given time interval (calculated by summing distances between each successive pair of locations during the given interval) and dividing by the total number of days in that interval.

All transmitters were equipped with mortality-mode switches (i.e., when the transmitter remains stationary for 6-8 hours, the pulse rate doubles). This allowed for quick location and recovery of dead birds. After necropsy, all recovered birds were classified as killed by avian, mammalian, or unknown predators, or as dying by other causes (e.g., road kill) (Einarsen 1956, Dumke and Pils 1973). In addition, each bird was equipped with a reward leg band that facilitated the identification of birds harvested during the hunting season (10 Oct – 29 Feb). Over the three-year study, the fate of 13% of tagged birds was unknown, most likely due to transmitter failure. To avoid any effect of short-term stress due to capture and handling or from transmitters, birds that died within 7 days of capture were not included in the analyses.

3.2.4 DATA ANALYSIS

If the risk of predation increases with movement distance or rate of movement, then movement rate should have a significant effect on bird survival. Because predation risk and movement rates vary over time we wanted to assess the effect of the rate of movement *at the time of each predation event* on the predation risk for all birds in the study. To accomplish this we used a method of survival analysis based on the extended Cox's proportional hazards model (White and Garrott 1990, Kleinbaum 1996, Hougaard 2000). While this semiparameteric model has been used only rarely in ecological studies, it is popular in clinical studies in the health sciences. The model estimates the hazard (i.e., the effect on survival time) for an individual due to one or more explanatory covariates. A particularly powerful characteristic of this model is its ability to handle both time-independent and time-dependent individual covariates.

3.2.5 GENERAL MODEL DESCRIPTION

The basic hazard model used in our analyses is expressed as:

$$\mathrm{h(t)} = \mathrm{h_0(t)}\exp\left(\beta_1\mathrm{SEX} + \beta_2\mathrm{STUDYAREA} + \beta_3\mathrm{YEAR} + \delta_2\mathrm{SITE(t)} + \delta_1\mathrm{RATE(t)}\right) \tag{1}$$

where the hazard function (*h*) for an individual at time *t* is a function of the baseline hazard function (h_o) and the covariates SEX, STUDY AREA , YEAR (study year), RATE (the movement rate of each individual expressed in m/d at time *t*), and SITE (familiar or unfamiliar space at time *t*). Time *t* is measured as the time (in days) since the start of the trapping period (1 August) each year. The hazard function (h_o) is considered the starting (or "baseline") version of the hazard function in that the formula reduces to this function if no covariates are included in the model (or all covariates = 0). The regression coefficients $ß_{1\text{-}3}$ and $\delta_{1\text{-}2}$ measure the degree to which each covariate in the model affects mortality due to predation. In our model the covariates SEX, STUDY AREA, and YEAR are time-independent. Movement rate (RATE) and site familiarity (SITE) may change over time and because this is due to behavior specific to an individual, they are termed “internal” time–dependent covariates (Kleinbaum 1996). Though the value of the covariate RATE changes over time, there is only a single coefficient (δ_1) for the time-dependent covariate in the model. Thus, the effect of the time-dependent variable RATE on the hazard at time *t* is based only on one value of RATE, the value being measured at time *t*. In practice, this means that a new movement rate was calculated for each individual bird in the study at each time *t* of interest, in this case, the date of each predation event. Likewise, the status of SITE for each bird was also updated on the date of each predation event.

We performed the analysis using PROC PHREG in SAS (SAS 8.1). PROC PHREG estimates regression coefficients for the hazard function using a partial likelihood function that considers probabilities only for those subjects preyed upon during the course of the study. All birds who are alive and for which we have data for a given day in the model make up the “risk set” for each predation event.

PROC PHREG estimates a hazard ratio for each covariate. The hazard ratio describes the relative risk between values of an individual covariate. If the hazard ratio is larger than one than an increment increase in the variable causes an increase in the risk of predation. A hazard ratio less than one signifies a decrease in the risk of predation. For example, the hazard ratio for the SEX covariate in our model is a measure of the relative predation risk of males versus females. Because males were coded as one and females as two in our analysis, a hazard ratio greater than one would indicate females experience an overall higher predation risk than males. When evaluating the relative risks for internal, time-dependent variables a slightly different interpretation of the hazard ratio is necessary. The variable RATE in our model is not distinguishing the relative risk between two separate groups (e.g. males vs. females) but is estimating the relative risk only *at any given time t* for an individual moving at some rate *r* compared to an individual moving at a rate of *r* + 1 m/d (Kleinbaum 1996). The hazard ratio for the variable SITE estimates the relative risk at any given time *t* of inhabiting familiar versus unfamiliar space.

If a regression coefficient is significantly different from zero, then a hazard ratio can be used to estimate the effect of that variable on predation risk. PROC PHREG uses the Wald statistic, which has a X^2 distribution, to determine if estimated regression coefficients are significantly different from zero.

Because overall annual survival rates (*S*) estimated with likelihood models using program MARK were significantly different for hatch-year birds (juveniles) ($S = 0.273$, SE = 0.039) and after-hatch-year birds (adults) ($S = 0.469$, SE = 0.38) (Swanson, *unpublished data*), we performed separate analyses for juveniles and adults. There was no evidence for significant differences in overall seasonal survival rates, with mortality spread evenly throughout the year. The origin point for an individual's survival time was 1 August of each year and we assumed that adult annual mortality was independent of age.

Because it is not clear exactly which time period of movement might be most important in determining predation rate, we ran three different models for each age class, all of which included SEX, STUDY AREA, YEAR, SITE, and RATE but differing in the period of time over which movements were used to calculate the time-dependent variable RATE. Each time period ended with the same date (at a predation event *t*) but had different initial dates. The three initial dates used were an individual's capture and tagging date, the date 14 days prior to the predation event, and the date of the individual's penultimate location (if it was located within 3 days of the predation event.) Thus, our analysis of the effect of movement rates on predation risk included a set of three models for both juveniles and adults:

$$\mathrm{h_c(t) = h_{0,c}(t)\exp}\left(\beta_1\mathrm{SEX} + \beta_2\mathrm{STUDYAREA} + \beta_3\mathrm{YEAR} + \delta_2\mathrm{SITE(t)} + \delta_1\mathrm{RATE_{capture}(t)}\right) \quad (2)$$

$$\mathrm{h_{14}(t) = h_{0,14}(t)\exp}\left(\beta_1\mathrm{SEX} + \beta_2\mathrm{STUDYAREA} + \beta_3\mathrm{YEAR} + \delta_2\mathrm{SITE(t)} + \delta_1\mathrm{RATE_{14day}(t)}\right) \quad (3)$$

$$\mathrm{h_3(t) = h_{0,3}(t)\exp}\left(\beta_1\mathrm{SEX} + \beta_2\mathrm{STUDYAREA} + \beta_3\mathrm{YEAR} + \delta_2\mathrm{SITE(t)} + \delta_1\mathrm{RATE_{3day}(t)}\right) \quad (4)$$

where $\mathrm{RATE_{capture}}$ is the movement rate calculated over the period *(t* - capture date) to *t*, $\mathrm{RATE_{14day}}$ is the movement rate calculated over the period (*t* – 14) to *t* and $\mathrm{RATE_{3day}}$ is the movement rate calculated over the period (*t* – 3) to *t.*

In order to investigate the effect of site familiarity on predation risk we included the time-dependent binomial variable SITE that varied according to the familiarity of the area inhabited by an individual at the time of a predation event. At any given predation event (*t*) an individual was classified as inhabiting familiar space if it was previously located within 500 m of that location during any point in its life prior to 14 days before *t*. Conversely, an individual was in unfamiliar space if it had never been located within 500 m of its current locations prior to the last two weeks. This definition of familiar space is somewhat arbitrary; however, a distance of 500 m is based on a mean home range size for grouse in our study (during non-dispersing periods) of 46 ha (Chapter 1) which corresponds to a circular area with a radius of 380 m. Therefore, we believe if an individual bird is found to be greater than 500 m from any previous location, it is highly likely that it is currently in an unfamiliar area. Likewise, any location within 500 m of any previous location may indicate the individual is still within a familiar home range or is returning to a previously occupied home range. While choice of a 14-day acclimation period is subjective, we believe an individual remaining in an area after a 14-day period has gained familiarity with the area. To ensure a valid determination of site familiarity status, we used only those birds for which we had at least 3 locations prior to 14 days before the time of the predation event.

The movements of two individuals that illustrate basic movement patterns found in the study are shown in Figure 3.1. Individuals may spend an entire year within a single home range, never moving into unfamiliar space (Figure 3.1A). Individuals also may exhibit one or more distinct shifts in range throughout a year with movements through unfamiliar space occurring during these shifts (Figure 3.1B).

To investigate differences in the effect of movement rate and site familiarity on the risk of being preyed upon by different types of predators, we repeated the above analyses with mortality due to predation from mammalian and avian predators separately. Finally, to investigate the effect of movement rate and site familiarity on the risk of being harvested, we repeated the above analyses with mortality due only to hunting.

3.3 RESULTS

During the 3-year study we obtained usable locations on a total of 193 birds (108 adults and 85 juveniles). The number of usable predation events occurring during this time was 44 for juveniles and 33 for adults. We were able to determine that 24 juvenile and 22 adult mortalities were due to avian predators and 13 juvenile and 8 adult mortalities were due to mammalian predators. Because we were unable to calculate a SITE status we did not include 6 juveniles and 8 adults that were preyed upon. Hunters harvested a total of 3 juveniles and 5 adults during the study.

Among juveniles, SITE had a consistently strong effect on the risk of being killed by a predator, with risk being 3 to 4.5 times greater in unfamiliar than familiar space (Table1; Figure 2). The effects of RATE, YEAR, SEX, and STUDY AREA were less obvious, either less consistent between models or having *p* values between 0.05 and 0.10. Although RATE never had a significant effect (at a significance level of $\alpha = 0.05$) on the hazard function, $\text{RATE}_{14\text{day}}$ and $\text{RATE}_{3\text{day}}$ had $p < 0.10$ and parameter estimates indicating an increase in mortality risk with decreasing movement rates (Table 1; Figure 2). One of the models indicated a significant difference in predation risk between sites (Table 1; Figure 2C). To illustrate model predictions (Figure 2), we used the rate parameter and all parameters with $p < 0.10$, using the mean predictions for males and females, years, and sites, to calculate the hazard function divided by the baseline hazard (h/h_o). Since the baseline function equals the hazard function when all covariates equal 0 (or are left out of the model), h/h_o is a measure of the overall effect of the covariates on the hazard function.

For adults as for juveniles, SITE had a consistently strong effect on mortality due to predation, with risk in unfamiliar space being 4 to 7.5 times greater than in familiar space (Table 2; Figure 3). Again, SEX, STUDY AREA, YEAR, and RATE were not as strong or consistent in their effects. $\text{RATE}_{3\text{day}}$ had a significant effect and $\text{RATE}_{\text{capture}}$

had $p = 0.07$, both showing increasing mortality risk with increasing movement rate (Table 2, Figure 3). Two of the models indicated a significant difference in predation risk between years (Table 2; Figure 3A-B). One of the models indicated a significant difference in predation risk between sites (Table 2; Figure 3C). Again, to illustrate model predictions (Figure 3), we used the rate parameter and all parameters with $p < 0.10$, using the mean predictions for males and females, years, and sites.

Because we suspected that movement rate might be correlated with moving through unfamiliar space we compared the proportion of birds inhabiting familiar and unfamiliar sites in relation to movement rate. We found that while birds inhabiting unfamiliar space tended to move at greater rates than those in familiar space, there was also great overlap in the distributions of movement rates between birds inhabiting the two site types (Figure 4).

Models including predation events due either only to mammalian or only to avian predators yielded similar results as those including all predation events. Among juveniles, SITE again had the strongest effect and was significant among all avian predation models and had either significant effects or p values <0.10 for all mammalian predation models. Among adults, the effect of SITE was significant in all avian and mammalian models and $\text{RATE}_{3\text{day}}$ was significant and positive in the model including only avian predation. None of the model covariates had a significant or near significant effect on the mortality risk due to hunting for either adults or juveniles.

3.4 DISCUSSION

Overall, we found inhabiting unfamiliar space to be the only consistently significant factor increasing the risk of being preyed upon for ruffed grouse. The effect of movement rate on predation risk varied greatly in strength between models within an age category and in direction between adults and juveniles. Two of the models for adult birds indicate that increased movement rates may also increase the risk of predation. Although not significant, the effect of increasing movement rates among juveniles was opposite that of adults, with increasing movement rates resulting in a decrease in the risk of predation.

A common assumption in behavioral ecology is that activity increases predation risk due to movement attracting the attention of predators, thereby increasing the likelihood of predatory encounters (Gotmark and Post 1996, Lima 1998). In addition to increasing the risk of predation, movement may have additional consequences during breeding or natal dispersal periods when both distance moved and rate of movement are often greater than during non-dispersal periods; dispersing individuals are more likely to suffer costs of high energetic demands (Lima 1986, McNamara and Houston 1990, Witter and Cuthill 1993) and spend time in unfamiliar space (Greenwood and Harvey 1982) than non-dispersing individuals.

Any effect of increased movement rate on predation risk seen in our results may theoretically be a result of movement *per se* (attraction of predators), inhabiting unfamiliar space, or a combination of both. However, because the model included both the effect of site familiarity and movement rate, our results clearly indicate that unfamiliar space increases the risk of predation independent of any effect of movement rate. In addition, while we found that birds inhabiting unfamiliar space tended to move at greater rates than those in familiar space, the overlap in the distribution of movement rates between the two habitat types (Figure 4) also indicates an independent effect of site familiarity on predation risk. A substantial number of birds moving through unfamiliar space moved at rates comparable to those in familiar space. This provides additional evidence that inhabiting unfamiliar space is dangerous and increases the risk of predation.

Individuals moving through unfamiliar space may suffer from decreased foraging efficiency (which also may affect energetic condition) or a decreased ability to avoid predators (Metzgar 1967, Ambrose 1972). A defense mechanism employed by ruffed grouse is concealment in dense brush and undergrowth. Being in unfamiliar space may compromise this defense mechanism. Grouse moving through unfamiliar space may be more vulnerable to predation during foraging. Lack of experience in a new area may lead to difficulty locating food sources that also provide good cover (e.g., wild grape vines in Ohio). Although we based the analysis on distinguishing between familiar and unfamiliar space, we cannot rule out the possibility that new territory is not only less familiar, but also of lower quality (i.e. with less available cover or food sources) than an individual's original home range.

While individuals are more likely to inhabit unfamiliar space during the fall dispersal period than at other times of the year, it is unlikely that energy depletion accounts for increased predation risk in this species. Fall is a season of abundant food supply (e.g., mast crops) and a time of significant weight gain for Ohio ruffed grouse (Stoll and McCLain 1988). We believe the cost of unfamiliarity for this species is more likely due to reduced ability to locate adequate cover or a willingness to inhabit more "dangerous" areas (either with higher predator densities or less available cover) than from a decrease in energetic condition. High predation risk in unfamiliar space may also account for exploratory behavior exhibited by a substantial proportion of both adults and juveniles in our study. During the fall and spring dispersal periods these individuals move into unfamiliar space but then return to their pre-dispersal home ranges (Yoder, *unpublished data*).

An increase in predation risk is often assumed to be the cause of differences in survival between dispersers and philopatric individuals (Gaines and McClenaghan 1980). Unlike most survival studies comparing dispersers and non-dispersers, data from four studies of gallinaceous birds do not indicate a greater mortality risk for dispersing individuals than for philopatric individuals (Hines 1986, Schieck and Hannon 1989, Beaudette and Keppie 1992) including one study examining survival during transience in ruffed grouse (Small et al. 1993). In their telemetry study over a 6-year period in Wisconsin, Small et al. (1993) found no significant differences in survival rates for juvenile ruffed grouse during transient vs. colonization (settlement) periods from autumn through spring.

Any effect of increased activity by dispersers would affect predation risk only during the actual transient phase of dispersal. The effects of inhabiting unfamiliar space could affect the predation risk of dispersers both during transience and settlement in a new territory. Small et al. (1993) may have failed to find differences in predation rates between transient and settlement periods because individuals were experiencing effects of unfamiliar space during both phases of dispersal. Because our results indicate the effect of inhabiting unfamiliar space is causing the greatest increase in predation risk, we suspect that most dispersers experience an increase in predation risk during both transience and early settlement periods. Those dispersers with relatively short transient phases and specific foraging or habitat requirements may actually experience the highest predation risk immediately after dispersal has taken place (while settling in a new and unfamiliar territory).

Previous studies attempting to directly measure predation risk in relation to activity cover a wide range of taxa (Daly et al. 1990, Skelly 1994, Lima 1998 and Norrdahl and Korpimaki 1998), but not birds. Two studies of small mammals also used radio telemetry to measure movement rates. Daly et al. (1990) found a positive relationship between the rate of movement and predation in a population of kangaroo rats (Dipodomys merriami). Norrdahl and Korpimaki (1998) found a similar relationship in field voles (Microtus agrestis) and sibling voles (M. rossiaemeridionalis). Both of these studies measured only short term (i.e. hourly or nightly) movement rates. They also did not attempt to distinguish effects of moving through from settling in unfamiliar territory.

Other studies attempting to compare survival rates during the transient portion of dispersal are not only biased towards mammalian species but also rely heavily on mark-recapture techniques (see Bélichon et al. 1996 for review). These techniques tend to underestimate dispersal distances by failing to detect long-range dispersers and are limited in their ability to accurately determine the fate of all individuals (Koenig et al. 1996). The combination of the limited size of most study sites and the inability to distinguish mortality from dispersal beyond trapping range may bias estimates of the survival of dispersing vs. philopatric individuals (Daly et al.1990). The use of radio telemetry can reduce the problem of disappearing individuals by allowing researchers to determine the fate of a much higher proportion of tagged individuals.

Because there exists no expected or control value for what the survival or predation risk would have been for a dispersing individual had they not dispersed, the true cost of dispersal is impossible to measure (Wolff 1994). But by comparing a quantifiable measure of activity, and controlling for covariates such as site familiarity between preyed-upon and surviving birds at the time of each predation event, it is possible to provide evidence that dispersers may experience one such cost, an increase in predation risk. This study highlights another tool to measure possible dispersal costs in addition to traditional comparisons between survival rates of dispersers and philopatric individuals. Our methods should be applicable to most radio-telemetry studies or any study in which individual fates are known and reasonably accurate estimates of movement distances can be made. Direct evidence in other avian species (as well as in other taxa) is sorely needed to support what many ecologists have long suspected; dispersal can be costly.

3.5 TABLES

Parameter	Parameter Estimate	Wald X^2	p	Hazard Ratio
SEX	-0.51	2.71	0.0999	0.60
SITE	0.66	3.70	0.0547	1.93
YEAR	-	0.89	0.3432	-
$\text{RATE}_{\text{capture}}$	1.8E^{-4}	0.03	0.8692	1.00
HABITAT	**1.08**	**7.05**	**0.0079**	**2.94**
SEX	-0.53	2.60	0.0964	0.59
SITE	-	0.78	0.3771	-
YEAR	-0.36	3.53	0.0601	0.70
$\text{RATE}_{\text{14day}}$	-0.003	2.82	0.0926	1.00
HABITAT	**1.51**	**11.97**	**0.0005**	**4.56**
SEX	-	1.80	0.1797	-
SITE	**1.43**	**14.53**	**0.0001**	**4.16**
YEAR	-	0.19	0.6597	-
$\text{RATE}_{\text{3day}}$	-0.003	2.79	0.0946	0.99
HABITAT	**1.27**	**6.83**	**0.0089**	**3.57**

Table 3.1. The risk of predation mortality for juvenile grouse modeled as a function of sex, study area, year, site (familiar or unfamiliar), and three estimates of movement rate. The Wald chi-square statistic is used to determine if the parameter estimate is significantly different from zero. If the Hazard Ratio is larger than one than an increment increase in the variable causes an increase in the risk of predation. Individual variables are defined in the text. There were a total of 85 juveniles tracked with 44 predation events occurring during the study.

Parameter	Parameter Estimate	Wald X^2	*P*	Hazard Ratio
SEX	-	0.003	0.9602	-
SITE	-	0.001	0.9802	-
YEAR	**-0.65**	**7.40**	**0.0065**	**0.52**
RATE$_{\mathrm{capture}}$	0.005	3.26	0.0712	1.01
HABITAT	**1.77**	**9.68**	**0.0069**	**4.08**
SEX	-	0.04	0.8412	-
SITE	-	0.58	0.4465	-
YEAR	**-0.77**	**11.03**	**0.0009**	**0.46**
RATE$_{\mathrm{14day}}$	$6.5E^{-5}$	0.01	0.9439	1.00
HABITAT	**2.02**	**13.77**	**0.0002**	**7.54**
SEX	-0.76	2.72	0.0988	0.47
SITE	**1.99**	**13.65**	**0.0002**	**7.40**
YEAR	-0.44	2.74	0.0974	0.64
RATE$_{\mathrm{3day}}$	**0.01**	**4.28**	**0.0385**	**1.01**
HABITAT	**1.54**	**4.01**	**0.0452**	**4.68**

Table 3.2. The risk of predation mortality for adult grouse modeled as a function of sex, study area, year, site (familiar or unfamiliar), and three estimates of movement rate. The Wald chi-square statistic is used to determine if the parameter estimate is significantly different from zero. If the Hazard Ratio is larger than one than an increment increase in the variable causes an increase in the risk of predation. Individual variables are defined in the text. There were a total of 108 adults tracked with 33 predation events occurring during the study.

3.6 FIGURES

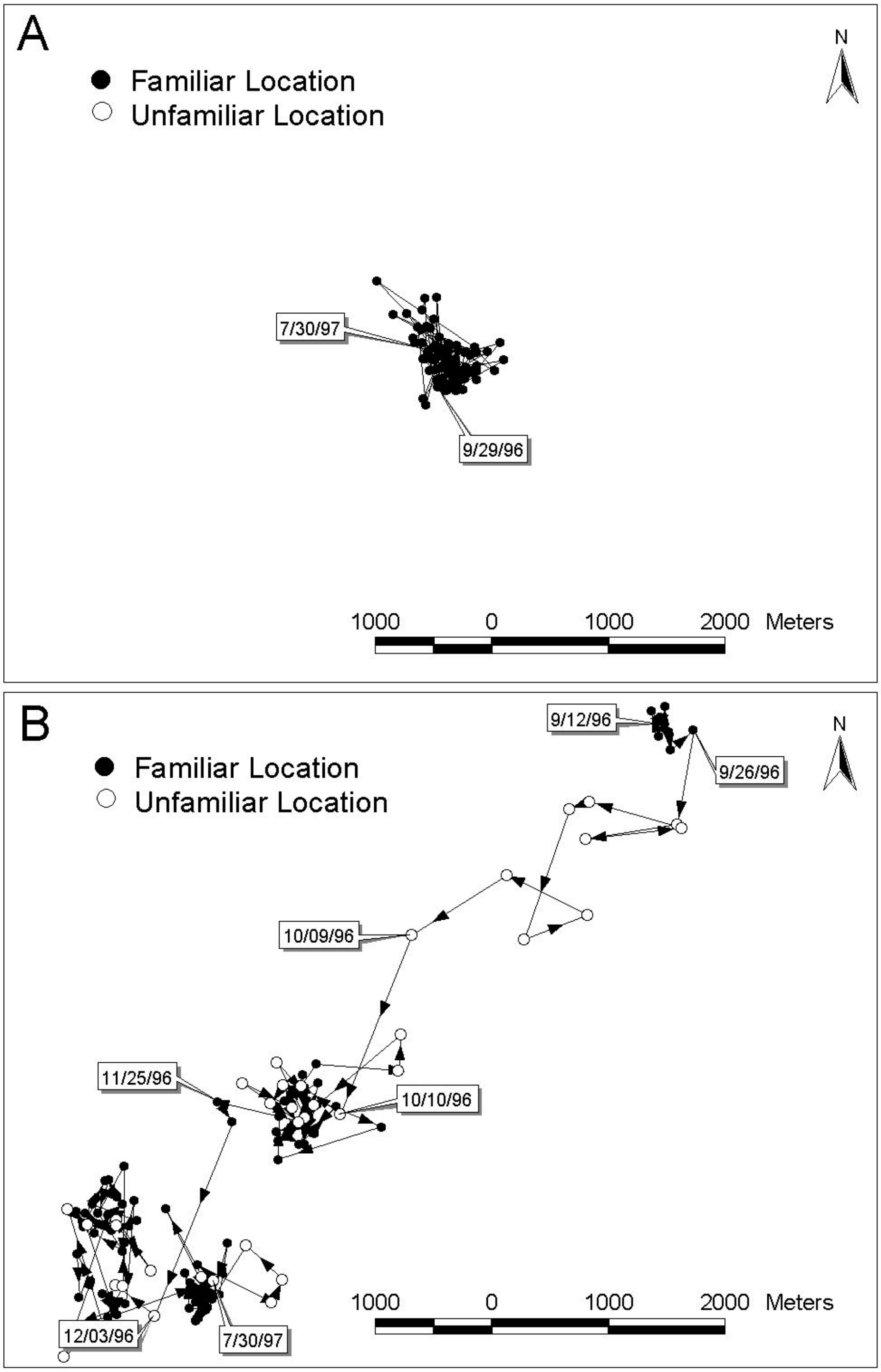

Figure 3.1. Locations and movement paths for two individual grouse during the study year 1996-97 that exemplify different movement scenarios. The bird in (A) survived the entire year and exhibited no movement into unfamiliar space. The bird in (B) also survived the year but exhibited at least 3 distinct shifts into unfamiliar space throughout the year.

Figure 3.2. The juvenile hazard function divided by the baseline hazard (h/h_o) as a function of (A) $\mathrm{RATE}_{\mathrm{capture}}$ in familiar and unfamiliar space, (B) $\mathrm{RATE}_{14\mathrm{day}}$ in familiar and unfamiliar space and (C) $\mathrm{RATE}_{3\mathrm{day}}$ in familiar and unfamiliar space in each study area. The effect of SITE was significant in (A – C) and the STUDY AREA effect was significant in (C). The hazard function divided by the baseline hazard function (h/h_o) is the portion of the overall hazard function ($h(t)$ as specified in Eq. 1 in the text) due to the effects of the model covariates

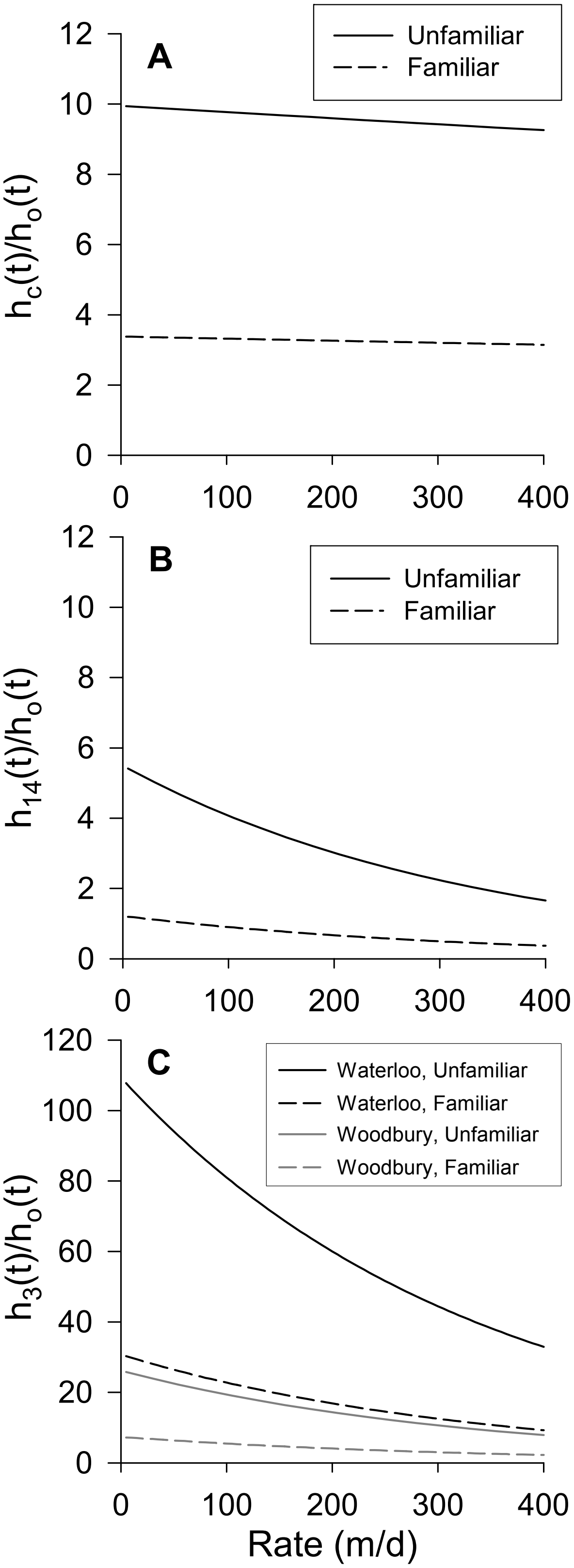
A
Unfamiliar
Familiar
$h_c(t)/h_o(t)$
0
2
4
6
8
10
12
0
100
200
300
400
B
Unfamiliar
Familiar
$h_{14}(t)/h_o(t)$
0
2
4
6
8
10
12
0
100
200
300
400
C
Waterloo, Unfamiliar
Waterloo, Familiar
Woodbury, Unfamiliar
Woodbury, Familiar
$h_3(t)/h_o(t)$
0
20
40
60
80
100
120
0
100
200
300
400
Rate (m/d)

Figure 3.2

Figure 3.3. The adult hazard function divided by the baseline hazard (h/h_o) as a function of (A) $\text{RATE}_{\text{capture}}$ in familiar and unfamiliar space in each year, (B) $\text{RATE}_{14\text{day}}$ in familiar and unfamiliar space in each year and (C) $\text{RATE}_{3\text{day}}$ in familiar and unfamiliar space in each study area. Significant covariate effects were SITE in (A-C), YEAR in (A-B), STUDY AREA in (C), and $\text{RATE}_{3\text{day}}$ in (C). The hazard function divided by the baseline hazard function (h/h_o) is the portion of the overall hazard function ($h(t)$ as specified in Eq. 1 in the text) due to the effects of the model covariates.

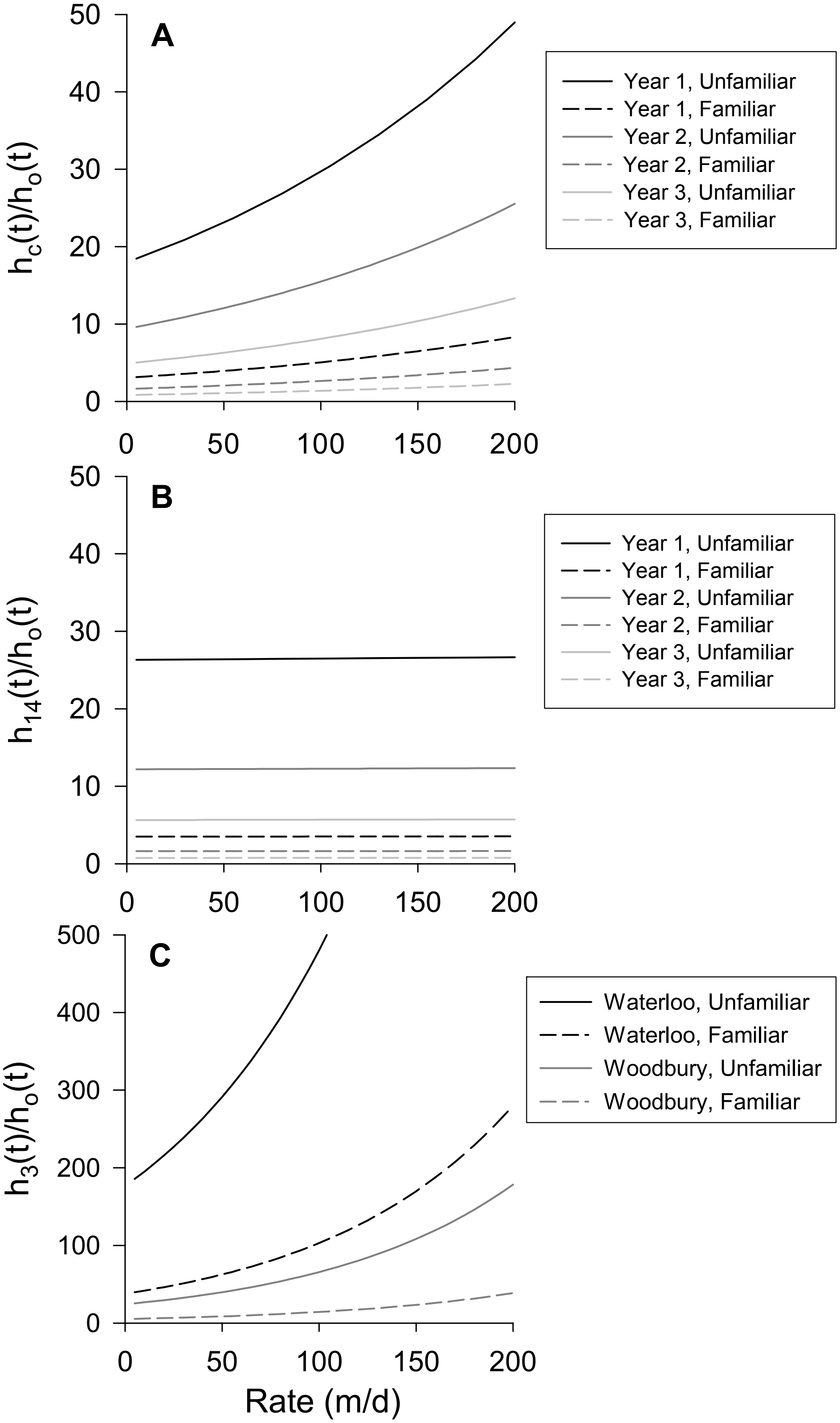
A
$h_c(t)/h_o(t)$
0
10
20
30
40
50
0
50
100
150
200
Year 1, Unfamiliar
Year 1, Familiar
Year 2, Unfamiliar
Year 2, Familiar
Year 3, Unfamiliar
Year 3, Familiar
B
$h_{14}(t)/h_o(t)$
0
10
20
30
40
50
0
50
100
150
200
Year 1, Unfamiliar
Year 1, Familiar
Year 2, Unfamiliar
Year 2, Familiar
Year 3, Unfamiliar
Year 3, Familiar
C
$h_3(t)/h_o(t)$
0
100
200
300
400
500
0
50
100
150
200
Rate (m/d)
Waterloo, Unfamiliar
Waterloo, Familiar
Woodbury, Unfamiliar
Woodbury, Familiar

Figure 3.3

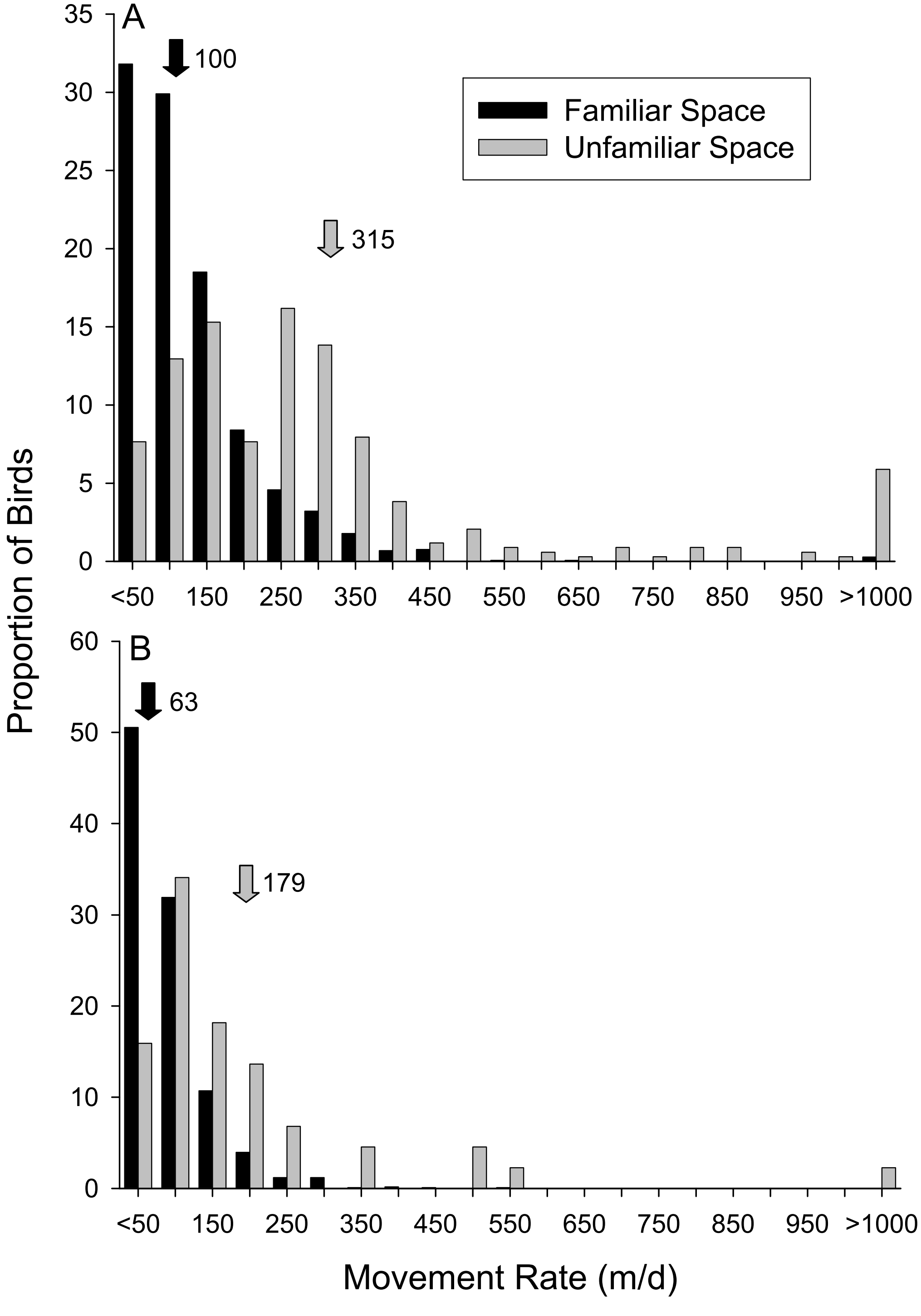

Figure 3.4. The proportion of (A) juvenile birds and (B) adult birds inhabiting familiar space (dark bars) and unfamiliar space (light bars) in relation to movement rate (m/day) calculated over the time period *t* to (*t* – 14 days). Arrows indicate mean movement rates for birds inhabiting familiar and unfamiliar space.

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APPENDIX A

COMPLETE RANKED LOGISTIC AND LINEAR REGRESSION MODELS USED IN AIC ANALYSES OF DISPERSAL DECISION, DISPERSAL DISTANCE, MOVEMENT RATE, AND HOME RANGE SIZE

buffer size (m)	Model	K	AIC_c	ΔAIC_c	w_i
500	PLAND, ED, SEX	5	35.6	0.0	0.212
	PLAND, ED	4	37.2	1.6	0.096
	PLAND, ED, GYRATE, SEX	6	37.3	1.7	0.091
	SEX	3	37.4	1.8	0.088
	PLAND, ED, GYRATE	5	37.9	2.3	0.066
	PLAND, ED, AREA, SEX	6	38.0	2.4	0.066
	PLAND, ED, AREA, GYRATE	6	38.2	2.6	0.059
	PLAND, GYRATE, SEX	5	38.5	2.9	0.050
	ED, SEX	4	38.7	3.1	0.046
	PLAND, ED, AREA, GYRATE, SEX	7	38.7	3.1	0.046
	PLAND, SEX	4	38.8	3.2	0.042
	PLAND, ED, AREA	5	39.1	3.5	0.036
	(null)	2	40.4	4.8	0.019
	PLAND, AREA, GYRATE, SEX	6	40.5	4.9	0.018
	PLAND, GYRATE	4	40.6	5.0	0.017
	PLAND, AREA, SEX	5	41.0	5.4	0.014
	PLAND	3	41.4	5.8	0.012
	ED	3	41.6	6.0	0.011
	PLAND, AREA, GYRATE	5	42.5	6.9	0.007
	PLAND, AREA	4	43.6	8.0	0.004
3000	PLAND, ED, AREA, GYRATE, SEX	7	30.8	0.0	0.270
	PLAND, ED, SEX	5	31.6	0.8	0.180
	ED, SEX	4	32.1	1.3	0.140
	PLAND, ED, AREA, SEX	6	33.1	2.3	0.087
	ED	3	33.3	2.5	0.076
	PLAND, ED	4	33.6	2.8	0.068
	PLAND, ED, GYRATE, SEX	6	34.1	3.3	0.051
	PLAND, ED, AREA	5	35.2	4.4	0.030
	PLAND, ED, AREA, GYRATE	6	35.4	4.6	0.027
	PLAND, ED, GYRATE	5	36.0	5.2	0.020
	PLAND, AREA, GYRATE, SEX	6	36.3	5.5	0.017
	SEX	3	37.4	6.6	0.010
	PLAND, SEX	4	38.6	7.8	0.006
	PLAND,GYRATE,SEX	5	38.6	7.8	0.006
	PLAND, AREA, GYRATE	5	40.1	9.3	0.003
	PLAND, GYRATE	4	40.2	9.4	0.002
	(null)	2	40.4	9.6	0.002
	PLAND, AREA, SEX	5	40.5	9.7	0.002
	PLAND	3	40.8	10.0	0.002
	PLAND, AREA	4	42.3	11.5	0.001

Table A1. Ranked logistic regression models explaining fall dispersal decisions for juvenile birds (n = 48) in landscapes buffered at 500 and 3000 meters. K is the total number of parameters (intercept, variance and individual independent variables). AIC_c values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC_c is the difference in AIC_c values from the lowest AIC_c value. AIC model weight (w_i) is the probability that model *i* is the best model in the set. The null model includes the intercept and variance but no additional variables.

buffer size (m)	Model	K	$QAIC_c$	$\Delta QAIC_c$	w_i
500	PLAND, ED, GYRATE	6	74.1	0.0	0.287
	PLAND, ED, GYRATE, SEX	7	74.9	0.8	0.190
	PLAND, ED, AREA	6	76.1	2.0	0.107
	ED	4	76.6	2.5	0.084
	PLAND, ED, AREA, GYRATE	7	76.6	2.5	0.081
	PLAND, ED, AREA, SEX	7	77.2	3.1	0.061
	ED, SEX	5	77.3	3.2	0.057
	PLAND, ED, AREA, GYRATE, SEX	8	77.6	3.5	0.051
	PLAND, ED	5	78.6	4.5	0.030
	PLAND, ED, SEX	6	79.3	5.2	0.022
	PLAND, AREA	5	81.3	7.2	0.008
	PLAND, GYRATE	5	82.8	8.7	0.004
	PLAND, AREA, SEX	6	82.9	8.8	0.004
	PLAND, SEX	5	83.1	9.0	0.003
	(null)	3	83.7	9.6	0.002
	PLAND, AREA, GYRATE	6	83.7	9.6	0.002
	PLAND, GYRATE, SEX	6	84.1	10.0	0.002
	SEX	4	84.4	10.3	0.002
	PLAND, AREA, GYRATE, SEX	7	85.4	11.3	0.001
	PLAND	4	85.8	11.7	0.001
3000	(null)	3	85.1	0.0	0.230
	SEX	4	85.1	0.0	0.227
	ED	4	86.5	1.4	0.112
	ED, SEX	5	87.2	2.1	0.079
	PLAND	4	87.3	2.1	0.078
	PLAND, SEX	5	88.0	2.9	0.053
	PLAND, ED	5	88.8	3.6	0.037
	PLAND, GYRATE	5	89.5	4.4	0.026
	PLAND, ED, SEX	6	89.5	4.4	0.025
	PLAND, AREA	5	89.5	4.4	0.025
	PLAND, ED, GYRATE	6	90.1	5.0	0.019
	PLAND, GYRATE, SEX	6	90.4	5.3	0.016
	PLAND, AREA, SEX	6	90.4	5.3	0.016
	PLAND, ED, AREA	6	90.8	5.7	0.013
	PLAND, ED, GYRATE, SEX	7	91.2	6.0	0.011
	PLAND, ED, AREA, SEX	7	91.7	6.6	0.008
	PLAND, ED, AREA, GYRATE	7	91.8	6.7	0.008
	PLAND, AREA, GYRATE	6	91.9	6.8	0.008
	PLAND, AREA, GYRATE, SEX	7	92.9	7.8	0.005
	PLAND, ED, AREA, GYRATE, SEX	8	92.9	7.8	0.005

Table A2. Ranked logistic regression models explaining fall dispersal decisions for adult birds (n = 63) in landscapes buffered at 500 and 3000 meters. K is the number of parameters. $QAIC_c$ values are Akaike Information Criteria values corrected for small sample sizes and overdispersion of the data. $\Delta QAIC_c$ is the difference in $QAIC_c$ values from the lowest $QAIC_c$ value. AIC model weight (w_i) is the probability that model *i* is the best model in the set. The null model includes no parameters.

buffer size (m)	Model	K	AIC_c	ΔAIC_c	w_i
500	ED	3	100.1	0.0	0.357
	ED, AGE	4	102.0	1.9	0.138
	PLAND, ED	4	102.4	2.3	0.114
	(null)	2	103.2	3.1	0.074
	PLAND, ED, AGE	5	104.1	4.0	0.048
	PLAND	3	104.4	4.3	0.041
	PLAND, ED, GYRATE	5	104.7	4.6	0.037
	PLAND, ED, AREA	5	104.7	4.6	0.036
	AGE	3	104.8	4.7	0.034
	PLAND, AGE	4	106.1	6.0	0.018
	PLAND, GYRATE	4	106.1	6.0	0.018
	PLAND, ED, AREA, AGE	6	106.5	6.4	0.015
	PLAND, ED, GYRATE, AGE	6	106.5	6.4	0.015
	PLAND, AREA	4	106.7	6.6	0.013
	PLAND, ED, AREA, GYRATE	6	107.0	6.9	0.011
	PLAND, AREA, GYRATE	5	107.3	7.2	0.010
	PLAND, GYRATE, AGE	5	107.8	7.7	0.008
	PLAND, AREA, AGE	5	108.4	8.3	0.006
	PLAND, ED, AREA, GYRATE, AGE	7	108.9	8.8	0.004
	PLAND, AREA, GYRATE, AGE	6	109.0	8.9	0.004
3000	ED	3	96.5	0.0	0.284
	ED, AGE	4	97.9	1.4	0.140
	PLAND, ED	4	98.7	2.2	0.098
	PLAND, ED, AREA	5	99.1	2.6	0.077
	PLAND, ED, AGE	5	99.9	3.4	0.051
	PLAND, ED, GYRATE	5	99.9	3.4	0.051
	PLAND, AREA, GYRATE	5	100.2	3.7	0.045
	PLAND	3	100.4	3.9	0.041
	PLAND, ED, AREA, AGE	6	100.8	4.3	0.033
	PLAND, ED, AREA, GYRATE	6	101.2	4.7	0.028
	PLAND, AGE	4	101.2	4.7	0.028
	PLAND, AREA, GYRATE, AGE	6	101.5	5.0	0.024
	PLAND, ED, GYRATE, AGE	6	101.6	5.1	0.022
	PLAND, AREA	4	102.2	5.7	0.016
	PLAND, GYRATE	4	102.5	6.0	0.014
	PLAND, ED, AREA, GYRATE, AGE	7	102.8	6.3	0.012
	PLAND, AREA, AGE	5	103.2	6.7	0.010
	PLAND, GYRATE, AGE	5	103.2	6.7	0.010
	(null)	2	103.2	6.7	0.010
	AGE	3	104.8	8.3	0.005

Table A3. Ranked logistic regression models explaining spring dispersal decisions of birds (n = 74) in landscapes buffered at 500 and 3000 meters. K is the number of parameters. AIC_c values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC_c is the difference in AIC_c values from the lowest AIC_c value. AIC model weight (w_i) is the probability that model *i* is the best model in the set. The null model includes no parameters.

buffer size (m)	Model	K	AIC_c	ΔAIC_c	w_i
250	YEAR	3	10.1	0.0	0.195
	(null)	2	10.5	0.4	0.166
	PLAND	3	11.3	1.2	0.110
	PLAND, YEAR	4	11.7	1.6	0.092
	ED	3	12.3	2.2	0.066
	SEX	3	12.4	2.3	0.063
	YEAR, SEX	4	12.5	2.4	0.060
	ED, YEAR	4	12.6	2.5	0.058
	PLAND, ED, SEX	4	13.6	3.5	0.035
	PLAND, SEX	4	13.8	3.7	0.032
	PLAND, ED	4	13.8	3.7	0.032
	PLAND, ED, YEAR	5	14.0	3.9	0.028
	PLAND, YEAR, SEX	5	14.3	4.2	0.025
	ED, SEX	4	14.7	4.6	0.020
	ED, YEAR, SEX	5	15.1	5.0	0.016
	PLAND, ED, YEAR, SEX	6	21.1	11.0	0.001
2000	YEAR	3	10.1	0.0	0.231
	(null)	2	10.5	0.4	0.197
	PLAND, YEAR	4	12.3	2.2	0.080
	SEX	3	12.4	2.3	0.074
	YEAR, SEX	4	12.5	2.4	0.072
	ED, YEAR	4	12.6	2.5	0.066
	ED	3	12.7	2.6	0.065
	PLAND	3	12.7	2.6	0.064
	PLAND, YEAR, SEX	5	14.8	4.7	0.022
	PLAND, ED, SEX	4	14.8	4.7	0.022
	ED, SEX	4	14.9	4.8	0.021
	PLAND, SEX	4	15.0	4.9	0.021
	PLAND, ED, YEAR	5	15.0	4.9	0.020
	PLAND, ED	4	15.2	5.1	0.019
	ED, YEAR, SEX	5	15.2	5.1	0.019
	PLAND, ED, YEAR, SEX	6	17.8	7.7	0.005

Table A4. Ranked least-squares regression models explaining fall dispersal distances for juvenile birds (n = 34) in landscapes buffered at 250 and 2000 meters. K is the number of parameters. AIC_c values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC_c is the difference in AIC_c values from the lowest AIC_c value. AIC model weight (w_i) is the probability that model i is the best model in the set. The null model includes no parameters.

buffer size (m)	Model	K	AIC_c	ΔAIC_c	w_i
250	PLAND	3	-267.1	0.0	0.202
	PLAND, YEAR	4	-266.6	0.5	0.161
	ED	3	-266.0	1.1	0.121
	ED, YEAR	4	-265.9	1.2	0.113
	PLAND, ED, SEX	4	-264.8	2.3	0.064
	PLAND, ED	4	-264.7	2.4	0.061
	PLAND, SEX	4	-264.6	2.5	0.059
	PLAND, ED, YEAR	5	-264.5	2.6	0.056
	PLAND, YEAR, SEX	5	-263.9	3.2	0.041
	ED, SEX	4	-263.9	3.2	0.040
	(null)	2	-262.5	4.6	0.020
	ED, YEAR, SEX	5	-262.4	4.7	0.020
	PLAND, ED, YEAR, SEX	6	-261.6	5.5	0.013
	SEX	3	-261.5	5.6	0.013
	YEAR	3	-261.1	6.0	0.010
	YEAR, SEX	4	-259.7	7.4	0.005
2000	ED	3	-263.6	0.0	0.193
	(null)	2	-262.5	1.1	0.111
	ED, YEAR	4	-262.4	1.2	0.105
	PLAND	3	-261.9	1.7	0.081
	PLAND, ED, SEX	4	-261.8	1.8	0.077
	SEX	3	-261.5	2.1	0.069
	PLAND, ED	4	-261.5	2.1	0.067
	ED, SEX	4	-261.4	2.2	0.065
	YEAR	3	-261.1	2.5	0.056
	PLAND, YEAR	4	-260.3	3.3	0.038
	PLAND, SEX	4	-260.1	3.5	0.033
	PLAND, ED, YEAR	5	-259.9	3.7	0.030
	ED, YEAR, SEX	5	-259.8	3.8	0.029
	YEAR, SEX	4	-259.7	3.9	0.027
	PLAND, YEAR, SEX	5	-258.0	5.6	0.012
	PLAND, ED, YEAR, SEX	6	-257.0	6.6	0.007

Table A5. Ranked least-squares regression models explaining fall dispersal distances for adult birds (n = 35) in landscapes buffered at 250 and 2000 meters. K is the number of parameters. AIC_c values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC_c is the difference in AIC_c values from the lowest AIC_c value. AIC model weight (w_i) is the probability that model *i* is the best model in the set. The null model includes no parameters.

buffer size (m)	Model	K	AIC$_c$	ΔAIC$_c$	*w_i*
250	AGE	3	-214.0	0.0	0.302
	(null)	2	-212.0	2.0	0.113
	PLAND , ED, AGE	4	-211.4	2.6	0.081
	PLAND, AGE	4	-211.4	2.6	0.081
	YEAR, AGE	4	-211.4	2.6	0.080
	ED, AGE	4	-211.3	2.7	0.080
	ED	3	-210.7	3.3	0.059
	PLAND	3	-210.7	3.3	0.057
	YEAR	3	-210.6	3.4	0.054
	PLAND, YEAR, AGE	5	-208.5	5.5	0.020
	ED, YEAR, AGE	5	-208.5	5.5	0.019
	ED, YEAR	4	-208.1	5.9	0.015
	PLAND, ED	4	-208.1	5.9	0.015
	PLAND, YEAR	4	-208.0	6.0	0.015
	PLAND, ED, YEAR, AGE	6	-205.4	8.6	0.004
	PLAND, ED, YEAR	5	-205.2	8.8	0.004
2000	AGE	3	-214.0	0.0	0.211
	PLAND, ED, AGE	4	-213.8	0.2	0.187
	ED, AGE	4	-213.0	1.0	0.128
	(null)	2	-212.0	2.0	0.079
	ED	3	-211.9	2.1	0.074
	PLAND, AGE	4	-211.5	2.5	0.060
	YEAR, AGE	4	-211.4	2.6	0.056
	PLAND	3	-210.6	3.4	0.039
	YEAR	3	-210.6	3.4	0.038
	ED, YEAR, AGE	5	-210.4	3.6	0.034
	PLAND, ED	4	-210.1	3.9	0.031
	ED, YEAR	4	-209.3	4.7	0.021
	PLAND, YEAR, AGE	5	-208.7	5.3	0.015
	PLAND, YEAR	4	-208.0	6.0	0.010
	PLAND, ED, YEAR, AGE	6	-207.7	6.3	0.009
	PLAND, ED, YEAR	5	-207.3	6.7	0.007

Table A6. Ranked least-squares regression models explaining spring dispersal distances for birds (n = 30) in landscapes buffered at 250 and 2000 meters. K is the number of parameters. AIC$_c$ values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC$_c$ is the difference in AIC$_c$ values from the lowest AIC$_c$ value. AIC model weight (w_i) is the probability that model *i* is the best model in the set. The null model includes no parameters.

buffer size (m)	Model	K	AIC_c	ΔAIC_c	w_i
250	PLAND, YEAR	4	152.3	0.0	0.573
	PLAND, YEAR, SEX	5	155.5	3.2	0.112
	PLAND, ED, YEAR	5	156.4	4.1	0.073
	ED, YEAR	4	156.7	4.4	0.061
	YEAR	3	157.3	5.0	0.046
	PLAND	3	158.0	5.7	0.033
	ED	3	158.4	6.1	0.027
	PLAND, ED, SEX	4	159.5	7.2	0.015
	YEAR, SEX	4	159.9	7.6	0.013
	PLAND, ED	4	159.9	7.6	0.013
	PLAND, ED, YEAR, SEX	6	160.4	8.1	0.010
	PLAND, SEX	4	160.5	8.2	0.009
	ED, YEAR, SEX	5	160.7	8.4	0.008
	ED, SEX	4	161.8	9.5	0.005
	(null)	2	164.0	11.7	0.002
	SEX	3	165.8	13.5	0.001
2000	ED	3	152.8	0.0	0.322
	ED, YEAR	4	154.1	1.3	0.169
	PLAND, ED, SEX	4	154.4	1.6	0.144
	PLAND, ED	4	154.8	2.0	0.117
	ED, SEX	4	156.1	3.3	0.063
	PLAND, YEAR	4	156.8	4.0	0.043
	PLAND, ED, YEAR	5	157.0	4.2	0.040
	YEAR	3	157.3	4.5	0.034
	ED, YEAR, SEX	5	157.9	5.1	0.025
	PLAND	3	159.2	6.4	0.013
	PLAND, YEAR, SEX	5	159.8	7.0	0.010
	YEAR, SEX	4	159.9	7.1	0.010
	PLAND, SEX	4	161.3	8.5	0.005
	PLAND, ED, YEAR, SEX	6	161.4	8.6	0.004
	(null)	2	164.0	11.2	0.001
	SEX	3	165.8	13.0	0.000

Table A7. Ranked least-squares regression models explaining fall movement rates for juvenile birds (n = 17) in landscapes buffered at 250 and 2000 meters. K is the number of parameters. AIC_c values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC_c is the difference in AIC_c values from the lowest AIC_c value. AIC model weight (w_i) is the probability that model *i* is the best model in the set. The null model includes no parameters.

buffer size (m)	Model	K	AIC_c	ΔAIC_c	w_i
250	(null)	2	65.9	0.0	0.706
	SEX	3	69.3	3.4	0.129
	YEAR	3	70.7	4.8	0.065
	PLAND	3	71.3	5.4	0.048
	ED	3	71.4	5.5	0.044
	YEAR, SEX	4	77.5	11.6	0.002
	ED, SEX	4	78.4	12.5	0.001
	PLAND, ED, SEX	4	78.4	12.5	0.001
	PLAND, SEX	4	78.6	12.7	0.001
	PLAND, YEAR	4	79.3	13.4	0.001
	ED, YEAR	4	79.9	14.0	0.001
	PLAND, ED	4	80.6	14.7	0.000
	ED, YEAR, SEX	5	96.0	30.1	0.000
	PLAND, YEAR, SEX	5	96.2	30.3	0.000
	PLAND, ED, YEAR	5	97.9	32.0	0.000
	PLAND, ED, YEAR, SEX	6	151.8	85.9	0.000
2000	(null)	2	65.9	0.0	0.694
	SEX	3	69.3	3.4	0.127
	YEAR	3	70.7	4.8	0.064
	PLAND	3	70.8	4.9	0.060
	ED	3	71.3	5.4	0.046
	YEAR, SEX	4	77.5	11.6	0.002
	PLAND, ED, SEX	4	78.4	12.5	0.001
	PLAND, SEX	4	78.5	12.6	0.001
	ED, SEX	4	78.6	12.7	0.001
	PLAND, YEAR	4	78.7	12.8	0.001
	ED, YEAR	4	79.7	13.8	0.001
	PLAND, ED	4	80.1	14.2	0.001
	PLAND, YEAR, SEX	5	95.8	29.9	0.000
	ED, YEAR, SEX	5	96.2	30.3	0.000
	PLAND, ED, YEAR	5	97.3	31.4	0.000
	PLAND, ED, YEAR, SEX	6	151.6	85.7	0.000

Table A8. Ranked least-squares regression models explaining fall movement rates for adult birds (n = 8) in landscapes buffered at 250 and 2000 meters. K is the number of parameters. AIC_c values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC_c is the difference in AIC_c values from the lowest AIC_c value. AIC model weight (w_i) is the probability that model *i* is the best model in the set. The null model includes no parameters.

buffer size (m)	Model	K	AIC_c	ΔAIC_c	w_i
250	(null)	2	75.8	0.0	0.737
	PLAND	3	79.8	4.0	0.103
	ED	3	80.7	4.9	0.064
	YEAR	3	81.4	5.6	0.045
	AGE	3	81.4	5.6	0.045
	PLAND, ED, YEAR	4	87.7	11.9	0.002
	PLAND, YEAR	4	88.0	12.2	0.002
	PLAND, ED	4	89.0	13.2	0.001
	PLAND, AGE	4	89.1	13.3	0.001
	ED, YEAR	4	89.9	14.1	0.001
	ED, AGE	4	90.0	14.2	0.001
	AGE, YEAR	4	90.8	15.0	0.000
	PLAND, AGE, YEAR	5	106.6	30.8	0.000
	PLAND, ED, AGE	5	107.7	31.9	0.000
	ED, AGE, YEAR	5	108.5	32.7	0.000
	PLAND, ED, AGE, YEAR	6	162.4	86.6	0.000
2000	(null)	2	75.8	0.0	0.621
	ED	3	78.0	2.2	0.209
	PLAND	3	79.8	4.0	0.084
	YEAR	3	81.4	5.6	0.038
	AGE	3	81.4	5.6	0.038
	PLAND, ED, YEAR	4	87.1	11.3	0.002
	ED, YEAR	4	87.1	11.3	0.002
	ED, AGE	4	87.3	11.5	0.002
	PLAND, ED	4	87.3	11.5	0.002
	PLAND, YEAR	4	89.0	13.2	0.001
	PLAND, AGE	4	89.1	13.3	0.001
	AGE, YEAR	4	90.8	15.0	0.000
	ED, AGE, YEAR	5	105.8	30.0	0.000
	PLAND, ED, AGE	5	105.9	30.1	0.000
	PLAND, AGE, YEAR	5	107.5	31.7	0.000
	PLAND, ED, AGE, YEAR	6	161.8	86.0	0.000

Table A9. Ranked least-squares regression models explaining spring movement rates for birds (n = 8) in landscapes buffered at 250 and 2000 meters. K is the number of parameters. AIC_c values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC_c is the difference in AIC_c values from the lowest AIC_c value. AIC model weight (w_i) is the probability that model *i* is the best model in the set. The null model includes no parameters.

buffer size (m)	Model	K	AIC$_c$	ΔAIC$_c$	w_i
500	PLAND	3	394.7	0.0	0.300
	ED	3	395.7	1.0	0.182
	(null)	2	396.7	2.0	0.110
	PLAND, ED	4	396.7	2.0	0.107
	PLAND, GYRATE	4	396.9	2.2	0.101
	PLAND, AREA	4	397.0	2.3	0.096
	PLAND, ED, AREA	5	399.1	4.4	0.032
	PLAND, ED, GYRATE	5	399.1	4.4	0.032
	PLAND, AREA, GYRATE	5	399.3	4.6	0.030
	PLAND, ED, AREA, GYRATE	6	401.7	7.0	0.009
3000	ED	3	395.5	0.0	0.318
	PLAND	3	396.6	1.1	0.188
	(null)	2	396.7	1.2	0.168
	PLAND, ED	4	397.8	2.3	0.102
	PLAND, GYRATE	4	398.6	3.1	0.070
	PLAND, AREA	4	398.8	3.3	0.062
	PLAND, ED, AREA	5	400.3	4.8	0.030
	PLAND, ED, GYRATE	5	400.3	4.8	0.030
	PLAND, AREA, GYRATE	5	400.8	5.3	0.023
	PLAND, ED, AREA, GYRATE	6	402.8	7.3	0.008

Table A10 Ranked least-squares regression models explaining fall adult home range sizes of birds (n = 54) in landscapes buffered at 500 and 3000 meters. K is the number of parameters. AIC$_c$ values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC$_c$ is the difference in AIC$_c$ values from the lowest AIC$_c$ value. AIC model weight (w_i) is the probability that model i is the best model in the set. The null model includes no parameters.

buffer size (m)	Model	K	AIC_c	ΔAIC_c	w_i
500	AGE	3	-18.1	0.0	0.224
	PLAND, AGE	4	-17.0	1.1	0.128
	(null)	2	-16.3	1.8	0.089
	ED, AGE	4	-16.1	2.0	0.082
	PLAND	3	-15.9	2.2	0.075
	PLAND, GYRATE, AGE	5	-15.9	2.2	0.073
	ED	3	-15.3	2.8	0.055
	PLAND, AREA, AGE	5	-14.8	3.3	0.043
	PLAND, GYRATE	4	-14.6	3.5	0.039
	PLAND, ED, AGE	5	-14.4	3.7	0.035
	PLAND, AREA, GYRATE, AGE	6	-14.4	3.7	0.035
	PLAND, AREA	4	-14.0	4.1	0.028
	PLAND, ED	4	-13.5	4.6	0.022
	PLAND, ED, GYRATE, AGE	6	-13.1	5.0	0.018
	PLAND, AREA, GYRATE	5	-12.4	5.7	0.013
	PLAND, ED, AREA, AGE	6	-12.1	6.0	0.011
	PLAND, ED, GYRATE	5	-12.0	6.1	0.011
	PLAND, ED, AREA, GYRATE, AGE	7	-11.6	6.5	0.009
	PLAND, ED, AREA	5	-11.4	6.7	0.008
	PLAND, ED, AREA, GYRATE	6	-9.7	8.4	0.003
3000	AGE	3	-18.1	0.0	0.201
	ED, AGE	4	-17.6	0.5	0.158
	ED	3	-17.1	1.0	0.123
	PLAND	3	-16.3	1.8	0.080
	(null)	2	-16.3	1.8	0.080
	PLAND, AGE	4	-16.0	2.1	0.069
	PLAND, ED, AGE	5	-15.1	3.0	0.044
	PLAND, GYRATE	4	-14.9	3.2	0.041
	PLAND, ED	4	-14.9	3.2	0.040
	PLAND, GYRATE, AGE	5	-14.4	3.7	0.032
	PLAND, AREA	4	-14.3	3.8	0.030
	PLAND, AREA, AGE	5	-13.8	4.3	0.024
	PLAND, ED, GYRATE	5	-12.7	5.4	0.013
	PLAND, ED, AREA	5	-12.6	5.5	0.013
	PLAND, ED, AREA, AGE	6	-12.5	5.6	0.012
	PLAND, ED, GYRATE, AGE	6	-12.5	5.6	0.012
	PLAND, AREA, GYRATE	5	-12.5	5.6	0.012
	PLAND, AREA, GYRATE, AGE	6	-11.9	6.2	0.009
	PLAND, ED, AREA, GYRATE	6	-9.9	8.2	0.003
	PLAND, ED, AREA, GYRATE, AGE	7	-9.6	8.5	0.003

Table A11. Ranked least-squares regression models explaining spring home range sizes (n = 41) of birds in landscapes buffered at 500 and 3000 meters. K is the number of parameters. AIC_c values are Akaike Information Criteria values corrected for small sample sizes and ΔAIC_c is the difference in AIC_c values from the lowest AIC_c value. AIC model weight (w_i) is the probability that model *i* is the best model in the set. The null model includes no parameters.