Nesting requirements of the Northern Goshawk (*Accipiter gentilis atricapillus*)
in southeastern British Columbia

by

William Laughton Harrower
BSc., University of British Columbia, 2002
Dipl. Envir. Sc., Camosun College, 1998

A Thesis Submitted in Partial Fulfillments of the
Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Biology

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ABSTRACT

The identification of resources animals select provides valuable insight into the factors that limit populations and control distributions. My objective in this thesis was to examine how the northern goshawk (*Accipiter gentilis atricapillus*) selects resources during the nesting and fledging life-history stages. This work was conducted in southeastern British Columbia, Canada, from 1998 to 2006. Using Information-Theoretic techniques, I described the forest characteristics selected by goshawks when locating their nest sites within their breeding territories, and the forest characteristics selected by fledgling goshawks around the nest while they are still dependent on their parents for food. I found that goshawks select nesting sites with a relatively large amount of high canopy cover (>40%) forest within 200 m of the nest. The amount of high canopy cover forest remained higher than comparison points up to 1100 m from the nest, but goshawks also will select for forest openings relatively close to the nest (~ 174 m). Fledgling goshawks selected for continuous areas of forest cover, particularly areas with higher amounts of forest between 40-80 years old within 525 m distance from the nest. Presumably, goshawks selected these younger stands in order to avoid

predation. Fledglings also selected areas with more high canopy cover forest and areas without large amounts of recently-harvested forest (<10 years of age) stands within 525 m of the nest. Thus, the structural characteristics of forests required by goshawks for nesting are complex, and different competing characteristics are selected at different distances from the nest. Although goshawks do require mature forest stands with high canopy cover close to the nest, a greater diversity of forest types appears to be either tolerated or required as the distance from the nest increases. Additionally, limited evidence suggests that the movements of fledgling goshawks may be governed by a combination of forest structure and inter-familiar interactions.

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ACKNOWLEDGMENTS

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I also need to thank Kari Stuart-Smith and Erica McClaren for introducing me to goshawks and avian ecology. Kari performed the incredible task of identifying an outstanding number of goshawk nest areas I used in this thesis, concurrent work, and future research. Beginning and maintaining her goshawk monitoring program took vision and perseverance without which little else could have been accomplished. She has gladly allowed me to use and extend her research, and without her trust and confidence this thesis could not have been completed. Erica has been a huge part of this project since its inception, and again my work could not have been completed without her. Although I had seen one goshawk at the outset of this project and realized goshawks had feathers, I knew little else about the birds, their ecology, or how to study them. Our long

talks brought me up to speed, helped me secure funding, taught me how to observe raptors, allowed me to frame questions, and kept my writing and assumptions on track. Kari and Erica's work are the foundations upon which my research was built and without this support my research would have surely crumbled.

I also benefit from the blood, sweat, and tears of a number of field assistants. Karl Bachman spent years monitoring goshawk nest sites, and his incredible organizational and observational skills allowed me to return to these sites. His smiles support, and insights are always welcome, not to mention his enormous collection of field footwear. Jon Michel, Rebecca Rozander, Debbie Bhattacharya, Barry Robinson, and Jay Finstad all spent a summer on the project collecting telemetry locations, tolerating my constant push for more locations, and dealing with either a lack of sleep or an overabundance of motor homes. Richard Klafki and Melissa Hogg lent their hard work and unique touch to the project, always reassuring me that everything was 'OK' while I was attached to my computer in Kamloops.

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CHAPTER 1: INTRODUCTION

Introduction

The identification of resources that animals exploit provides valuable insights into factors that limit populations and control distributions. Resources may be food, shelter, or breeding sites or can be an area where the risk of predation or competition is low. Thus, a *resource* is any environmental component or variable that assists an animal to survive and reproduce. Understanding what resources animals select provides useful knowledge of how animals interact with their environment (Weins 1989, Krebs 2001, Manley et al. 2002).

The quantification of the resources animals' acquire from their environment requires the definition of terms (Manley et al. 2002). Resources *used* by animals can be described by measuring the quantity acquired by an individual or population (Manley et al. 2002). However, this approach describes which resources the animals are exploiting, and does not indicate if these resources are limiting (Manley et al. 2002). Thus, applied ecologists are more interested in *selection*, because selection occurs when a resource is used more or less often than it is *available* to the animal (spatially or temporally). Along with *preference* (the likelihood a resource is chosen over another equally available resource), selection provides a quantification of the importance of resources (Manley et al. 2002). Following from these definitions, *habitat* is a general term that describes a location or area comprised of one or more beneficial resources and thus forms the usual or favoured surroundings of an individual or population (Morrison et al. 1992). Additionally, defining the spatial and temporal scale of both use and availability is essential. Two

important aspects of spatial scale that must be clarified are 'extent' and 'grain' (Fortin and Dale 2005). Spatial *extent* is the study area of interest. Spatial *grain* is the size of the sample unit or the area used to collect data (Fortin and Dale 2005).

Since the selection of resources often varies among different components of a population (Aebischer et al. 1993), identifying these differences is essential in assessing the importance of resources. Selection can vary by one or a combination of factors such as year, season, sex, age class, reproductive condition, predation risk, resource availability and/or disturbance patterns. Thus, working definitions of extent and grain may need to be adjusted to match specific investigations of different life-history stages of the animals being examined. The challenge to ecologists is to quantify which resources affect the fitness of individuals at each life-history stage and then to determine the sensitivity of populations to changes in fitness at each of their stages. In this way, ecologists are able to determine the resources having the largest impact on the distribution and abundance of species.

Breeding birds offer an excellent opportunity to examine resource selection across different life-history stages and at multiple spatial scales. Since birds are restricted in their breeding site to a central location (the nest), nearly all resources required to reproduce during this season must be acquired within a relatively short distance. Hence, the availability of resources is restricted, and this geographic limit simplifies the quantification of which resources are selected during particular life-history stages. Territorial birds further segregate resource use, because each individual pairs nests in discrete geographic areas. Furthermore, resource selection in birds may occur at multiple

spatial scales (Weins 1989), each of which may be tied to an ecologically functional unit. For example, selection of a territory can be tied to landscape conditions, selection of a nest site to conditions within the territory, and selection of a nest location to conditions within the nest site. Thus, we are able to define both the extent and grain of investigation in a way that is potentially meaningful to the animal, and at the same time, improve our understanding of the importance of differences in resource selection among life-history stages.

The northern goshawk (*Accipiter gentilis*) is a relatively large raptor that is well adapted to life in a broad range of forested ecosystems (Squires and Reynolds 1997). Goshawks have short, stout wings and a long tail that allow rapid manoeuvring through dense forest (Squires and Reynolds 1997). In western North America, goshawks utilize a wide variety of forest types, including boreal spruce (Doyle and Smith 1994), sub-boreal spruce (Mahon and Doyle 2003), temperate hemlock-Douglas-fir (McClaren et al. 2005), ponderosa pine (Graham et al. 1999), and Douglas-fir/lodgepole pine and Douglas-fir/western larch (this study). Less frequently, goshawks use deciduous-dominated forests such as high-elevation sites or low-elevation mature aspen stands (Younk and Bechard 1994, Graham et al. 1999).

During the breeding season, the movements and resource selection of goshawks can be divided into a number of hierarchical levels, including nesting territories, breeding areas, nest areas, nest sites, and the post-fledging area (Figure 1). How goshawks distribute their nests on the landscape can be described using the ideal pre-emptive distribution (Fretwell and Lucas 1970, Pulliam and Danielson 1991), as the nesting territories of

breeding pairs are regularly spaced across the landscape (Kruger and Lindstrom 2001, Reich et al. 2004). The components and terminology describing nesting territories can be defined by the behaviour of goshawks during the various life-history stages (Figure 1). The *nest area* encompasses all the nest trees in a breeding pair's nesting territory; this area is thought to be defended by a breeding female during courtship, incubation, and the early fledgling-dependency period (Squires and Kennedy 2006). For approximately 40 days after fledging, juvenile goshawks may extensively use a portion of forest surrounding and including the nest area for learning to fly and for protection from predators. This period is termed the *fledgling-dependency period* (FDP) and during this time, fledglings are completely dependent on their parents for food (Kenward 2006, Squires and Kennedy 2006). The area traversed by fledglings during the FDP is the *post-fledging area* (Squires and Kennedy 2006). Although overlap occurs between the nest area and post-fledging area (PFA), these areas are not identical (Figure 1). Hereafter, I term the combined area of all possible PFAs over many years and the nest area as the *breeding area* for that individual nesting territory (Figure 1). The breeding area therefore encapsulates the entire area required to maintain successive nesting events over multiple years, at a particular site. It is not defined by a single breeding pair and is maintained despite breeding pair turnover. Surrounding and including the breeding area are the *foraging areas* of adults. These areas constitute the entire area traversed by the adult birds during the breeding season and are the areas where these birds hunt for food (Reynolds et al. 1992). Following from these definitions, I define a *nesting territory* as the area in which other goshawks are excluded from nesting due to the presence of other nesting goshawks.

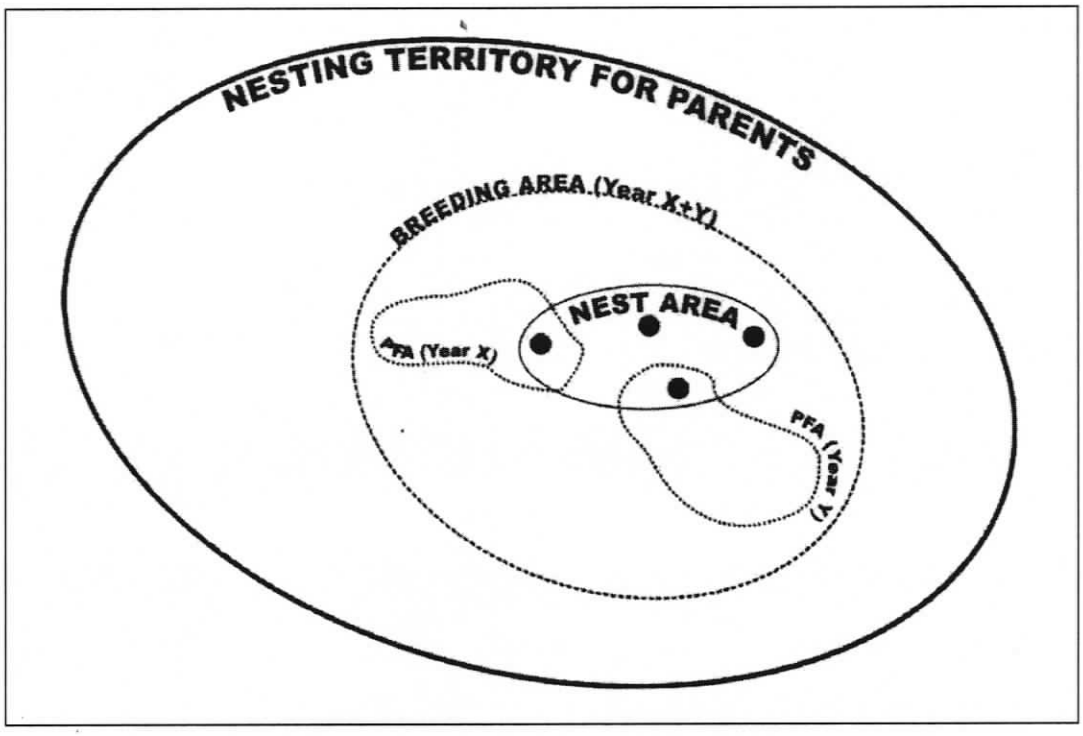

Figure 1: The use of space by different northern goshawk (*Accipiter gentilis*) life-history stages during the breeding season. Dots indicate potential nest trees each used in an individual year. I define the nest area by the distribution of these trees over many years. The post-fledgling areas (PFA) for two hypothetical years (x+y) are shown along with the breeding are resulting from the nest area and all possible PFAs from many years. Adapted from Reynolds et al. 1992.

Goshawks and other forest-dwelling species are an increasing concern in the management of forests. Market forces requiring forest certification, federal and international pressure on local agencies, and public opinion have shifted towards the protection of biodiversity. The growing numbers of threatened or endangered species means that managers are confronted with the overwhelming task of ensuring sustainable populations of a large number of species. The use of *indicator species* has been widely touted as one means to simplify the management of many species on the landscape (e.g., Lambeck 1997, Simberloff 1998). Maintaining viable populations of an indicator species

ensures that the resource requirements for a large number of other species are met, thus alleviating the need to plan, manage, and monitor for each individual species individually. Further, management of the forest for the protection or persistence of a host of *focal species*, each representative of a specific suite of forest values, may provide a simplified framework that encompasses many more forest values than just those protected by managing for a single indicator species (Roberge and Angelstam 2004). Thus, by managing and monitoring for a small number of focal species, forest managers are able to concentrate their limited time and money on the management and monitoring of a reduced number of species and still meet sustainable forest-management objectives.

The goshawk is one of a series of candidates for use as an indicator of forest management that incorporates the protection of biodiversity and maintenance of ecological function into forest harvest plans. The rationale for consideration of the goshawk as an indicator species is that this species has been associated with old and mature forests (Reynolds et al. 1992, Kenward 2006, Squires and Kennedy 2006). Furthermore, the goshawk feeds on mid-sized prey such as hare, grouse, and squirrels (Squires and Reynolds 1997). Goshawks also require suitable, large trees in which to perch and nest. Therefore, the presence of nesting goshawks is thought to suggest suitable mature forest structure as well as abundant prey species surrounding nesting stands (Reynolds et al. 1992). These and other general requirements of the goshawk are well known; however, precise data are lacking on such topics as the amount of forest required in breeding areas. The lack of these data restricts both the development of operational level harvest plans by forest companies and the creation of strategic level

plans, which use the nesting requirements of the goshawk to guide sustainable forest management objectives.

In southeastern British Columbia (BC), the goshawk has emerged as a key candidate species for monitoring the sustainable use of forests. In this region, forest harvest has occurred in valley bottoms for over 100 years and higher elevations have seen increasing harvest since the 1950s. Thus logging, along with the manipulation of historic disturbance patterns (e.g., fire suppression), has resulted in a highly modified landscape. Despite these changes, the goshawks continue to be observed throughout the region. However, changes in the distribution and loss of connectivity in the forests of this region raise concerns that the number of nesting locations may be decreasing. Thus, research into the types of forests goshawks select could provide useful information into their potential nesting requirements and help address the concerns that the number potential nest areas is decreasing. Tembec Industries Inc. (a Canadian forest company with large holdings of public forest lands in southeastern BC) has developed a sustainable forest management plan geared at meeting it's objectives of maintaining Forest Stewardship Council certification and managing forests in a sustainable fashion. My research supports one component of that plan, and will feed information directly into Tembec's Criteria and Indicators Framework for Sustainable Forest Management.

In this thesis, I investigate the selection of forest resources by northern goshawks (ssp. *atricapillus*) at nest-sites in southeastern BC. My overarching goal is to better understand how the selection of forest resources, at different spatial scales, by two different age-classes of goshawks, combines to define the nesting requirements of this

species. I examine resource selection during the breeding season because this is when goshawks may be limited by the availability of nest sites or the abundance of effective rearing areas. Although these may not be the only factors limiting goshawk populations, they are the factors that may be most affected by anthropogenic change, such as logging and fire suppression, and thus are the factors that resource managers have the greatest ability to manipulate at a local level.

I describe the selection of nest sites within territories by adult breeding goshawks and the selection of forest types by fledgling goshawks prior to dispersal. Goshawks may select resources at different scales and the influence of individual resources on nest-site occupancy may vary with the spatial grain used to measure that resource (McGrath et al. 2003). For example, less shrub cover may occur near a nest than in the surrounding forest, in order to provide easy access to the nest by parents with large food items; however, young dense forest may be selected further from the nest in order to provide escape cover for fledglings. Both of these resources may be important factors that combine to influence nest-site occupancy, but each is available to goshawks during a different life-history stage and at different spatial grains.

Study Area

Nest sites occupied by goshawks were observed from 1998 to 2006 in southeastern British Columbia, Canada. Additionally, I observed the movements of fledgling goshawks around occupied nest sites from 2004 to 2006 in the same area. My study area occupies the operating area of Tembec Industries Inc. within the Rocky Mountain Forest District (RMFD) of southeastern British Columbia, Canada. The RMFD is an area of

approximately 2.6 million hectares in southeastern British Columbia and Tembec's operating area covers a large portion of the southern part of this district (Figure 2). I confined my investigations to Tembec's operating areas as these are the only areas that provided up-to-date digital forest harvest information to me.

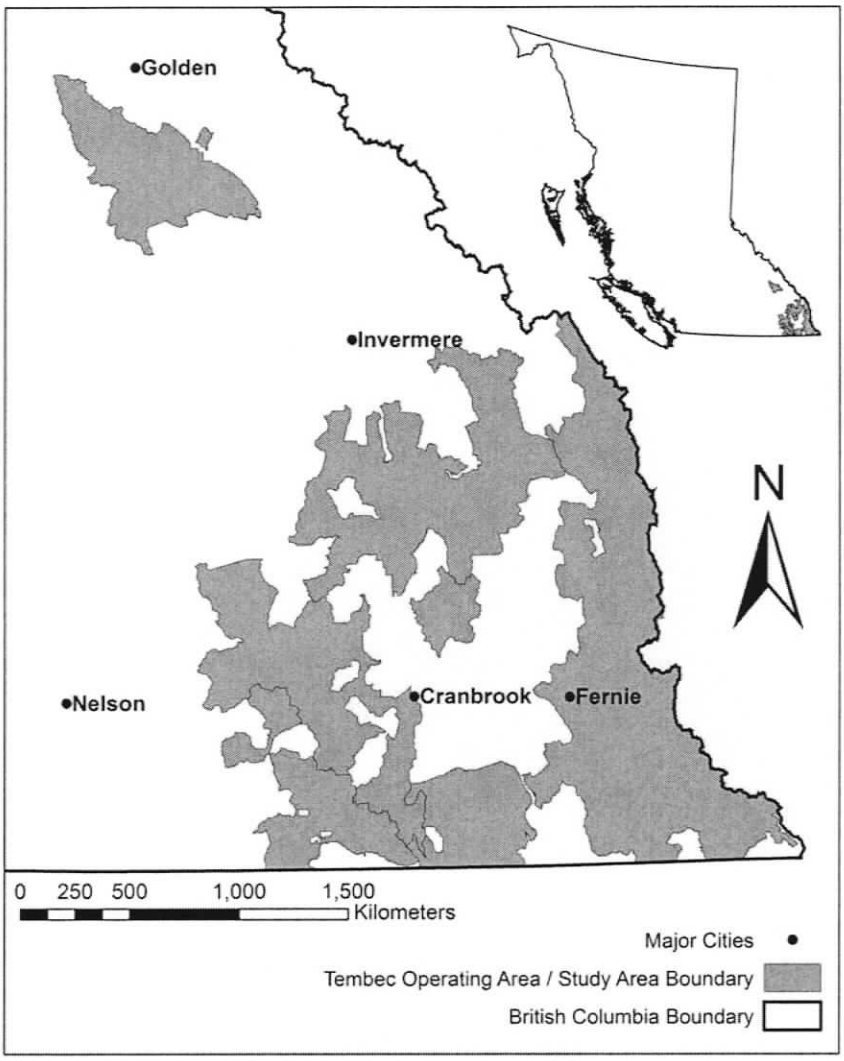

Figure 2: Study area for investigation of resource selection by goshawks in southeastern British Columbia, Canada. Observations were restricted to the forested, operating areas of Tembec Industries Inc.

Southeastern BC (i.e., the East Kootenay Region) is a diverse area of the province characterized by grassland, forest, and alpine ecosystems. It has grassland and wetland river valleys (i.e., Southern Rocky Mountain Trench Ecoregion) extending though a mid-elevation forest belt to high alpine tundra and unvegetated areas (i.e., Columbia Mountains and Highlands, and Southern Rocky Mountains Ecoregions). The climate is characterized by warm dry summers, and cold winters (Figures 3 and 4). Dry valley bottoms occur due to the rain shadow effects of the Columbia Mountains on the western border of the region; however, with increasing elevation, precipitation increases significantly and forest and alpine ecosystems become more prominent.

Goshawks occur within the forested areas of this region. Tree species are diverse and the forests area subject to a wide range of natural and anthropogenic disturbances (e.g., fire and logging, respectively). Anthropogenic disturbance of forest lands in the RMFD consists primarily of logging, fire suppression, and cattle grazing: with greater than 1.6 million m^3 of wood harvested each year (http://www.for.gov.bc.ca/drm/DistrictMap/about.htm, accessed July 8, 2007). Additionally, substantial amounts of coal mining occur locally within the Elk Valley and other small mining operations dot the region. The tourism industry is increasing yearly, adding substantial development to valley bottoms. However, logging and fire suppression are the main anthropogenic impacts on goshawk populations at present.

I chose this study area for a number of reasons. First, a local forest company, Tembec Industries Inc., had been identifying and monitoring goshawk breeding areas and describing the surrounding forest since 1998. Thus, a relatively large database of nest

locations was available, and this information was instrumental in finding and radio-tagging an appropriate sample of fledgling birds and their parents. Second, this sample of goshawk breeding areas occurred in a region with a diverse range of forest types and a wide range of disturbance patterns. Thus, nests in this area occur in low- to high-elevation forests, at both dry and wet sites, and with a range of disturbance patterns surrounding each nest. This sample provided me with an excellent range of variation with which to investigate the patterns of resource selection by nesting goshawks. Finally, a full set of fine-scale descriptions of the forest cover immediately surrounding goshawk nest sites was available for me to use in my analysis.

My field observations of goshawks began in 2004, although I used information from Tembec's data base to conduct a retrospective analysis of goshawk nest sites from 1998-2005. During the years of this work (1998-2006), mean monthly temperatures and precipitation values generally lay within the long-term monthly norms (Figures 3 and 4, respectively). From 2004 to 2006, I collected data on nest sites and their occupancy along with Tembec biologists, and merged this information with that previously collected by Tembec from1998 to 2003. I used the larger, resultant data-set to examine selection of nest sites within territories by adult breeding pairs from 1998-2005 (Chapter 2). From 2004 to 2006, I captured and radio-tagged fledgling and adult goshawks at a select number of occupied nests, and in Chapter 3 I use this information to examine fledgling movements and resource selection. In Chapter 4, I provide a brief summary of my major results, their implications to goshawk ecology and forest management, and suggestions for future investigation.

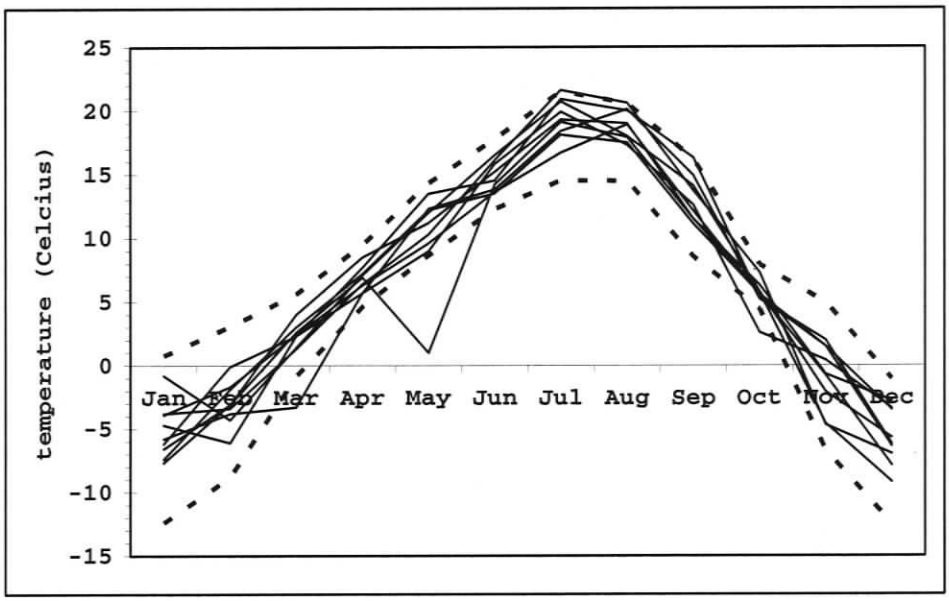

Figure 3: Mean monthly temperatures for Cranbrook City Environment Canada weather station from 1998 to 2006 (solid lines) and 95% confidence intervals for 20-year mean monthly temperatures from 1980-2000 (dashed lines).

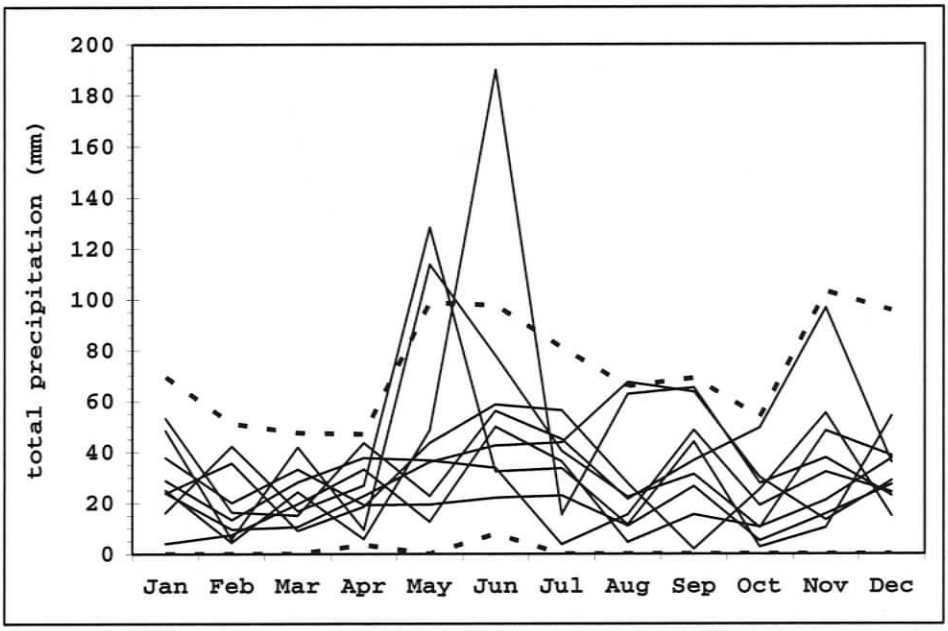

Figure 4: Total precipitation for Cranbrook City from 1998 to 2006 (solid lines) and 95% confidence intervals for 20-year mean monthly temperatures from 1980-2000 (dashed lines).

CHAPTER 2: NORTHERN GOSHAWK NEST-SITE SELECTION AT MULTIPLE SPATIAL SCALES

Introduction

In both Europe and North America, the nesting habits of Northern Goshawk (*Accipiter gentilis*) have received considerable attention, , due to the perceived adverse impact of logging on goshawk breeding requirements (Reynolds et al. 1992, Kenward 2006, Squires and Kennedy 2006). Although the characteristics of goshawk nest trees and nest stands have been well described, fewer studies have specifically examined how these characteristics differ across multiple spatial scales (McGrath et al. 2003, Squires and Kennedy 2006). Penteriani (2002) reviewed 43 published accounts, theses, and technical reports from across the goshawk's Holarctic range and found only nine papers that compared nest-site conditions with the conditions of the areas available for nesting, and only six studies that examined nesting requirements at the scale thought necessary to assess between stand selection (>0.08 ha). In the absence of detailed comparative studies that provide information on the extent of the general nesting requirements of goshawks (i.e., large trees, high canopy cover forest, and low understory vegetation), current assessments may be an over-simplification of the more diverse nesting requirements of this species (Kenward 2006).

The establishment of a nest by goshawks may be viewed as series of hierarchical choices operating at multiple spatial extents (Johnson 1980, Reynolds et al. 1992). Intuitively, a bird may select the attributes associated with a particular tree within a forest stand. Beyond the stand, the bird may select particular attributes measured at a larger spatial

scale (i.e., patch level metrics). I use the terms *nest tree* and *nest stand* to refer to these two orders of selection (Johnson 1980), respectively. A further order of selection is the landscape-level selection of nesting territories by goshawks. Goshawk nests have been described as being regularly spaced across the landscape (Kruger and Lindstrom 2001, Reich et al. 2004) and this distribution may be analogous to the ideal premptive distribution (Fretwell and Lucas 1970, Pulliam and Danielson 1991). Although breeding pairs may not defend these areas during foraging, it appears that pairs are restricted from placing their nests within a certain distance of other goshawk pairs (Kenward 2006). Thus, the selection of nesting territory from the available landscape is an important level in the hierarchical process of placing a nest.

Over 300 variables have been used to describe the location (i.e., the area immediately surrounding a goshawk nest tree) of goshawk nest trees (Penteriani 2002), but only a small number of variables seem to consistently describe the area around the nest tree (Squires and Kennedy 2006). For example, goshawks nest in both deciduous and coniferous trees and so it appears that goshawks choose a nest tree based more on the structural characteristics of the tree rather than the species of tree (Kenward 2006, Squires and Kennedy 2006). Goshawks often nest in one of the largest trees in the stand, but the height and diameter of nest trees vary widely (Kenward 2006, Squires and Kennedy 2006). Typically, goshawks nest in stands of large, mature trees with relatively closed canopies and open understories (Kenward 2006, Squires and Kennedy 2006). Goshawks have been described nesting at sites with higher basal areas and higher tree densities than surrounding sites (Squires and Kennedy 2006). However, these two variables are correlated, and as mentioned few studies have compared the values of these

variables at the nest tree to the landscape conditions surrounding the nest (Squires and Kennedy 2006).

Most investigations of goshawk nest locations have focused on a 1- to 2-ha area surrounding the nest, examined less than 40 nests, and used a fixed grain of measurement (McGrath et al. 2003). Therefore, it is difficult to generalize nesting requirements to the nest-stand level. Goshawks typically choose to nest in mature forest stands with relatively high canopy cover and relatively low understory vegetation (Penteriani 2002, Kenward 2006, Squires and Kennedy 2006), although they have been observed nesting in younger, middle-aged stands (Kenward 2006, Squires and Kennedy 2006). Often canopy cover is higher in nest stands than in the stands of the surrounding forest (Squires and Kennedy 2006). Goshawk nests also have been associated with a number of landscape features, such as roads, forest edges, and water features. Nests have been described as occurring near a canopy break, sometimes provided by roads or trails (Squires and Kennedy 2006). Goshawks may nest close to forest openings such as clearings and other open areas presumably to improve access to the nest. However, goshawks are reported to avoid paved roads and other developed areas (Penteriani and Faivre 1997), despite more recent evidence suggesting they will nest in urban centers (Kenward 2006). Goshawks may place their nests close to water features, but this behaviour is variable and may be correlated with forest type or the proximity to a break in the forest canopy associated with the water feature (Squires and Kennedy 2006). Despite these findings regarding nest-stand level selection, generalizations applicable across a range of forest types are difficult to make because of differences in sampling

regimes (extent of investigation), inconsistencies in definitions of resource variables (the grain of measurement), and differences in the definition of variables.

The objective of my study is to investigate selection of nesting locations within territorial boundaries by the northern goshawk (ssp. *atricapillus*), at multiple spatial extents and grains, in order to identify forest characteristics important in predicting nest-site location, and thus identify the resources required by goshawks when nesting. Based on previous studies, I hypothesized that compared to surrounding trees goshawks would select nest trees within stands that had greater amounts of high canopy cover and lesser amounts of understory vegetative cover. I further predicted that goshawks would select nest stands based on most common tree species in the stand, stand age, patch size, edge length, and their distance to roads, water, and recently-harvested forest stands.

Methods

Between 1998 and 2006 occupied nests were identified by investigating reported sightings of aggressive birds during the breeding season (March through August). Most these reports came from field workers in the forest industry. Each report was confirmed as a goshawk nest by visiting the site and noting indications of use (nestlings, fledglings, or adults present, fresh green branches in the nest, whitewash streaks near the base of the nest tree, prey remains or pellets nearby) and broadcasting calls (adult alarm or juvenile begging calls) and listening for a response. Nest trees were marked and their location recorded with a Garmin76 GPS device (Global Positioning System; GARMIN Corporation, Olathe, Kansas) with the aid of an external antenna (GPS 17-HVS GPS Sensor, GARMIN Corporation, Olathe, Kansas).

I classified a nest as active if a goshawk was seen incubating eggs, is nestlings were seen, or if fledglings were observed in or around the nest. Although previous studies have used the defence of a nest area or nest tree as a measure of use, goshawks may defend a nest area during the courtship and nesting periods but not lay eggs in it (Squires and Kennedy 2006, personal observations). I included these nests in calculations of nest area size, distance between nests, and number of nests per nest area, but they were not included in the nest-tree or nest-stand selection analysis.

I defined nest-tree selection as selection of a tree within a circle with a radius of 200 m (12.6 ha) in order to represent the typical size of a goshawk nest stand. To assess how the characteristics of the nest tree differed from the characteristics of trees available for nesting within the stand, I employed a *used versus unused design* (Sampling Protocol C, Design III: Manley et al. 2002). The forest characteristics at each nest tree (used) and at seven comparison trees (unused) situated at random distances (1-200 m) and random bearing (1°-360°) from the nest tree were described by Tembec personnel and I used these data to in my analysis.

I defined nest-stand selection as the selection of a nest tree within a nesting territory (i.e., comparison points selected within 5 km). Forest cover variables were measured at nest trees (used) and 10 comparison points (unused) placed randomly within 5 km of the nest tree (Sampling Protocol C, Design III: Manley et al. 2002). I chose a distance of 5 km to represent the minimum distance between the geographic centres of nest areas and thus approximate nesting territory size. The geographic centre of nest areas was

determined by calculating the weighted mean of the Euclidean distance between nest area centres. I used a conservative estimate of nesting territory size based on my minimum-observed inter-nest-area distance (mean = 4.67 km, SE = 4.49, n = 35).

I quantified characteristics of the nest tree, and when possible, compared them to the analogous data collected from nest-tree comparison plots. Combinations of variable and fixed radius plots were used to characterize the area around each nest tree and comparison point (Table 1). Canopy closure was measured with a spherical densitometer (averaging 4 measurements from each of the cardinal directions taken 1 m from the tree), and estimated the percent cover of small trees and shrubs visually within fixed radius plots (small trees were measured in 3.99-m plots, and shrubs were measured in 5.64-m plots). Data was also collected for a number of other variables thought relevant to goshawks (Table 1).

I measured a series of stand- and patch-level variables to determine the differences between nest trees and comparison points (Table 2). I identified four grains of measurement for explanatory variables that I perceived relevant to goshawks when they were selecting a nest location. These grains were: (1) the nest stand and primary area used prior to hard-penning of fledgling feathers (a 200-m radius buffer, 13-ha [Reynolds et al. 1992 and personal observations]), (2) a standard conservative post-fledging area (a 500-m radius buffer; 79-ha [Woodbridge and Detrich 1994]), (3) the initial post-fledging area estimate (a 800-m radius buffer; 201-ha [Kennedy et al. 1994 and personal observations]), and (4) roughly the largest area observed between alternative nests (1100-m radius buffer; 380-ha).

Table 1: Summary of variables used to describe the characteristics of goshawk nest trees, nest stands, and randomly selected areas within 200 m of the nest tree in southeastern British Columbia, Canada.

Variable	Description +/or Method of measurement
Nest Tree Diameter	Diameter at breast height measured in cm
Nest Tree Elevation (m)	TRIM[1] DEM[2] from 30m raster
Nest Tree Slope (degrees)	TRIM[1] DEM from 30m raster
Nest Tree Aspect (degrees)	TRIM[1] DEM from 30m raster
Nest Tree Canopy Cover (%)	Average value of 4 measurements of spherical densitometer
Tree 2-10m Canopy Cover (%)	visual estimate from 3.99 m fixed radius plot
Tree <2m Canopy Cover (%)	Visual estimate from 3.99 m fixed radius plot
Small Tree (<10 m) Canopy Cover (%)	visual estimate from 3.99 m fixed radius plot
Shrub Canopy Cover (%)	visual estimate from 5.64 m fixed radius plot
Veteran Tree Height (m)	height in meters of the trees that are older and taller than the trees comprising the main tree canopy and are remnant from the stand that occupied the site prior to a major disturbance (i.e., stand initiating event)
Dominant Tree Height (m)	height of the trees in the nest stand that are more vigorous than the trees comprising the main tree canopy
Main Canopy Tree Height (m)	height of the trees that comprise the largest amount of the tree canopy
Sub-canopy Tree Height (m)	height of trees over 10 m in height but that do not reach the main tree canopy, these trees may form a secondary canopy in multi-layered stands

[1] TRIM = British Columbia Terrain Resource Inventory Mapping
[2] DEM = Digital Elevation Model

Table 2: Summary of variables used to describe the characteristics of goshawk nest trees and nest-stand level comparison plots within 5 km of the nest tree in southeastern British Columbia, Canada.

Variable	Description +/or method of Measurement
Distance to Road (m)	Euclidean distance measured to the nearest permanent road, including forestry roads
Distance to Water (m)	Euclidean distance measured to either the nearest mapped wetland, lake, or permanent stream
Distance to Harvest (m)	Euclidean distance measured to the nearest harvested forest stand logged since 1971 (i.e., <36 years old)
% of Young Forest[1,2]	Proportion of the area in each of four circular buffers[1] with 41-80 year old stands
% of Mature Forest[1,2]	Proportion of the area in each of four circular buffers[1] with >80 year old stands
% of Larch Forest[1]	Proportion of the area in each of four circular buffers[1] with larch as the leading tree in the stand
% of Doug-fir Forest[1]	Proportion of the area in each of four circular buffers[1] with Douglas-fir as the leading tree in the stand
% of Canopy Cover >40%	Proportion of the area in each of four circular buffers[1] with stand canopy cover >40%
Average Stand Area (m^2)	Average area of all stands within circular buffer, stands are defined by each unique combination of age[2] and species[3] classification
Total Edge Length (m)	Total length of the edge of all stands within circular buffer, stands are defined by each unique combination of age[2] and species[3] classification

[1] Four circular buffers used to define explanatory variables (200 m, 500 m, 800 m, 1100 m)
[2] Three age classes defined: Initiation (0-40 years), Young (41-80 years), and Mature (80+ years)
[3] Seven species classes defined: Mixed Pine (Lodgepole pine leading by <80% canopy cover), Spruce-Balsam (Spruce or Sub-alpine fir leading), Larch (western larch leading), Pine (lodgepole pine leading and >80% of canopy cover), Deciduous (a deciduous tree species leading), Fir (Douglas-fir leading), other (a tree species other than those listed is leading), and non-forest (the polygon is not forested).

I reclassified digital forest cover information originally developed by the BC Ministry of Forests and Range and maintained by local forest licensees. I categorized stands by their dominant tree species and age class, and defined a *stand* as an area of forest composed of trees of relatively uniform tree composition and age. Age-classifications for stands that had not been harvested were based on projected age classes and projected canopy cover from the date of aerial photo interpretation, corrected for forest harvest by year. My classification of forest types was based on break points that I considered relevant to goshawks (Table 2). Seven tree species classes were defined. These are Mixed Pine (Lodgepole pine leading by <80% canopy cover), Spruce-Balsam (Spruce or Sub-alpine fir leading), Larch (western larch leading), Pine (lodgepole pine leading and >80% of canopy cover), Deciduous (a deciduous tree species leading), Fir (Douglas-fir leading), other (a tree species other than those listed is leading), and non-forest (the polygon is not forested). For each point I calculated the distance to the nearest road and the distance to the nearest recently harvested forest stand (<36 year old). I included these in my models as linear, rather than quadratic terms, as linear predictors better fit the data. A 30-m pixel size was used to determine all stand measurements and a 10-m pixel size was used to measure proximity variables.

I assessed the multivariate selection of explanatory variables using Information-Theoretic (IT) approaches (Burnham and Anderson 2002) and matched case-control multivariate logistic regression (Hosmer and Lemeshow 2000). I estimated the best plausible approximation of the information in my data, by assessing the relative Kullback-Leibler distance between multiple competing models (Burnham and Anderson 2002). I was able to assess the relative importance of only those variables I assumed to

be important to goshawks *a priori*. Unlike standard logistic regression, matched case-control logistic regression allows the pairing of used sites with comparison points. This pairing controls for the random effect between strata (nest-areas in this case) and reduces some autocorrelation problems typical of spatial and temporal data (Whittington et al. 2005; Hosmer and Lemeshow 2000). A matched case-control logistic model's interpretation is identical to standard logistic regression and, because the number of controls per case reduces error, I was better able to sample my unused areas by using multiple control points per case (Whittington et al. 2005, Manley et al. 2002, Hosmer and Lemeshow 2000).

I selected variables for inclusion in my candidate set of models by examining the collinearity between explanatory variables. For pairs of variables with Spearman rank correlations >0.7, I selected the variable that explained the greatest amount of variation in the data for inclusion in my candidate set (i.e., variable with the lowest AIC_c score: Burnham and Anderson 2002). For the nest-stand selection investigation, I removed variables that were deemed uninformative by examining the Wald statistic of the single variable statistical model and removing variables with a p-value <0.10. I developed my final set of candidate models for nest-site and nest-stand levels within two operating constraints: the number of explanatory variables needed to be 1/10 the number of observations (Peduzzi et al. 1996), and the number of candidate models (R) was required to be less than the number of observations (R<n [Burnham and Anderson 2000]).

I ranked candidate models in order of decreasing parsimony using Akaike's Information Criterion for small samples (AIC_c). Final models were developed using a model-

averaging approach for all variables from models with a <4 AIC-unit change from the most parsimonious candidate. Since I employed a *used versus unused* design, I assessed model fit by calculating the area under the receiver operating characteristic (ROC) curve (Boyce et al. 2002, Hosmer and Lemeshow 2000). All geographic analysis and data collection were performed in ARCGIS, ArcEditor 9.1 (Environmental Systems Research Institute, Redlands CA) and statistical analyses performed in R v.2.4.1 (R Core Development Team 2007).

Results

Thirty-six goshawk nest areas were located between 1998 and 2005, and females were observed incubating eggs in nests at 65 individual trees (Table 3). Nests were primarily in Douglas-fir (*Pseudotsuga menziesii*, 48%) and western larch (*Larix* spp., 32%) trees, with other nests located in lodgepole pine (*Pinus contorta*, 8.0%), spruce (*Picea* spp., 6%), and deciduous (4%) trees. The majority of nests were in trees that comprised the main tree canopy (62%), but additional nests were located in large old trees that reached above the main tree canopy (29%), and trees more than 10 m in height, but below the main canopy (9%). Generally, nests were located 1/3-1/2 of the way up the tree, usually on the first major branch whorl, and were always against the trunk of the tree. Nest trees occurred in six different biogeoclimatic subzones (31% dry moist, Interior Douglas-fir; 31% dry cool, Montane Spruce; 17% moist warm Interior Cedar-Hemlock; 15% moist cool, Interior Cedar-Hemlock; 6% dry cool, Engelmann Spruce-Sub-alpine Fir) and occurred in 8 different stand types (25% mature larch; 20% mature Douglas-fir; 23% mature spruce-balsam; 12% young mixed-pine or other stand type; 3% mature, pure-pine or deciduous; and 2% mature, mixed-pine). Neither nests nor comparison points

were located on any particular aspect relative to those available on the landscape (used mean = 94.2°, p-value 0.4312; unused mean = 88.0°, p-value = 0.2451). The average distance between nest trees within the 36 nest areas was 203.6 m (SE = 19.91, n = 96). I examined the vegetative cover by vegetation class and the height of tree canopy class (i.e., veteran, dominant, main canopy, and sub-canopy) variables to see if selection for these variables occurred at the nest site (Table 3). The height of tree canopy class variables and the cover of trees <10m in height (2 variables) were correlated with other variables and explained relatively less of the variation in my data (i.e., had higher AIC_c values than the remaining canopy cover variables), and were omitted from the final set of candidate models.

I examined all combinations of the remaining variables and each model received substantial support (Table 4), but when the models were averaged, the variables representing the canopy cover surrounding the nest tree had the strongest influence (Table 5). However, an examination of model fit provided an ROC score of 0.56, suggesting the model had no discriminatory power (Hosmer and Lemeshow 2000) and thus does not provide any information about selection.

Table 3: Mean values, standard errors (SE), and range of values for descriptions of the characteristics of goshawk nest trees and nest-tree level comparison plots within 200 m of the nest tree in southeastern British Columbia, Canada.

Variable (n)	Nest Plots			Comparison Plots		
	mean	SE	range	mean	SE	range
Nest Tree Diameter (cm, n=65)	49.5	1.99	17.0-91.0	-	-	-
Nest Height (m, n=65)	14.6	0.51	7.1-25.0	-	-	-
Nest Tree Elevation (m, n=65)	1283	23.3	865-1680	-	-	-
Nest Tree Slope (%, n=65,650)	18.0	1.00	1.9-34.5	-	-	-
Stand Canopy Cover (%, n=63, 466)	89.7	1.98	15.0-99.7	81.1	0.89	3.0-100.0
Tree 2-10m Canopy Cover (%, n=63, 466)	6.4	0.89	0.0-27.0	7.0	0.40	0.0-75.0
Tree <2m Canopy Cover (%, n=63, 466)	2.3	0.48	0.0-20.0	2.7	0.32	0.0-70.0
Small Tree Canopy Cover (%, n=63, 466)	8.7	1.2	0.0-40.0	9.7	0.64	0.0-100.0
Shrub Canopy Cover (%, n=63, 466)	12.2	1.8	0.0-75.0	14.7	0.79	0.0-95.0
Veteran Tree Canopy Height (%, n=17,95)	33.8	1.61	22.5-44.9	33.3	0.66	19.1-47.3
Dominant Tree Canopy Height (n=61,430)	27.9	0.81	18.1-42.0	26.8	0.31	15.3-85.2
Main Tree Canopy Height (n=48,369)	22.8	0.75	10.2-37.0	20.5	0.22	11.3-35.0
Sub-canopy Tree Height (n=33,236)	15.0	0.55	10.0-21.8	14.3	0.18	10.0-24.0

Of all variables examined at the nest-stand level, 22 were significant at the Wald <0.10 level (Table 6). Variables measured across different spatial grains were highly correlated. For each explanatory variable, I chose the spatial grain that explained the most variation in my data (i.e., had the lowest AIC_c value). Thus, the final variables included in my candidate set of models were percentages of the following forest attributes: mature forest stands at 800 m, larch leading stands at 800 m, Douglas-fir leading stands at 800 m, stands with canopy cover >40% at 200 m, and the average stand size within 500 m and the total length of stand edge within 1100 m. The distance to nearest water, permanent road, and recently harvested stand measurements were all included in the final set of candidate variables. To ensure I had ≥10 data points for each explanatory variable, I developed a set of plausible candidate models, each with <7 parameters (6 explanatory variables and 1 conditional requirement). In this set I included as many combinations of variable types as possible (i.e., stand type, canopy cover, age class, distance to landscape feature, and patch characteristics) and tested each variable individually. My final candidate set included 64 different models.

Table 4: Model negative log-likelihood (-loglik), number of parameters (K), Akaike's information criterion for small sample sizes (AIC_c), the change in Akaike's information criterion for small sample size from most parsimonious model (ΔAIC_c), and Akaike's weight (ω) for the final candidate set of models used to examine nest-tree selection by goshawks in southeastern British Columbia, Canada.

Model	-loglik	K	AIC_c	ΔAIC_c	ω
Stand canopy cover	122.74	2	249.68	0.0000	0.5077
Stand canopy cover + shrub canopy cover	122.37	3	251.14	1.4644	0.2441
Stand canopy cover + small tree canopy cover	122.74	3	251.88	2.1989	0.1691
Stand canopy cover + small tree canopy cover+ shrub canopy cover	122.37	4	253.41	3.7313	0.0786

Table 5: Model-averaged regression coefficients (β), standard errors (SE), Wald statistics (β/SE) and relative importance of explanatory variables (ω+). Selection based on $\Delta AIC_c<4$, and models are ordered by their decreasing explanatory strength (ω+). ROC = 0.5621.

Variable	β	SE	Wald	ω+
Stand canopy cover	4.7921e-02	1.4588e-02	3.28489	0.9995
Shrub canopy cover	-8.9139e-03	1.4078e-02	-0.63318	0.3227
Small tree canopy cover	-6.1493e-04	1.4299e-02	-0.04301	0.2477

ω+ indicated the sum of ω in the previous table

Table 6: Mean values, standard errors (SE), and range of values for descriptions of the characteristics of goshawk nest trees and nest-stand level comparison plots within 5 km of the nest tree in southeastern British Columbia, Canada.

Variable	Grain (m)	Nest Points (n=65)			Comparison Points (n=715)		
		Mean	SE	range	mean	SE	range
Dist to Road (m)	NA	170.4***	24.87	18.2-1509.0	486.1	24.90	0.3-4062.0
Dist to Water (m)	NA	249.3**	23.77	6.7-1058.0	198.6	7.26	0.0-1181.0
Dist to Harvest[1] (m)	NA	384.5***	68.05	0.0-3876.0	791.6	33.4	0.00-4007.0
% of young	200	14.3	3.02	0-100	18.7	1.14	0-90
	500	15.3	2.28	0-100	18.4	0.97	0-70
	800	16.8	2.32	0-100	18.0	0.88	0-70
	1100	17.8	2.30	0-90	18.0	0.82	0-70
% of mature	200	54.8*	4.06	0-100	47.3	1.34	0-1.0
	500	50.2**	2.80	0-100	43.9	1.07	0-80
	800	48.1**	2.45	0-100	42.9	0.94	0-80
	1100	45.3	2.35	0-100	42.3	0.85	0-80
% of larch leading	200	29.5	3.29	0-100	30.6	1.20	0-100
	500	31.1	2.18	0-100	34.5	1.01	0-80
	800	31.9*	2.01	0-100	36.0	0.88	0-80
	1100	6.6**	0.98	0-50	4.5	0.27	0-20
% of Douglas-fir leading	200	19.6	3.09	0-100	21.3	1.21	0-90
	500	22.6	3.03	0-90	19.6	0.98	0-80
	800	22.5**	3.04	0-90	18.7	0.88	0-70
	1100	21.3*	2.88	0-80	18.4	0.82	0-70
% of high-canopy-cover[2]	200	74.5***	3.38	0-100	55.0	1.31	0-100
	500	65.0***	2.82	0-100	52.4	1.08	0-100
	800	60.8***	2.52	0-100	51.5	0.95	0-90
	1100	58.2**	2.26	0-100	51.0	0.85	0-90
Average Stand Area (ha)	200	4.04***	0.342	0.97-13.00	5.20	0.140	0.63-13.00
	500	7.41***	0.432	1.78-15.70	16.00	0.706	0.68-78.52
	800	9.91***	0.594	2.01-22.34	24.04	1.520	1.26-200.00
	1100	11.61***	0.645	2.77-25.00	28.11	2.382	2.13-380.00
Total Edge Length (km)	200	45.75*	3.985	8.54-140.00	40.15	1.099	4.07-140.00
	500	75.50**	4.351	27.10-151.82	61.57	1.223	7.02-157.34
	800	97.78***	4.294	50.53-180.00	82.78	1.425	7.02-220.00
	1100	125.22***	4.906	58.38-200.00	104.96	1.752	7.60-270.00

Significance Levels (Wald) = *** <0.001, ** <0.05, *<0.10

[1]harvested stands are those logged within the last 36 years

[2]high-canopy-cover is all stands with canopy cover >40%

From my final candidate set, six different variables were included in plausible models (ΔAIC_c <4, Table 7) and these two models received considerable support (ω+=0.8833, Table 8). Only one additional variable (% mature forest within 800 m) was included in models that received any support (ΔAIC_c <10) and it was included in only one model that received little support (ω=0.0150). Goshawks selected nest sites with relatively more area of stands with >40% canopy cover within 200 m of the nest, for locations with relatively more stand edge within 1100 m, and locations with a smaller average stand size within 500 m of the nest. Goshawks preferred to nest farther from water features but closer to forest roads and recently-harvested forest stands (<36 years). The final model received an ROC score of 0.8311 suggesting excellent discriminatory power by this model (Hosmer and Lemeshow 2000).

Table 7: Model negative log-likelihood (-loglik), number of parameters (K), Akaike's information criterion for small sample sizes (AIC_c), the change in Akaike's information criterion for small sample size from most parsimonious model (ΔAIC_c), and Akaike's weight (ω) for plausible models used to examine nest-stand level selection by goshawks in southeastern British Columbia, Canada. Selection was based on $\Delta AICc$ <10

Model	-loglik	K	AIC_c	ΔAIC_c	ω
dist.rd[1]+dist.water[2]+dist.cut[3]+cc.200[4]+ area.500[5]+edge.1100[6]	104.23	7	224.43	0.0000	0.4857
dist.rd+dist.water+cc.200+ area.500+edge.1100	105.61	6	224.67	0.2430	0.3976
cc.200	107.73	2	228.90	4.4743	0.0495
dist.cut	109.34	2	229.69	5.2648	0.0334
dist.water	108.54	2	230.53	6.0970	0.0220
dist.rd+dist.water+dist.cut+ ma.800[7]+edge.1100	110.13	6	231.29	6.8573	0.0150

[1]distance to nearest road, [2]distance to nearest water, [3]distance to recently harvested forest stand, [4] % canopy cover >40% within 200 m, [5]average patch area within 500 m, [6]total edge length within 1100 m, [7] % of mature forest within 800 m.

Table 8: Model-averaged regression coefficients (β), standard errors (SE), Wald statistics (β/SE) and relative importance of explanatory variables ($\omega+$). Selection based on ΔAICc<4 and models are ordered by their explanatory strength ($\omega+$). ROC = 0.8311

Variable	β	SE	Wald	$\omega+$
% of cc.200[1]	0.0272	0.0075	3.63239	0.9328
distance to nearest water	2.5582e-03	8.8523e-04	2.91676	0.9203
distance to nearest road	-3.2108e-03	8.8820e-04	-3.61495	0.8983
length of edge.1100[2]	1.2794e-05	6.9184e-06	1.84938	0.8983
average patch area.500[3]	-1.3467e-05	4.3848e-06	-3.07185	0.8833
distance to harvested forest stand	-5.5737e-04	8.1224e-04	-0.68621	0.5341

$\omega+$ indicated the sum of ω in the previous table
[1]high canopy cover within 200 m, [2]total amount of stand edge within 1100, [3]average patch size within 500 m

Discussion

The goshawk nests I observed in this study were typical of those observed across the goshawks' range (Kenward 2006, Squires and Kennedy 2006). Douglas-fir and western larch were the most common trees used for nesting, and these species of trees often were the largest trees within the older forest stands, thereby providing good physical structure (i.e., branching structure) for nesting. The specific diameter and height reported for goshawk nest trees varies widely between biomes, but the birds have been reported to nest in trees with larger diameters and taller heights than other trees in the stand (Squires and Kennedy 2006). Ninety-one percent of nests I observed were in trees that were either part of the dominant tree canopy of the stand, or in trees relatively older and taller than the dominant trees.

I investigated whether selection occurred for higher canopy cover and lower understory cover at nest trees and although I developed a model to describe selection, it performed poorly at predicting nest-tree location within a stand. I assessed vegetative cover classes,

variables which have been identified by numerous studies throughout the goshawk's range as some of the best predictors of nest site location. For example, overhead canopy cover and understory cover have been found to be good predictors of goshawk nest site location within 200 m of the nest or 12.6 ha (Squires and Kennedy 2006). Overhead canopy cover may provide increased protection from predators and adverse environmental conditions, and lower amounts of understory vegetation may provide easy access to the nest and clear sight lines for hunting (Kenward 2006, Squires and Kennedy 2006). Thus, although I did not assess all possible variables influencing the selection of nest trees by goshawks, I did assess some of those that have been consistently associated with goshawk nest trees by other researchers. However, within this study and at this spatial extent, these commonly-identified variables were not strongly tied to the location of the nest site within a stand.

My results suggest that goshawks may not be selecting the features I examined at this spatial extent. I ranked the three variables that I hypothesized would be important in determining nest-tree location in a stand. My results suggested that overhead canopy cover explains the location of a nest within a stand better than understory vegetative cover. As mentioned above, this coincides with previous observations (Squires and Kennedy 2006). However, the identification of Akaike's best model ensures neither statistical nor biological significance (Guthery and Bingham 2007, Burnham and Anderson 2002). Thus, although my final model of nest site location may be the best that I could construct to predict nest location, it did not discriminate between my observed and comparison points. Thus, selection for particular resources may occur at the nest-site level and may very well be occurring for high canopy cover sites; however, high canopy

cover, by itself or with measures of understory vegetation, is neither the only nor the primary resource selected by goshawks at this spatial scale.

My final model describing nest-tree selection may have poor discriminatory ability because I did not examine the appropriate variables. A multitude of forest metrics may be assessed at the nest-tree level, but basal area has been shown to be a more important descriptor of nest stands than canopy closure in the northwestern United States (McGrath et al. 2003). However, basal area is extremely variable between study areas, and by itself may not be the best metric. Tree density must be considered in tandem with basal area to clearly describe the characteristics of a forest stand (i.e., small trees in dense stands and large trees in open stands may have the same basal area). Stand density has been reported more frequently in goshawk nest description studies, although numbers again vary widely (Squires and Kennedy 2006) with values both higher and lower at nest trees and stands than in surrounding forests. Any further examinations at this extent should consider basal area, tree density, and their interaction to provide a better picture of how these variables influence nest-site-level selection.

I found that selection did occur for nest stands with a number of stand- and patch-level descriptors of forests. At the nests I observed, goshawks selected for a greater amount of overhead canopy cover within 200 m of the nest, more stand edge within 1100 m of the nest, and smaller average stand size within 500 m of the nest. Goshawks placed their nests farther from water sources, closer to roads, and closer to recently-harvested forest stands comparison points. Although goshawks were selecting larger amounts of high canopy cover forest at all spatial grains, selection was strongest at the 200 m spatial

grain. Likewise, selection was strongest for the amount of stand edge and average patch size at all spatial grains, but the 1100 m and 500 m grains provided the greatest strength of evidence. Goshawks' avoidance of water features simply may be the result of nests being located away from riparian areas, as these areas have less understory vegetation and thus greater access to the nest outside riparian areas. Additionally, goshawks have been reported to use openings, such as roads and meadows, to improve access to the nest and my analysis identified two such variables: distance to the nearest road and distance to nearest harvested stand. However, selection by goshawks for sites that are closer to roads (mean = 170.4 m SE = 24.87, n = 65) and closer to recently-harvested stands (mean = 384.5 m SE = 68.05, n=65) suggests that these features were outside the nest stand.

My results further support the observations that large areas of continuous forest with *mature* characteristics may be less critical for nesting than previously supposed (see Kenward 2006 for review). For example, Daw and DeStephano (2001) found that late forest structure was important near the nest and that its importance decreased as one moved away. They also observed goshawks nesting near forest openings. Penteriani and Faivre (1997) examined site, stand, and landscape conditions surrounding nest sites in Italy, and found goshawks nesting in mid-elevation forests, at sites with high canopy closure, and larger trees. However, they measured crown closure, tree height, and the diameter of trees at 10 m intervals extending 150 m out from the nest tree and found that these metrics decreased quickly with distance away from the nest. Penteriani and Faivre (1997) also observed extremely high variability in the landscape values they examined beyond the nest stand. McGrath et al. (2003) found mature forest characteristics to be

important predictors of nest-site location at small scales (< 30 ha, 309 m radius circular buffer) and they identified 83 ha (514 m radius circular buffer) as the scale at which the structural conditions of the forest best predict nest-site location. My results support these findings. Thus, it appears that a core area exists around goshawk nests, within which the structural conditions of the stand provides adequate shelter and protection from predators for nesting (Kenward 2006), but that these characteristics combine with other features, such as forest openings, at distances beyond 200-500 m of the nest tree .

Little information exists on patch-level landscape characteristics selected by goshawks for nesting or foraging, and my results are only a first step in examining these relationships. McGrath et al. (2003) performed a rigorous multi-grain analysis of nest-site selection and found that many variables showed extensive overlap between scales, but that particular scales were more important than others at describing the influence of individual variables. They concluded that variables measured at different scales and in combination interact to provide the best descriptions of nesting habitat. My results concur, suggesting that different competing variables, all measured at different spatial grains, combine to describe the characteristics of the nest site. However, my definitions of forest stands may not be the most appropriate stand- and patch-level metrics. I used classifications of stand age (initiating, young, and mature) and common leading tree species to define stand boundaries, and thus total edge length and average stand size are variables derived from relatively minor changes in forest type resulting from the many possible combinations of age class and leading tree species. If these variables were defined using *hard* boundaries, such as the boundaries created by forest harvest between mature forest and recently harvested stands, they may provide a more pronounced

description of selection. These new classifications of forest stands could be combined with additional metrics. Connectivity and diversity metrics (McGarigal et al. 2002) could be combined with the area and patch variables I examined to explore different distributions of forest stands. Additionally, I defined *roads* as all permanent roads within my study area. This definition included many forestry and spur roads that see little traffic. Future analyses should classify roads with regard to their traffic volumes and right-of-way width.

CHAPTER 3: RESOURCE SELECTION AND MOVEMENTS OF FLEDGLING NORTHERN GOSHAWKS

Introduction

In raptors, the fledgling-dependency period (FDP) is a vital portion of the reproductive process (Newton 1979), linking the selection of territories by parents with the success of their offspring. Although during this time the young birds remain dependent on their parents for food, they begin traversing the post-fledging area (PFA) near the nest, learning to fly and hunt (Kenward et al. 1993a, Ward and Kennedy 1996, Dewey and Kennedy 2001). However, their limited flight skills early in this stage (Kenward et al. 1993a), coupled with their need to develop hunting skills, may increase the mortality from predation (Newton 1979, Kenward et al. 1993a; Weins 2004). It follows that the fitness of both the adult and juvenile birds will depend, to some extent, on the initial selection of the nest site and the manner in which the fledglings use the PFA during their transition from dependent nestling to independent juvenile.

For the northern goshawk (*Accipiter gentilis*), the PFA generally encompasses the nest tree of that year and may include a large portion of the *nest area* (Reynolds et al. 1992, Squires and Kenney 2006), which is the immediate area defended by adult birds during the breeding season (Figure 1, Chapter 1). The nest area is the combination of core area of forest surrounding all alternative nests in a breeding area (Chapter 2). Reynolds et al. (1992) first described an area corresponding to the post-fledging area (PFA) for goshawks, and since then it has received considerable attention; however, until recently this area has not been rigorously defined by direct observation of fledgling birds

(McClaren et al. 2005). The size of the PFA is presumably determined by the fledglings' ability to fly, the forest structure available to them, and their need to remain close to the nest. Thus, fledgling movements should be governed by a series of hierarchical choices, and as the age of the fledglings and their mobility increases, they are able to move farther from the nest (Kenward et al. 1993a, Kennedy and Ward 2003, Kennedy et al. 1994, McClaren et al. 2005). With improved flight capabilities, they are, in theory, able to progressively gain access to larger areas, but in some cases, they may become restricted by unsuitable forest types. However, the distances the fledglings travel away from the nest during the FDP do not expand indefinitely (Kenward et al 1993a, McClaren et al. 2005, Kenward 2006). Adults deliver food in close proximity to the nest, and if a fledgling remains in this area, it is assured food. Finally, if there are multiple fledglings from a single nest, competition for food will occur (Squires and Kennedy 2006), placing an emphasis on of each fledgling's ability to intercept the parent delivering food. The cessation of feeding by the parents appears to coincide with dispersal by the young goshawks, in approximately mid- to late-August (Kenward et al. 1993a, Kennedy and Ward 2003).

Previous studies have suggested that a combination of forest stand characteristics may be necessary for successful nesting by goshawks. The PFA is thought to be comprised of an area of mature forest with dense canopies and small openings, and it is intermediate in its landscape connectivity between the nest areas and foraging areas (Daw and DeStephano 2001, Mahon and Doyle 2003, McGrath et al. 2003). Additionally, the reduction or loss of forest connectivity around the nest may allow competitors or predators of goshawks to become established near nest stands (La Sorte et al. 2004), or

may reduce the amount of appropriately-structured forest around the nest to levels not tolerated during nest-site selection. However, some evidence suggests that goshawks may tolerate at least some disturbance around their nests (Kenward 2006, Squires and Kennedy 2006), but it is unclear how this tolerance relates to the nature of the disturbance and the minimum nesting requirements (Kenward 2006). Weins (2004) suggested that fledgling goshawks may require areas with dense understories in order to avoid predation. This suggested requirement is counter to the conditions thought to be selected by nesting adult birds, that is stands with open understories. Thus, goshawks may require a combination of both mature forest with open understories and either younger dense stands or older stands with dense understories.

Because of the obvious relationship between the PFA and goshawk reproductive success, the management of forests for this species has relied to a large extent on the description of both the PFA and the nest area. Protection of goshawk nesting opportunities is primarily concerned with reducing the disturbance around existing nest areas and their possible PFAs. In the southwestern United States, Reynolds et al. (1992) suggest that management targets a 120- to 240-ha area of forest with canopy cover >50% and well-developed understories. They also suggest that this area should be managed to maintain habitat attributes of the critical prey species of goshawk in the region. In coastal British Columbia, McClaren (2004) suggests the management of a 200-ha *core area* surrounding each nesting area, where there is no road construction, or forestry activity. She also suggests, where necessary, the management treatment surrounding the core area, to reduce external disturbance (e.g., wind throw) in core area. Although the PFA is thought to include areas of increased cover for fledglings to escape

predation, both sets of management recommendations call for the management of the core area for only nesting characteristics and not for fledgling escape cover, since they focus on existing nest sites that presumably were already recognized by goshawks to contain appropriate PFAs. Additionally, only limited information and general guidelines are available for the long-term or landscape-level management of nest areas. Thus, proactive management guidelines are required that help create or maintain the number of nest areas on the landscape, to compensate for the change in forests over time, and after both natural (e.g., pest infestation and/or fire) and anthropogenic disturbance. A better understanding of the function, composition, and size of the PFA will help guide the development of management guidelines, and provide a better understanding of goshawk breeding requirements (Kenward 2006) that can account for these long-term and large-scale changes.

Estimates of PFA size vary considerably, but studies estimating PFA size through direct observation of fledgling movements have produced consistent trends. The PFA has been estimated at ca. 168 ha in New Mexico (Kennedy et al. 1994, n=16), ca. 19 ha in north-central British Columbia (Mahon and Doyle 2003, n=34), and 59 ha in size on Vancouver Island British Columbia, for the Queen Charlotte goshawk (ssp. *laingi*) (McClaren et al. 2005; n=15). PFA size presumably varies with local conditions (Squires and Kennedy 2006), but the large difference in Kennedy et al.'s (1994) estimate may result from their use of adult female movements and a circular buffer to estimate PFA size, rather than the strict use of fledgling movements (McClaren et al. 2005). Despite this, many management recommendations have used the 170-ha area as representative of the PFA when examining selection of forest characteristics by goshawks during nesting

(e.g., Daw and DeStephano 2001; Finn et al. 2002, McGrath et al. 2003), as it is presumed that adult goshawks are selecting a nest site that would benefit their young. This large circular area may include many of the alternative nest sites within that nest area and a great portion of the PFA, but the relationship between the PFA, nest site, and nest area remains uncertain (McClaren et al. 2005). For example, managing for a single nest tree or only for the nest area may not include all the features important to goshawk nesting over many years (McClaren et al. 2005).

Potential problems with using larger, non-spatial estimates of the PFA come into play when analysing the types of forests required by fledglings. The PFA may not be described by the same forest characteristics that describe the nest tree (Chapter 2) or nest area (Chapter 2). Again, most multi-scale, resource selection studies of goshawks use a 170-ha (736-m) circular buffer to approximate the PFA (Daw and DeStephano 2001, Finn et al. 2002, McGrath et al. 2003), and then characteristics measured at this grain are compared to other sites to describe adult selection of a nest site within the PFA (Chapter 2). However, smaller areas may better describe the core area around goshawk nest trees that adult birds select for their mature forest characteristics (e.g., 83 ha McGrath et al. 2003 131 ha, La Sorte et al. 2004 24 ha, Chapter 2). Thus, the 170-ha area surrounding the nest may be comprised of a diversity of forest types including young to old seral stages and the PFA may not be completely composed of forests with mature characteristics. Additionally, circular buffers may not adequately describe how fledgling goshawks travel around the nest site (Kenward et al. 1993a, McClaren et al. 2005). To accurately describe the PFA, assess how fledgling travel within it and ultimately to

determine its function, detailed comparisons of the areas where fledglings are observed to the areas available to them are required.

The objective of my study was to monitor the movements of fledgling goshawks as a means of quantifying the PFA, but more specifically, to investigate how the characteristics of the forests surrounding the nest tree are selected by fledgling goshawks. In addition to describing the patterns of resource selection by fledglings, I provide a preliminary examination of how the movements of fledgling birds correspond to the direction that adult female birds travel away from the nest. I conducted my research in southeastern British Columbia, Canada, as previous goshawk monitoring efforts in this region provided a relatively large sample of nests at which to observe fledglings, and because this region is composed of a diverse range of forests that has seen considerable and ongoing forest harvest (Chapter 1).

I observed the movements of fledgling northern goshawks (ssp. *atricapillus*) and documented forest characteristics of the areas they used in order to identify the resources that were important to them in their PFAs. I predicted that fledglings would select PFAs within forest stands that had a larger amount of high canopy cover forest and a larger proportion of young forest: both of these would provide cover from predation. I further hypothesized that fledglings would select their PFAs based on characteristics important to their parents in selecting a nest site, such as the area of the primary tree species of the stand, the area of mature forest, and the distance to permanent roads and recently harvested forest stands. Furthermore, I hypothesize that fledgling goshawks adjust their movements not only in relation to the characteristics of the forest, but in response to the

behaviour of their parents. Briefly, I explore the supposition that fledglings will move away from the nest in order to intercept mothers.

Methods

From 2003 to 2006, I captured and radio-tagged fledgling and adult goshawks in the East Kootenay region of southeastern British Columbia, Canada. Birds were located by identifying active nests through an annual nest monitoring program (Harrower et al. 2004). I chose to radio-tag birds at nest areas offering a range of amounts mature forest stands (>80 years old) within 500 m of the nest. Not all nest areas have continuous mature forest surrounding the nest, and I therefore attempted to select sites with clear boundaries between young (41-80 years) and mature (>80 years) forest (Table 2). These selection criteria provided a clear contrast to fledglings between suitable and unsuitable areas. I monitored active nests using binoculars and spotting scopes over a minimum of two days in order to target the age of the nestlings (following Boal 1994), and determine the most effective date of capture of both adult and fledgling birds.

When nestlings were approximately 20-25 days old, I accessed the nest in order to radio-tag the young birds. The adult female goshawks were netted by prompting the birds to fly into a modified Dho-gaza trap, using as a lure either a captive tame Great Horned Owl (*Bubo virginianus*), or a robotic replica. The adult females were outfitted with an 18-g backpack style radio-transmitter (Biotrack Limited, Dorset UK, Model# TW51 with mortality switches) and banded with USFW Service and colour auxiliary bands (Acraft Sign and Nameplate Co. Ltd. Edmonton, AB, Canada). All nestlings were outfitted with a colour auxiliary band (Acraft Sign and Nameplate Co. Ltd. Edmonton,

AB, Canada), a USFW Service silver metal band, and a 9-g, tarsal-mounted, radio-transmitter equipped with a mortality sensor (Advanced Technology Services, Isanti, MN, USA). Leather jesses were used to attach radio-tags and were designed to allow the bird to remove the transmitter after the transmitter had failed (McClaren et al. 2005). The sex of each bird was determined with tarsal width measurements, following Kenward et al. (1993a).

Nestlings were monitored until they dispersed from the PFA. I recorded *fledge date* as the first day that a nestling was observed perching on a tree other than the nest tree, and marked the initiation of dispersal after locating the bird farther than 1.6 km from the nest site for two consecutive days (Weins 2004). All locations on fledglings were obtained by homing in on their location using radio-telemetry receivers (Communications Specialists Inc. R-1000, Orange, California) until the bird was sighted. The location was recorded in a handheld GPS unit (Garmin 76GPS or 72GPS, Global Positioning System, GARMIN Corporation, Olathe, Kansas) by averaging 100 successive locations and until the variance reached some minimal target of under 15 m. When possible, an external antenna (GPS 17-HVS GPS Sensor; GARMIN Corporation, Olathe, Kansas, USA) was used to increase the accuracy of locations. All attempts were made to minimize the disturbance to fledglings. Many locations were recorded by marking the location of the bird and determining the coordinates at a later time.

Two monitoring schedules were followed to determine the location of fledgling birds. First, I attempted to locate all fledglings at least once per day in order to document their broad-scale movements within the PFA. These data were used to define the PFA and to

determine which forest characteristics the fledglings were selecting. To supplement this information and to provide data for future investigations of the fine-scale movements of fledglings (Harrower unpublished data), I performed a series of short-term, intensive monitoring sessions at selected sites. During these daily sessions, fledglings were located hourly. I document movements from one hour before and one hour after these times, and the timing of sunrise and sunset were determined by standard local calculations.

Preliminary observations of fledgling movements suggest that fledglings made a movement >30 m no more than once per hour. I therefore used this as the minimum distance for achieving a valid trade-off between location and/or forest cover error and movement patterns (Jerde and Visscher 2005). Additionally, I observed that fledglings were able to traverse the entire PFA available to them during any one movement. Thus, hourly locations were assumed to be biologically independent, and I used the locations collected during the intensive monitoring sessions to supplement the other non-focal data. Although this rationale may be subject to debate, the information gained by increasing the number of locations used in the analysis, for a life-history stage of limited duration, supports a more liberal approach to statistical independence (Kernahan et al. 2001).

Adult goshawks were relocated opportunistically throughout the FDP and their locations determined through standard triangulation techniques of >3 strong bearings (Kenward 2001). Bearings were plotted on 1:20 000 topographic forest cover maps and the most probable location determined. Following assessment of the blind re-location of

stationary transmitters, and through the estimation of the quality of plotted bearings, I estimate the average telemetry error to be 316 m (SE = 52.3, n = 22), which was an error estimate I felt adequately placed birds within forest stands. My goal in the location of adult birds was simply to document their general location as I did not intend to analyze their fine-scale movements or resource selection.

All locations were entered into a Geographic Information System (GIS) for subsequent data collection and analysis. The Euclidean distance and bearing to the nest was calculated for each location. I estimated the 95% fixed kernel home range sizes for each fledgling using program HOME RANGER (version 1.5, Ursus Software, Revelstoke, BC Canada). Kernel home ranges were calculated using an *ad hoc* estimation of the smoothing parameter and error rates were obtained from bootstrap estimates derived from 1000 repetitions. Because a different nest could be used in the same nest area in different years, forest structure within 500 m of active nest trees could differ between years due to logging, and sibling fledglings exhibited a high degree of overlap in their movements. I pooled all locations from radio-tagged siblings in the same year.

I quantified selected variables in order to describe the characteristics of the PFA, and compared them to randomly located comparison points, during both the early (<21-days post-fledging) and late (≥21-days post-fledging) period. I chose these scales because they represented the areas available to fledglings during different life-history stages (pre- and post-hard-penning of feathers). I chose specific radii from the nest to estimate resource availability, based on my observations of fledglings' movements. I used five randomly chosen comparison points for each telemetry location, and assessed all

locations collected during either the early or late time periods during analyses. To measure resource variables (Table 1, Chapter 2), I reclassified digital forest cover information by categorizing stands by their dominant tree species and age class using data developed by the BC Ministry of Forests and Range from air photo interpretation. I defined a *stand* as an area of forest that is composed of trees of relatively uniform tree composition and age. Age classifications for stands that had not been harvested were projected age classes from the date of aerial photo interpretation and corrected for forest harvest by year (see Chapter 2).

For each location or comparison point, I calculated the distance to the nearest permanent road and distance to nearest harvested forest stand <36 years old. I included these in my models as linear, rather than quadratic terms, as linear predictors better fit my data, and thus I assume a linear response of goshawk to my proximity measurements. Young forest stands were defined as those stands between 41- and 80-years of age and mature stands were >80 years old. Non-forested stands were those that were either logged within the last 10 years or where no forest occurs (e.g., wetland or other opening). I classified high canopy cover stands as those canopy cover >40% estimated from aerial photo interpretation as this was the mean canopy cover present in my study area. Larch, Douglas-fir, and pine stands were those with *Larix* sp., *Pseudotsuga menziesii*, or *Pinus contorta* as the leading tree species, respectively.

I conducted a multivariate analysis of explanatory variables using Information-Theoretic (IT) approaches (Burnham and Anderson 2002) and matched case-control multivariate logistic regression (Hosmer and Lemeshow 2000). I estimated the best plausible

approximation of the information in my data, by assessing the relative Kullback-Leibler distance between multiple competing models (Burnham and Anderson 2002). Unlike standard logistic regression, matched case-control logistic regression allows the pairing of used sites with comparison points. This pairing controls for the random effect between strata (nest areas in this case) and reduces some autocorrelation problems typical of spatial and temporal data (Whittington et al. 2005; Hosmer and Lemeshow 2000). The interpretation of a matched case-control logistic model is identical to standard logistic regression (Whittington et al. 2005, Manley et al. 2002, Hosmer and Lemeshow 2000).

I selected variables for inclusion in the set of candidate models by examining the collinearity between explanatory variables. For pairs of variables with Spearman rank correlations >0.7, I selected the variable that explained the greatest amount of variation in the data for inclusion into my set of candidate models. I developed my final set of candidate models for each FDP time period while working within two constraints: the number of explanatory variables needed to be <1/10 the number of observations (Peduzzi et al. 1996), and the number of candidate models needed to be less than the number of observations (R<n; Burnham and Anderson 2000). I ranked candidate models in order of decreasing parsimony using Akaike's Information Criterion for small samples (AIC_c). Final models were developed using a model-averaging approach for all variables, from models with a <4 AIC-unit change from the most parsimonious candidate. I assessed model fit by calculating the area under the receiver operating characteristic (ROC) curve (Boyce et al. 2002, Hosmer and Lemeshow 2000).

I compared the movements of fledglings to female parent location and to the primary forest type variables identified by my previous resource selection analysis. I used the Watson test and Q-Q plots to see if the fledgling movements fit the von Misses distribution (the circular distribution is analogous to the normal distribution) and Rayleigh's general unimodal test to determine if the movements were directional (Zar 1999). I compared the movement direction of fledglings to the geographic mean of adult female locations and the variables selected by fledglings using Rayleigh's test with a specified mean direction (Zar 1999). All geographic analysis and data collection were performed in ARCGIS, ArcEditor 9.1 (Environmental Systems Research Institute, Redlands CA) and statistical analyses performed in R 2.4.1 (R Core Development Team 2007).

Results

During the breeding seasons of 2004, 2005, and 2006, I radio-tagged 34 fledgling goshawks, and 20 adult female goshawks at 15 nest sites, in 10 nest areas. Twenty-six of these nestlings survived to disperse from the PFA. Of the eight nestlings that did not survive, four were preyed upon by either an avian or mammalian predator prior to fledging, and three were killed by avian predators after fledging and were not eaten, plucked, or otherwise disturbed. One female fledgling starved to death. This bird had two female siblings and died during a mid-summer snow storm. Only 2 of the 17 (11.8%) nests did not produce fledglings after adult females were seen incubating eggs. At both of these sites a single nestling hatched, and then was killed by a mammalian predator prior to fledging.

I recorded the location of fledglings 1148 times with an average of 44 locations/fledgling (SE = 1.4, range = 24-81) and 77 locations/PFA (SE = 1.7, range = 29-158). Ninety-five percent of the fledglings' locations were within 450 m of the nest (mean = 168, median = 126, SE = 4.3, n = 1148). Within the first 21-days after fledging (when feather growth and hardening was not completed), 95% of locations were within 298 m of the nest (mean = 120, median = 94, SE = 3.7, n = 713). Locations recorded 21-days post-fledging, but while the fledglings were still in the FDP, were within 525 m of the nest 95% of the time (mean = 246, median = 201, SE = 8.2, n = 435). Although I located fledglings farther from the nest following the completion of feather development, all of the birds returned frequently to the area surrounding the nest site. This behaviour was highly variable between sites and individuals, but fledglings did spend considerable time close to the nest tree. I determined the azimuth of each fledgling's location from the nest tree, and compared the mean azimuth between siblings at sites with more that one fledgling. No differences were observed between siblings so I pooled all locations from each nest area (88.48%, SE = 5.83, range = 77.08-97.69%, n = 10). Fledglings' movements from the nest were directional at all nest areas but one (Table 9).

An average number of 77 locations per site (SE = 9.7, range = 29-158, n = 15) was used to estimate 95% fixed kernel PFA sizes (Table 10), which ranged from 10.3 ha to 70.9 ha (mean = 36.7 ha, SE = 6.58, n = 15). Since all locations were used to calculate PFA size, I estimated the degree of independence between points using Swihart and Slade's Independence Index (Kernahan et al. 2001). The values of this index ranged from 0.00 to 2.56 across nest areas, suggesting a low autocorrelation between points, and supporting

my previous observation that individuals were able to traverse their entire range between relocations.

Table 9: Summary of the directional movements of fledgling goshawks observed from 2004-2006 at nest trees located in southeastern British Columbia, Canada. Fledgling locations were pooled by nest area and year. The only non-significant movement away from the nest tree was at WB4_2004 ($p=0.14$). All other p-values were <0.001 except TP2_2006 ($p=0.0220$).

Breeding Area	Mean Azimuth (deg)	Circular Variance	n
BT4_2005	35	0.086	153
CO3_2005	101	0.605	71
GC1_2006	22	0.205	29
GC2_2005	27	0.227	68
JC2_2004	75	0.309	69
KS6_2005	147	0.585	104
MD1_2005	117	0.659	158
MD2_2006	162	0.192	65
RM4_2004	47	0.553	92
RO2_2004	889	0.389	38
SW3_2004	15	0.488	68
TP2_2004	42	0.617	83
TP2_2006	36	0.732	53
WB1_2006	117	0.594	51
WB4_2004	79	0.794	46

I examined nine attributes of PFA's (Table 11); however, areas with a high percentage of non-forest area were strongly avoided, and thus were removed from the overall analysis. The percentage of non-forested area was by far the greatest predictor of PFA location, receiving the largest amount of support when compared to other candidate models ($AIC\omega = 0.9769$). From the remaining variables, five plausible variables were identified and model averaging was used to produce a predictive equation from locations collected during both the early- and late-PFA (Table 12-13). When selection during the early FDP was examined (298 m from the nest) the area of non-forest ($AIC\omega = 0.6079$) and the distance to nearest harvested forest stand ($AIC\omega=0.3217$) were the only

plausible variables, receiving a combined support of 92.9% over all other models. During the late FDP (525 m from the nest) the area of non-forest (AICω = 0.8235) and area of forest with canopy cover greater than 40% (AICω = 0.1541) were the only plausible variables combining to receive 97.8% of the support over other models. Fledglings avoided areas of non-forest while selecting for areas with high canopy cover.

Table 10: Estimated post-fledging areas for northern goshawk (n=15) in southeastern British Columbia, Canada, calculated with 95% fixed kernel home ranges with an *ad hoc* estimate of the smoothing parameter, using program HOME RANGER.

Nest Tree	n	95% Fixed Kernel (ha)	Bootstrap (SE)	Bootstrap Range (Max, Min)
BT4_2005	153	20.23	1.166	23.05, 30.13
CO3_2005	71	32.45	2.359	32.10, 47.28
GC1_2006	29	28.32	2.669	25.30, 43.70
GC2_2005	68	21.31	1.481	19.25, 29.36
JC2_2004	69	10.31	0.753	10.44, 14.82
KS6_2005	104	23.12	1.460	25.18, 35.21
MD2_2006	65	36.29	2.851	35.62, 53.18
MD1_2005	158	43.15	2.279	42.49, 60.31
RM4_2004	92	22.77	1.506	22.05, 31.66
RO2_2004	38	15.28	1.523	14.23, 23.69
SW3_2004	68	70.88	5.714	69.65, 103.99
TP2_2006	53	22.64	2.071	23.06, 37.95
TP2_2004	83	15.30	1.007	14.24, 20.36
WB1_2006	51	70.16	6.148	73.41, 107.39
WB4_2004	46	50.19	4.158	43.72, 69.76

Table 11: Summary of average measurements for each explanatory variable used in resource selection analysis to determine selection by northern goshawk fledglings in southeastern British Columbia, Canada. Available areas were defined as the entire area within a 525 m radius of the nest.

Variable	post-fledging area (n=11)			available area (n=11)		
	mean	SE	range	mean	SE	range
% larch stands	39.54	11.486	0-95	32.07	8.485	0-78
% Douglas-fir stands	22.44	11.157	0-100	25.29	9.748	0-90
% pine stands	22.11	9.134	0-84	15.82	6.387	0-62
% >40 canopy cover stands	88.81*	05.425	39-100	78.37	5.035	51-100
% young stands	38.53	12.675	0-97	26.74	9.799	0-88
% mature stands	54.68	13.107	3-100	51.73	10.334	8-94
% non-forest stands	6.66	2.370	0-24	21.26	4.889	3-51
distance to road	191.2	26.60	103.0-396.0	199.3	31.67	75.8-369.1
distance to harvest <10	295.3	108.32	38.7-1161.9	272.8	110.04	28.0-1178.9

Significance Levels (Wald) = *** <0.001, ** <0.05, *<0.10

Table 12: Model negative log-likelihood (-loglik), number of parameters (K), Akaike's information criterion for small sample sizes (AIC_c), the change in Akaike's information criterion for small sample size from most parsimonious model (ΔAIC_c), and Akaike's weight (ω) for plausible models used to examine resource selection by fledgling goshawks during the entire dependency period in southeastern British Columbia, Canada. Plausible variables have $\Delta AIC_c<4$.

Model	-loglik	K	AIC_c	ΔAIC_c	$AIC\omega$
% young stands	4.7118	2	13.6173	0.0000	0.3796
% >40 canopy cover stands	5.2173	2	14.6281	1.0108	0.2290
distance to harvest	5.7430	2	15.6796	2.0623	0.1354
% larch stands	6.0872	2	16.3679	2.7507	0.0959
% pine stands	6.3110	2	16.8154	3.1982	0.0767
% fir stands	7.1008	2	18.3952	4.7780	0.0348
% mature stands	7.4104	2	19.0145	5.3973	0.0255
distance to road	7.5138	2	19.2211	5.6039	0.0230

Table 13: Model coefficients (β), standard errors (SE), Wald statistics (β/SE) and relative importance of explanatory variables (ω) of plausible variables from the analysis of resource selection by fledgling goshawks during the entire dependency period in southeastern British Columbia, Canada. Plausible variables include all variables with $\Delta AIC_c<4$ and models are ordered by their explanatory strength (ω). ROC = 0.7335

Variable	β	SE	Wald	AICω
% young stands	0.1660	0.12700	1.3070	0.4141
% >40 canopy cover stands	0.1060	0.06490	1.6333	0.2498
distance to cut	0.0510	0.03890	1.3111	0.1477
% larch stands	0.8650	0.06010	1.4393	0.1047
% pine stands	0.9780	0.08340	1.1727	0.0836

The movements of fledglings and female parents were correlated at the majority of nest sites (Figure 5). At six of eight nest sites, the direction the PFA was offset from the nest was the same as the direction to the geographic center of the female parents' locations (Table 14). At only 4 of 11 nest sites was the direction to young forest the same as the direction of PFA offset from the nest. At these four sites the area of young forest within the PFA was extremely low, measuring between 0 and 10% of the PFA and between 0 and 4% of the available area. The direction of stands with canopy cover >40% was the same as the direction the PFA was offset from the nest at 4 of 11 nest sites. At these four sites, the amount of high canopy cover was high, measuring >94% of the PFA and >83% of the available area. However, the amount of high canopy cover stands within both PFAs and available areas was high in nearly all cases. At the single nest area where I estimated the PFA in multiple years under consistent forest cover, the direction the PFA was offset from the nest site was the same (rbar = 0.2143, $p<0.001$, n = 158,65) across years despite the fact the parental birds used different foraging sites.

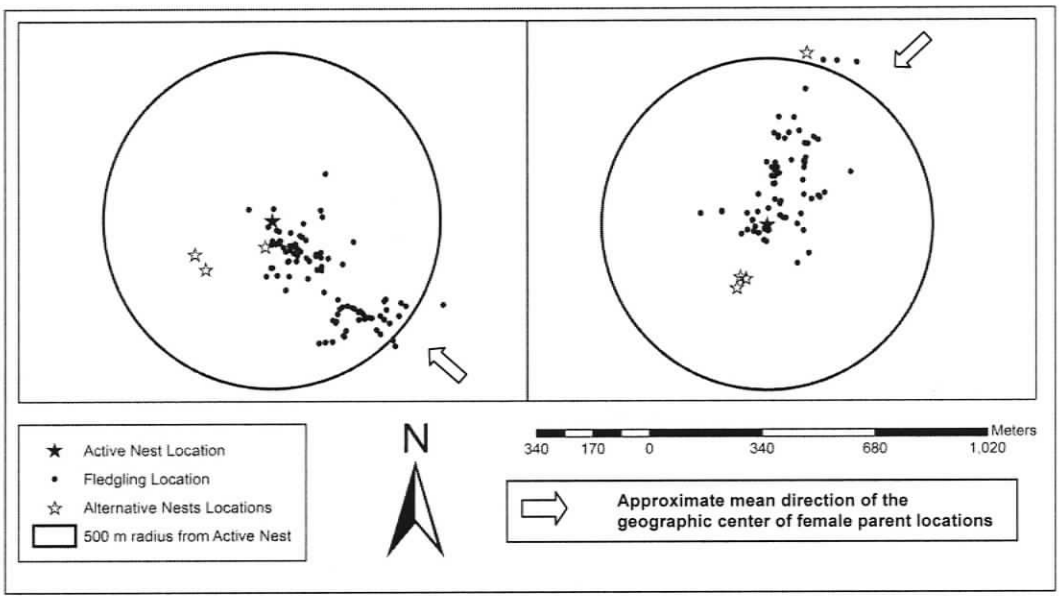

Figure 5: Two representative northern goshawk nest areas traversed by fledglings in southeastern British Columbia, Canada. Post-fledging areas are offset towards the geographic center of their mother's breeding season locations and do not necessarily encompass alternative nest sites.

Table 14: Number of locations and probability values for the similarity between the geographic center of the female parent's relocations, the proportion of highly-selected resources in post-fledgling areas (PFA), and proportion of resources available to fledglings (avail) at each nest site. Data are from observations of goshawks from 2004 to 2006 at selected nest sites in southeastern British Columbia, Canada

Nest sites	Fledgling Sample Size	Adult Sample Size	p-value[1]	% young PFA	% young avail	% cc PFA	% cc Avail
BT4_2005	153	11	<0.001***	0.0***	0.0	98.0***	83.4
CO3_2005	71	9	0.039**	73.2	54.6	39.4	60.6
JC2_2004	69	-	-	66.7	27.5	98.6	86.7
KS6_2005	105	-	-	1.0	5.8	89.7	51.7
MD1_2005	158	11	0.005**	96.2	88.0	98.7	92.9
MD2_2006	65	-	-	96.9	76.9	100	85.5
RM4_2004	92	16	0.083***	0.0***	3.7	100***	100
RO2_2004	38	21	0.143	0.0***	0.00	97.4	86.3
SW3_2004	68	15	0.027***	73.5	30.9	76.5	50.6
TP2_2004	-	13	0.945	-	-	-	-
WB1_2004	51	24	0.078*	9.8***	2.0	94.1***	88.2
WB4_2006	46	-	-	6.5	4.8	84.8	76.1

Significance Levels (Wald) = *** <0.001, ** <0.05, *<0.10

[1] p-value from Rayleigh test of the mean direction of fledgling movements with the center of breeding season movements

Discussion

My observations of fledgling goshawk movements are similar to those made previously at other locations (Kenward et al. 1993a, Kennedy et al. 1994, McClaren et al. 2005). However, fledglings continued to visit the area immediately around the nest during the entire FDP. I did not observe a dramatic change in the movement patterns of fledglings. Likewise, I observed that fledglings did not shift their center of activity, but rather expanded their range as the FDP progressed. In Sweden, Kenward et al. (1993a) reported fledglings were always within 1000 m of the nest, with the majority of locations within 800 m; 91% of the observations made by Kennedy et al. (1994) in New Mexico

were within 800 m of the nest; and nearly all of the observations made by McClaren et al. (2005) on Vancouver Island (ssp. *laingi*) were within 800 m. However, the majority of locations from all of these studies were within 600 m of the nest. I observed very few locations greater than 800 m from the nest, with 98.6% of locations within 600 m. These data suggest that fledgling goshawks limited the distance they will move from the nest. Even after obtaining full flight capability, fledglings are attracted to the nest site presumably because this is a central location to obtain food from their parents.

Variability in movement patterns may result from fledgling sex, sibling competition, and forest structure around the nest. Kenward et al. (1993b) reported that although male and female patterns did not seem to differ during the early FDP, males were near the nest less often in the later stages of the FDP. However, these results varied with the sexual composition of the brood (Kenward et al. 1993b). McClaren et al. (2005) speculated that differences in the sizes of PFA estimates between Vancouver Island and New Mexico may have resulted from their almost exclusive use of female birds to estimate the PFA and from the influence of distinct forest edges in restricting movements within their study area. I did not test for differences in movement patterns between the sexes, because at all sites the sibling fledglings showed a large correlation in their movements.

My estimates of PFA size (36.7 ± 6.6 ha) differs slightly from those reported elsewhere (Mahon and Doyle 2003, Kennedy et al. 1994, McClaren et al. 2005) because of sampling methods or local environmental conditions (see Methods). I sampled all fledglings arising from a particular nest, and collected a large number of radio-telemetry-aided visual locations at each site thereby directly estimating the size of the

PFA. At no time did I attempt to locate a fledgling and fail. Only the McClaren et al. (2005) study has used similar methods to mine in order to avoid error in PFA estimation associated with the unaided relocation of fledglings; however, in that study a lower number of locations per site (mean = 17.8 ± 0.6) were collected, possibly under-sampling and thus not estimating of PFA size correctly. Mahon and Doyle (2003) used a combination of visual observations and radio-telemetry relocations, and found no difference between the location of radio-tagged birds and visual search methods for untagged birds. However, without radio-tags, it is difficult to determine if fledglings are being disturbed when entering the stand, raising the possibility of bias in PFA size estimates. Thus, my methods are more rigorous than previous studies and reduce many of the sources of error previously identified.

I account for potential sources of error by using a large number of relocations on all fledglings arising from a nest, and by obtaining radio-telemetry assisted locations to reduce disturbance. Despite differences in methods, my estimates fall within the range of those reported by both McClaren et al. (2005) and Mahon and Doyle (2003), suggesting similar PFA sizes across British Columbia. Local conditions around the nest, such as forest type or forest openings, may account for differences both within and between studies. Additionally, fledgling movements may be influenced by both the movements of their parents and siblings and the local forest conditions that determine the nature of the PFA at a particular site. Thus, future investigations should concentrate on the location of the PFA and how it is offset from nest sites.

If the variables shown here to be important to the selection of forests by fledglings are compared to those identified as being important to adults during nest-site selection (Chapter 2), it appears that the fledglings selected different forest characteristics than their parents. My analysis suggests that 5 of the 9 variables (Table 11) were useful in describing the PFAs used by fledglings; however, 2 of these variables (the % of larch leading stands and the % of pine leading stands) may be dependent on the prior placement of the nest site by adult birds (Chapter 2). Thus, fledglings selected, first and foremost, to avoid areas with a high percentage of non-forested area. Secondly, fledglings selected areas with a larger percentage of younger stands and areas with a larger percentage of high canopy cover forest. However, at the scale of the PFA, the types of forest surrounding the nest are limited, and thus selection for forest type may simply be an artefact of nest-site selection by adults. In short, nest-site selection by the parent(s) logically dictates the set of choices available to the fledglings. However, my data show differences in the types of forests fledgling select within what was available as determined by their parents.

Despite differences in which variables were selected during early, late, and total stages of the FDP, I suggest that a combination of 3 resources (% canopy cover, % young forest, and % non-forest) best predict PFA location. I observed differences in selection between the total, early, and late FDPs and these differences may be the result of sampling intensity and the high selection against areas of non-forest. During all periods, fledglings were not found in non-forested areas. However, I did document selection for other variables. During the early FDP, the distance to the nearest harvested stand was a plausible variable, suggesting that young fledglings prefer forest interiors, presumably

where the risk of predation is reduced. During the late FDP, fledglings selected areas with less non-forest and more, high canopy cover forest. However, as fledglings became more mobile, I often observed them close to forest edges, experimenting with flight and hunting techniques. The identification of young forest as an explanatory variable when early and late period locations are pooled may result from the increased resolution provided by the larger sample size obtained by pooling locations. Selection for young forest simply may result from the restriction of forest types available to fledglings attempting to avoid non-forested areas. However, the area of young forests observed around nests was not identified as a plausible variable at any spatial grain in my investigations of nest-stand selection.

My analysis of the correlation between fledgling movements and those of their mother is far from conclusive, it suggests that although forest structure provides the set of locations available to fledglings, their specific movements are determined to some extent by intra-family interactions. At the majority of sites, fledgling movements were offset in the same direction from the nest as their mothers foraging area. Likewise, when I examined the forest structure variables selected by fledglings, I found only a limited number of cases in which the direction to the forest structure and the offset of the PFA were the same. Adult male goshawks do the majority of the hunting during the breeding season (Kenward 2006, Squires and Kennedy 2006), but food deliveries to the nest are presented to the adult female in many cases (Kenward 2006, personal observations) and the female then transfers this food to fledglings. Even if the mother does not feed the fledglings regularly during the FDP, fledglings have much more interaction with their mother during the FDP as she generally remains much closer to the nest site (Kenward

2006, Squires and Kennedy 2006). Because of this, and because I had a larger amount of data on adult female movements than on adult male movements, I examined how the direction of fledglings' movements related to the geographic center of female locations during the FDP. My assessments of the correlations between the movements of fledglings and adults are far from complete; however, they do point towards the need for more investigation into the causes of fledgling movements.

CHAPTER 4: SUMMARY AND CONCLUSIONS

The major findings of my thesis are: (1) a core area exists around the nest site where there is a high proportion of forest >80 years old with canopy closure >40% , (2) beyond 200 m from the nest, forest cover is less intact, (3) fledgling goshawks select for forests between 40 and 80 years old, a characteristic not necessarily selected by their parents during the location of a nest site, and (4) the movements of fledglings may be governed by factors other than forest cover, specifically the movements of the mother. Although these results are not dissimilar to other recent investigations of goshawk nesting requirements, they do help quantify the spatial scale at which resources are required, and raise important questions as to the nature of what resources are required beyond 200 m from the nest. However, the results of my thesis, like any other resource selection investigation, are subject to interpretation and constraint by the terminology and approaches used to define units of measurement and describe the areas available to animals.

The scale at which availability is defined and the type and grain of resource variables examined interact to allow an adequate quantification of selection (Weins 1989), and my definitions of extent and grain allow me to better document resource selection in the goshawk. I defined availability at two spatial extents (nest-tree and nest-stand) and found that the strength of selection differed between them. Models for predicting nest location performed poorly at the nest-tree level, but adequately described selection at the nest-stand level. Despite using variables that were thought to best describe goshawk nest-tree location within a stand (high overhead cover and low understory cover) my

model was no better than random (Hosmer and Lemeshow 2000) at predicting the location of a nest tree within 200 m of the nest. Nest-stand-level models had better discrimination than nest-site-level models and thus showed an excellent ability (Hosmer and Lemeshow 2000) to predict the location of nests within goshawk territories. The strongest variable in both these models was overhead canopy cover. Although these metrics are not identical (each was measured in a manner suitable to its spatial scale of reference), they both represent the amount of cover available around the nest. My results suggest that canopy cover, an important correlate with nest location, provides information on the location of the nest only at a particular spatial scale (the nest-stand level).

My results further suggest that goshawks breeding requirements in my study area are more plastic than originally proposed, and that large areas of mature forest may not be required to preserve nesting locations; however, appropriate forest management techniques still are required to maintain goshawk population numbers. Goshawks have long been proposed as a flagship species (Lambeck 1997, Simberloff 1998) for the protection of old-growth forest in North America; however, European studies suggest that goshawks will nest in small isolated woodlands (Kenward 2006, Rutz et al. 2006), and breeding populations have even become re-established in seven European cities (Rutz et al. 2006). However, these populations have access to suitable nesting sites, abundant prey populations, and areas with limited disturbance (e.g., prosecution and predation [Rutz et al. 2006]). These are all conditions of the forest that can presumably be provided by sustainable forest management techniques. For example, removing substantial amounts of forest cover can shift the availability of suitable nesting locations

in favour of red-tailed hawks (*Buteo jamaicensis*), a competitor of goshawks (La Sorte et al. 2004). This situation may be analogous to that of interactions between the common buzzard (*Buteo buteo*) and goshawk in the United Kingdom (Kenward 2006). Thus, the management of forests beyond the 200 m of the nest is essential in maintaining viable prey populations, foraging areas, and reducing competition for goshawks, and these techniques may well benefit other forest species (Carroll et al. 2006). However, the conditions of the landscape beyond the nest area that are required by goshawks are poorly understood (Anderson et al. 2005, Kenward 2006, Squires and Reynolds 2006) and may be essential in determining population productivity (Kenward 2006). Thus, future research should be focused on landscape conditions and nest productivity metrics other than nest occupancy.

To extend my work on the factors influencing the nesting requirements of goshawks in southeastern British Columbia I suggest the following investigations:

(1) apply and validate the result of both nesting and fledgling selection models and test if the application of the fledgling model can increase the ability to distinguish occupied sites;

(2) examine how measures of nest site productivity, such as number of young fledged or dispersed, or surrogates of nest area productivity, such as number of years occupied, are influenced by the composition of the forest in both breeding territories and foraging areas; and

(3) continue to examine how the movements of fledgling birds and thus the placement of the PFA are influenced by interactions between fledglings and their parents, and fledglings and their siblings.

I have provided detailed descriptions of the forest characteristics selected by fledgling goshawks when locating their PFAs. My observations of fledgling mortality and my PFA size estimates are similar to those reported elsewhere (Weins 2004, McClaren et al. 2005, Mahon and Doyle 2003). However, my descriptions of the offset of the PFA from the nest site and the selection of young forest provide valuable new information towards a better understanding of the function of the PFA and its relationship to the nest site and nest area. A discrepancy exists between the forest characteristics selected by adult goshawks when they are selecting their nest sites (Chapter 2) and the forest characteristics selected by fledglings when they are selecting their PFA (Chapter 3). However, the selection of young forests by fledglings, a variable presumably not identified by their parents, is not surprising. Fledgling goshawks are highly susceptible to predation and thus require escape cover during the FDP. However, this insight, when combined with my nest-site selection results, suggests that the forest composition and shape of the PFA required may be more complex than previously thought. Management guidelines currently focus on protecting high canopy cover forest within 200 m of the nest. Beyond this distance, both my nest-site selection results (Chapter 2) and my PFA selection results (Chapter 3) suggest that the area beyond 200 m may be important in nesting and require more complex, and possibly more active, (i.e., silvicultural prescriptions and/or logging) management. Additionally, the location of the PFA may not be completely governed by the forest characteristics surrounding the nest. Further investigations into factors influencing the specific movements of fledglings are required to understand the function of the PFA and how inter-familiar interactions influence PFA location.

Some discrepancies exist in both the research directions taken in Europe and those in North America (Kenward 2006), but the observations made by researchers on these two continents seem more similar as new information becomes integrated into local research efforts and into a global understanding of this species' requirements. Human use of forests has resulted in widespread and dramatic change in the composition, structure, and distribution of forests in both Europe and in eastern North America. Research and conservation efforts in western North America have attempted to document and monitor goshawks in order to maintain populations, and thus avoid the population declines, extirpation, and re-colonization cycles seen in large parts of this species' range. However, without knowledge of which resources limit goshawk populations, observational and mensurative studies will fail to document essential requirements of this species. These studies still are essential as they provide the natural history framework within which applied ecologists can develop effective questions to test our assumptions of nesting requirements. It is from these foundations that questions concerning the spatial extent and grain of resource selection can be examined and thus resource limitations identified.

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