

## Bookends 0.3

### Introduction

Once valued primarily for high timber yields, temperate rainforests of the Pacific Northwest are now managed with increased emphasis on the conservation of biodiversity (Thomas et al. 2006). Among the drivers of this shift are declining populations of species whose life histories depend on old-growth forests. Some of these species have been placed under federal, provincial, or state protection: the marbled murrelet (*Brachyramphus marmoratus*) is protected under the Species at Risk Act in Canada (COSEWIC 2014), and the coastal population of the pacific marten (*Martes caurina*) is protected under the Endangered Species Act in the United States (US Fish & Wildlife Service 2020). Management under these types of legislation is typically reactive and focuses on conserving each imperiled species on a case-by-case basis (Simberloff 1998). This approach has been widely criticized for failing to provide management for broader ecosystems, including the very ecosystems on which the imperiled species depend (Lambeck 1997). Alternatively, focusing on the larger scales of landscapes or ecosystems should preserve the ecosystem processes and services on which wild species and humans alike depend (Franklin 1993). Yet ecosystem-based management is itself beset by numerous practical, theoretical, and even philosophical challenges which have made it difficult to implement (Lambeck 1997, Simberloff 1998).

Managers have often turned to surrogate species as a solution for the dilemma posed by the single-species and ecosystem-based management debate. At the core of the surrogate species concept is the belief that the requirements or wellbeing of a single species, or a small suite of species, can stand in for the needs and health of numerous co-occurring species or entire ecosystems (Caro 2010). A myriad variations and conflicting definitions are present in the literature, but the original may be the concept of the *indicator species*. The presence and population size of an indicator species is believed to reflect ecosystem processes or the populations of other species (Landres et al. 1988). Perhaps more widespread than indicator species is the *umbrella species* concept. Protections which benefit umbrella species—typically wide-ranging habitat specialists—are assumed to confer protection to co-occurring species with smaller ranges and less restrictive habitat requirements (Roberge & Angelstam 2004, Seddon & Leech 2008). A related concept is the *flagship species*, a species whose protection, like an umbrella species, confers benefit on other species, but which is selected for its charisma and ability to serve as a rallying point for conservation (Andelman & Fagan 2000). These concepts all attempt to extend the relative simplicity of single-species methods to achieve the promise of ecosystem-based management (Lambeck 1997).

No species better embodies the challenges of managing forest species and ecosystems in the Pacific Northwest than the Northern spotted owl (*Strix occidentalis caurina*). The spotted owl is strongly associated with old-growth forest (Forsman et al. 1984) and has at various points been proposed as an indicator (Lee 1985), an umbrella (Tracy & Brussard 1994), and a flagship species ( ) for this ecosystem. In the late 1980s, public outcry and litigation in the United States led to the development of a spotted owl conservation strategy concurrent with the species' listing as threatened under the Endangered Species Act (Thomas et al. 1990). This single-species plan rapidly expanded to include other species, particularly the marbled murrelet and several salmon stocks, and ultimately evolved into the Northwest Forest Plan. The Northwest Forest Plan remained rooted in spotted owl management, but also included protections for watersheds, monitoring of rare species, and a sustainable annual timber harvest (DeSala & Williams 2006). Not all the Northwest Forest Plan's goals have been achieved—notably, spotted owl and marbled murrelet populations have continued to decline, although at a slower rate—and some parts of the plan have been eroded under subsequent presidential administrations (DeSalla et al. 2015). Yet the Northwest Forest Plan remains a powerful example of an ecosystem-scale management plan with a single species at its core.

The story of the northern goshawk (*Accipiter gentilis*) in North America parallels that of the spotted owl. Goshawks are present in boreal forests across the continent and in the west range as far south as the high-elevation forests of the American Southwest and northern Mexico. Two subspecies (*A. g. atricapillus* and *A. g. laingi*) are widely recognized and a third (*A. g. apache*) is recognized by some authors (Squires et al. 2020). Goshawks are not associated with old-growth forest to the same degree as the spotted owl, but do show a clear preference for extensive tracts of mature forest with large-diameter trees and closed canopies (Andersen et al. 2005, Squires & Kennedy 2006). Like the spotted owl, goshawks have been proposed as a flagship (Sergio et al. 2006), an indicator (), and an umbrella species (Ozaki et al. 2006). While the Northwest Forest Plan was developing in the Pacific Northwest, alarms were sounded over the impact of timber harvest on northern goshawks in the American Southwest (Crocker-Bedford 1990). Decades of litigation failed to result in listing the southwestern population (proposed subspecies *apache*) under the Endangered Species Act, but a new management plan was developed under the National Forest Management Act in the 1990s (revised in Peck 2000). This single-species management plan disallowed timber harvest near known nests and required a minimum amount of mature forest within the larger home range surrounding known nests (Reynolds et al. 1992). Notably, the plan also specified the inclusion of younger forest, small clearings, snags, and woody debris to provide habitat for eight important goshawk prey species. This recommendation was based on the assumption that goshawks are habitat generalists limited by the abundance, not the availability, of prey—an assumption which has been the subject of heated debate (Greenwald et al. 2005, Reynolds et al. 2007). However, by incorporating multiple species, dynamic ecosystem processes, and human use, the goshawk management plan approaches the principles of ecosystem-based management and shows its potential to scale up to a more cohesive plan in the style of the Northwest Forest Plan (Graham et al. 1994, Peck et al. 2000).

In the Pacific Northwest, naturalists described a small, dark subspecies of goshawk unique to the coastal temperate rainforests of Haida Gwaii and Vancouver Island (Taverner 1940). The size and plumage characteristics of *A. g. laingi* may be an adaptation the dark, dense forests the subspecies inhabits (Ethier 1999) and the agile avian prey believed to dominate its diet (Penteriani et al. 2013, McClaren et al. 2015). The precise range of *laingi* is unclear; based on morphometrics, genetics, and ecosystem mapping, it is believed to extend along the west coast and islands of British Columbia, from Southeast Alaska south to Washington’s Olympic Peninsula (NGRT 2008, Sonsthagen 2012). In the portion of its range within the United States the *laingi* subspecies has no additional protections, but in Canada it is designated as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). The *laingi* subspecies is further Red-listed by the British Columbia Conservation Data Centre and is an Identified Wildlife Species under the Forest Practices Code (COSEWIC 2013). Existing management plans call for the creation of buffers around known goshawk nests and the maintenance of a minimum amount of mature forest within the larger home range (McClaren et al. 2015, Parks Canada Agency 2018), similar to the plan from the American Southwest, but do not include recommendations for goshawk prey species. To some extent this is due to the single-species focus of this plan, but it is also a result of several knowledge gaps. Goshawk managers have acknowledged that a landscape-scale plan would be superior to the current fine-scale plan, and ecosystem-based management has been implemented elsewhere in British Columbia, most notably the Great Bear Rainforest (Price et al. 2009). Together these suggest an ecosystem-based approach incorporating the goshawk as a focal species may be possible for coastal rainforests elsewhere in British Columbia. Yet while *laingi* nesting habitat is relatively well documented, foraging behavior and habitat of goshawks remains poorly understood across North America in general and coastal British Columbia in particular. These knowledge gaps hinder current single-species and potential ecosystem-based management alike.

My thesis attempts to fill one small knowledge gap by providing basic ecological information regarding the breeding season diet of goshawks in coastal British Columbia. This first chapter provides background on endangered species conservation in relation to forest management and establishes a rationale for my research. The second chapter describes my research quantifying goshawk diet in coastal British Columbia and investigating potential links between dietary variation and goshawk reproductive success. The final chapter summarizes my results in the context of Pacific Northwest forest management and suggests both implications for management and direction for further research.

# Conclusion

## Overview

Specialist and generalist predators differ in their dependence on prey species, with cascading consequences for many aspects of their life history (Korpimäki & Norrdhal 1991, Resano-Mayor et al. 2016). Specialists are highly efficient hunters of their main prey at the cost of decreased efficiency when hunting others, whereas generalists exhibit less variation in foraging efficiency across multiple prey species (Terraube et al. 2011). A specialist is relatively ill-equipped to compensate with other prey when its preferred prey becomes scarce, but generalists readily switch to alternate prey (Steenhof & Kochert 1988, Terraube & Arroyo 2011). As a result, specialists are highly dependent on their main prey and respond to declines with pronounced reductions in local density, productivity, or total population size (Korpimäki & Norrdhal 1991, Terraube et al. 2011). Specialists may even be limited in geographic range or habitat use by the presence and abundance of their main prey (Ferrer & Negro 2004, Peers et al. 2003). In contrast, generalists are not dependent on any one prey species and exhibit relatively greater population stability (Hanski et al. 1991, Andersson & Erlinge 1977).

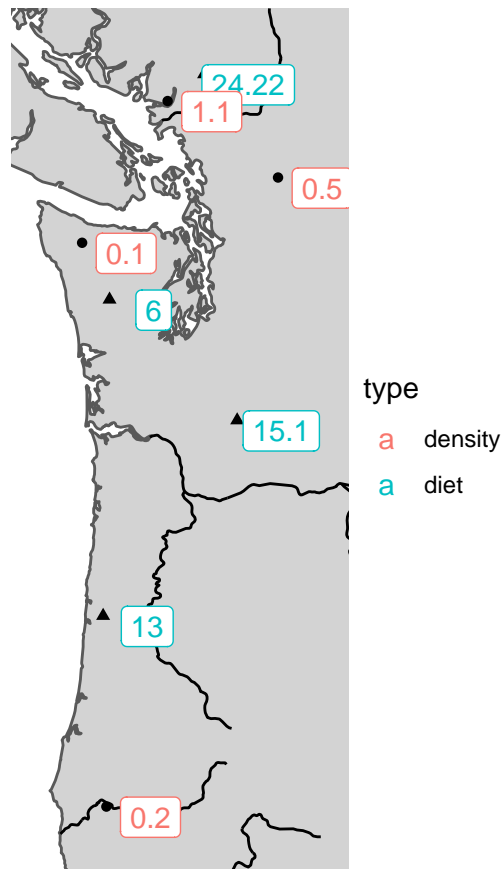
This dichotomy between specialist and generalist species is, however, an oversimplification. Most species exist on a continuum of specialization and generalization, and for a generalist predator the abundance of a single prey species can be a major driver of reproductive success (Elmhagen et al. 2000, Resano-Mayor et al. 2006). In a single species, some populations (Salamolard et al. 2000, Roth et al. 2007) or some individuals within a population (Woo et al. 2008) may be more or less specialized. Even a single individual may shift its position along the specialist-generalist continuum over its lifetime in response to age and experience (Rutz 2006) or to changing conditions (that one lynx paper). The degree of specialization, and its associated impact on demographic parameters, can scale up from individuals through populations to entire species, with profound consequences for conservation (Terraube et al. 2011, Resano-Mayor 2016).

The complex relationship between dietary specialization and conservation is exemplified by the northern spotted owl. Spotted owls depend on old-growth forests, but the cause of this association has been a source of speculation from the earliest years of spotted owl research (). In part, the selection of old-growth forest appears to be driven by the spotted owl's relatively specialized diet (Carey et al. 1992, Ward et al. 1998). More than half the biomass spotted owls consume comes from just two taxa, flying squirrels (*Glaucomys sabrinus*) and woodrats (bushy-tailed woodrat *Neotoma cinerea* and dusky-footed woodrat *N. fuscipes*; reviewed in Carey et al. 1992). This pattern remains constant across the subspecies' range, although the relative contribution of each taxa varies with geographic region and forest type to reflect local prey abundance. In Washington's Olympic Peninsula, where woodrats are absent, spotted owls consume primarily flying squirrels (Carey et al. 1992), whereas in northern California flying squirrels make up a relatively small portion of the diet and woodrats, which are more abundant, dominate (Ward et al. 1998). Even within a single population, some individuals specialize to a greater degree on one taxa or the other (Zabel et al. 1995). Home range sizes in the flying squirrel-dependent Olympic Peninsula are among the largest ever recorded for spotted owls (Carey et al. 1992), and where both flying squirrels and woodrats are consumed, owls which consume more flying squirrels have larger home ranges than those which consume more woodrats (Zabel et al. 1995). Evidently diet and prey abundance do affect some demographic parameters, including breeding density, but not others, such as spotted owl productivity (Rosenberg et al. 2003). Instead, productivity appears to be the result of complex interactions between climate and prey abundance (Glenn et al. 2011). Increasing prey abundance has been recommended as a management tool to aid spotted owl recovery (Forsman et al. 2014).

In contrast to the spotted owl's reliance on a few prey species, the northern goshawk is considered a generalist predator and consumes an enormous diversity of prey across its wide geographic range (reviewed in Drennen 2006). I identified **25** different prey species in the diet of goshawks in coastal British Columbia, consistent with a generalist foraging strategy. Some goshawk populations appear to be strongly generalist (Salafsky et al. 2007), while in others a key prey species is a major driver of productivity, survival, and other demographic parameters (Doyle & Smith 1994, Tornberg et al. 2005). Over 60% of goshawk diet in my study area was composed of tree squirrels (*Tamiasciurus* spp.), which indicates a level of specialization even greater than that of the spotted owl. However, I found no effect of the degree of dietary specialization on goshawk productivity. There are three main explanations for this finding. First, specialization may be the result of preference:

some individuals strongly prefer tree squirrels and select them disproportionate to their abundance, but this specialist strategy confers no fitness advantage over a generalist strategy (Woo et al. 2008). Second, specialization may be the result of opportunity and goshawks take tree squirrels proportionate to their abundance, but it is total prey abundance rather than tree squirrel abundance which drives productivity. Finally, as in the spotted owl, prey abundance and diet during the breeding season may not be as great a driver of productivity as other factors, such as weather or winter prey abundance.

Tree squirrels are the same key prey identified on Vancouver Island (Ethier 1999) but not from other regions of the Pacific Northwest, where the key prey is generally grouse (Watson et al. 1998, Thraikill et al. 2000, Bloxton 2002, Lewis et al. 2006). The key prey from my study area is more similar to those identified elsewhere in western North America, where the most important prey species is also mammalian, generally either a sciurid or a leporid. This unexpected result may be in part the product of methodological differences between my study and others conducted in the Pacific Northwest. When the results from studies across temperate rainforest ecosystems are standardized (data from pooled pellets-and-remains or remains only, measured by counts), the difference between British Columbia and other regions in the Pacific Northwest is much less pronounced. However, the proportion of mammalian prey in the diet, particularly tree squirrels, remains markedly higher within my study area (see figure). This is likely the result of relatively high tree squirrel abundance within my study area, which is much greater (Ransome & Sullivan 2003) than in other temperate rainforest ecosystems (reviewed in Carey et al. 1995). No Pacific Northwest study has assessed goshawk diet and absolute prey abundance simultaneously (but see Ethier 1999), but regional data on tree squirrel abundance hint that, as abundance varies, so may goshawk specialization. Across two ecological zones present in my study area I observed only minor variation in goshawk diet and no variation in the dominance of tree squirrels in the diet, indicating a slight difference in the prey community of these two zones but a similar abundance of tree squirrels. Overall, these results suggest goshawks in my study area pursue a specialized generalist (Elmhagen et al. 2000) foraging strategy—a generalist predator opportunistically exploiting a locally abundant prey source.



## Directions for future research

Comparing the northern spotted owl and the northern goshawk highlights significant knowledge gaps regarding goshawk biology. The controversy surrounding the spotted owl, combined with its position at the heart of a major management plan, has made it one of the most-studied birds in the world (Gutierrez et al. 2020). The northern goshawk, although also shrouded in controversy, has not received the same level of study. It is also far more difficult to generalize results for the widespread, generalist northern goshawk than for the more restricted, relatively specialized spotted owl. As a result, there is a pressing need for detailed, local information on goshawks in the Pacific Northwest in general and coastal British Columbia in particular.

One major knowledge gap related to the work presented here is how goshawks respond to variation in prey abundance. Dietary specialization like that exhibited by goshawks in my study may be the result of a preference for the main prey or simply an absence of other options, and most of the possible explanations for my results cannot be evaluated without differentiating between these two possibilities. Data on prey abundance is required to understand the mechanism of goshawk specialization and whether it is the result of high selectivity for tree squirrels, high abundance for tree squirrels, or some combination of both. This information could be further used to evaluate how changes in key prey abundance and total prey abundance influence goshawk demographic parameters, particularly productivity. This in turn could be used to improve understanding of the factors limiting goshawk populations in coastal British Columbia.

A second knowledge gap is how the amount and type of habitat goshawks use for foraging varies with prey abundance and diet. Goshawk home range size varies significantly across their geographic range and goshawks have been observed foraging a wide variety of habitat types, leading to persistent controversy over how and why goshawks select habitat, particularly foraging habitat (Greenwald et al. 2005, Reynolds et al. 2008). Research on spotted owls indicates that home range size is inversely related to prey abundance and foraging habitat selection varies with the identity of the main prey (Zabel 1995). Diet and prey abundance may likewise explain some of the variation in habitat use in goshawks (Kenward 1982, Penteriani et al. 2013). If so, foraging habitat management recommendations made for one goshawk population could be applied to others only with great caution, if at all. Filling this knowledge gap with information specific to coastal British Columbia is therefore a high priority and has been identified as a priority by goshawk managers (NGRT 2008, Parks Canada 2018).

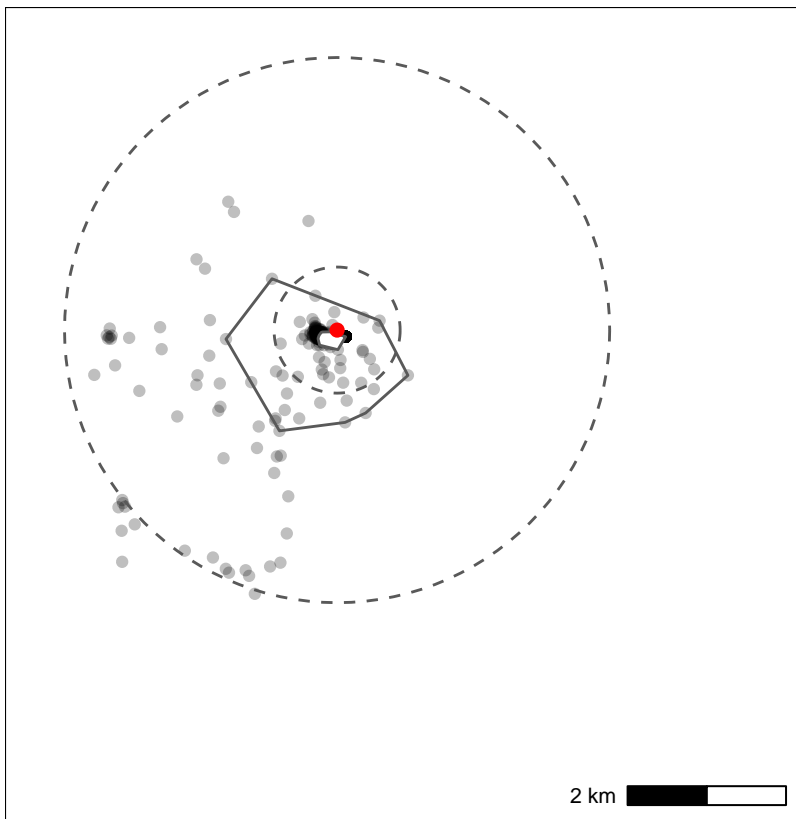
As a pilot study of goshawk foraging habitat use in coastal British Columbia, the British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development (FLNRORD) and I tagged 13 goshawks in 2018-2020. We tagged 4 males and 9 females and over the course of the study period we had only one probable mortality. Captures were conducted during the early breeding season using a dho-gaza trap with a live great-horned owl (*Bubo virginianus*) as a lure (Bloom et al. 2007). Goshawks were fitted with a 14-gram geolocator tags (Ecotone Telmetry brand, Harrier model) attached via backpack-style harness. Tags were programmed to take a location point every 15 minutes and to download data to a base station when within range (approximately 100 m). Base stations were placed beneath or above nests and tags checked for proximity to the station every 15 minutes. From each tag we collected between 0 and 73 days of breeding season (20 April - 15 September) data. Of the tags from which at least one day of data were retrieved, we collected between 3 and 73 (mean  $37.89 \pm 26.69$  standard deviation) days of data, with an average of 31.03 locations per tag per day.

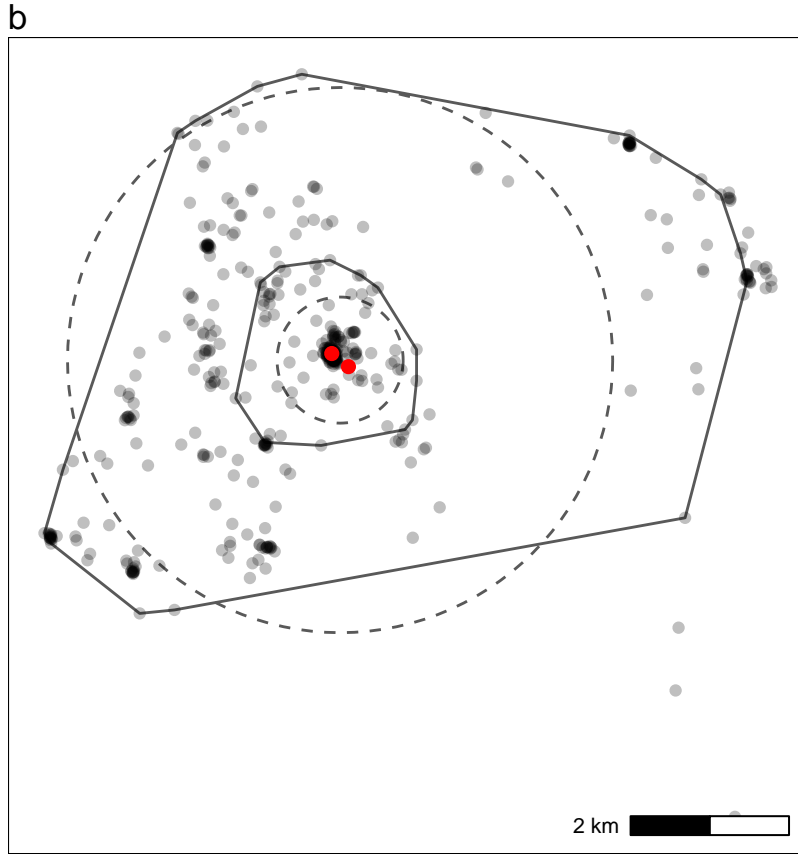
The mean breeding season home range was 2008.89 ha (95% minimum convex polygon) but I observed a large difference in home range size between males and females. Mean male home range was 4409.16 ha whereas mean female home range was much smaller, 829.13 ha. Core-use areas were more similar, but still larger for males at 851.51 ha (50% minimum convex polygon) than for females at 151.87 ha. The smaller female home range was due to the amount of time females spent on the nest. An average of 66.48% ( $\pm 36.09$ ) of female location points were taken within range of the base station ( $< 100$  m from the nest), while only 2.87% ( $\pm 4.26$ ) of male points were taken at the nest. Males also traveled further from the nest. The mean furthest distance from the nest a male traveled was 7.05 km, while females on average only ventured 2.86 km from the nest. As the breeding season progressed, the length of time spent away from the nest increased noticeably for males but less so for females.

ID	Site	Days of data collected		N. days	Relation to nest		% points taken at nest	Home range (50% MCP)
		first	last		N. points	Max. distance from nest (m)		
HAR12	FMT	2020-06-25	2020-06-28	3.0	104	2,302.320	3.850	0.680
HAR03	GRV	2020-06-08	2020-06-28	20.0	2,964	2,441.140	95.880	0.000
HAR10	MTC	2019-05-02	2019-06-29	58.0	315	5,456.710	78.410	0.350
HAR02	RLK	2020-06-13	2020-07-08	25.0	977	4,013.480	72.060	5.440
HAR08	TCR	2019-06-10	2019-06-27	17.0	45	76.500	82.220	0.000
AVERAGE				24.6	-	2,858.030	66.484	1.294
HAR09	MTC	2019-05-02	2019-07-02	61.0	409	4,413.190	2.440	530.110
HAR04	RLK	2019-06-22	2019-07-08	16.0	532	7,773.290	9.020	423.000
HAR05	SKA	2019-06-23	2019-09-04	73.0	1,557	8,026.150	0.000	1,548.170
HAR07	TCR	2018-07-08	2018-09-14	68.0	637	7,976.540	0.000	904.780
AVERAGE				54.5	-	7,047.292	2.865	851.515

We encountered several challenges over the course of the three-year pilot. The dho-gaza method favors the capture of females and resulted in a much larger number of females than males in our sample. Because males provide most of the food during the breeding season, this provided us with relatively little foraging location data. Further, the geolocator tags only download data when within 100 m of the base station, on a 15-minute cycle. Males spend little time near the nest except briefly while making prey deliveries, so we obtained only infrequent data downloads from males. Overall, our methods favored collection of location data from females, which offered little relatively little insight into foraging habitat use. We also struggled to relocate tagged birds in subsequent years and so were unable to obtain location data for multiple breeding seasons or for winter movement. It is difficult to determine the fate of these missing birds. Several were tentatively resighted but could not be definitely relocated, and it is unclear if they nested the year after being tagged. We cannot rule out the possibility that tags negatively impacted these birds' ability to reproduce in subsequent years. However, we observed only one probable mortality and the same tags and methodology have been used elsewhere on goshawks without significant negative effects (Blakey et al. 2020). The location data we were able to retrieve, although less than anticipated, was of much higher resolution than VHF data and much higher accuracy than satellite data. Despite setbacks, this technology may therefore be uniquely well-suited to studies of foraging habitat selection.

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My preliminary results show several interesting patterns and offer some suggestions for management. The high fidelity of females to the nest area confirms the importance of protected buffers around nests to prevent disturbance of this critical habitat. However, the large distances traveled by males and the irregular shape of their home ranges shows that circular buffers based on estimates of mean home range size are not good approximations of true space use. Home ranges were rarely circular but rather shaped by geographic constraints such as coastlines or mountains peaks. Within home ranges, kernel density estimates show habitat use is not even across a male's territory. Instead, there are clusters of activity around high-use areas which are likely high-quality foraging habitat. These areas usually fall outside the nest area and so would not be captured by current habitat protections. Goshawks readily crossed narrow barriers such as roads, rivers, and powerline cuts, and sometimes appeared to use these features for travel or foraging. On the other hand, goshawks seemed to generally route around larger barriers such as lakes or clearcuts. This suggests managed areas around nests should be tailored to the amount and configuration of suitable foraging habitat in the surrounding landscape, and that any timber harvest within the foraging area should prioritize preserving connectivity between patches of high-quality foraging habitat. However, a great deal of additional research is needed to confirm and refine these suggestions, particularly regarding what defines suitable and high-quality foraging habitat.

### Management implications

Although my thesis found no evidence of a link between productivity and the dominance of squirrel in the diet, data from multiple other studies suggests it is likely that squirrel abundance does affect productivity, although I was not able to test for this in my thesis. If this is the case, it would have important implications for management. In particular, squirrel abundance is itself tied to a cyclical food source, the conifer cone crop. Previous work on Vancouver Island found a correlation between cone crop size and goshawk productivity, supporting the supposition that goshawks in coastal British Columbia are impacted by squirrel populations. However, in some goshawk populations early spring weather, not prey abundance, has been found to be a greater factor in goshawk productivity. Resolving which is the primary driving factor in coastal British



Columbia is a worthy goal in its own right, but is especially pertinent in light of global climate change. Currently little is known or even speculated about how climate change will affect northern goshawks, but as both cone crop and spring temperatures are expected to be affected by climate change this represent a crucial direction for future research.

My thesis examines a single population of goshawks on the south coast of British Columbia which is currently classified as belonging to the subspecies *laingi*. The boundaries of the *laingi* subspecies have always been unclear; a combination of morphometric and genetic data, along with ecosystem mapping, has tentatively defined the eastern edge of its range within British Columbia as the Coast Mountains. This range is the foundation for goshawk management in British Columbia. However, recent genetic evidence has called this distribution into question. Gerald et al. (2019) identified the Haida Gwaii population as highly unique and distinct from populations on Vancouver Island and the south coast. They further found little genetic distinctness between populations in Vancouver Island, the south coast, and elsewhere in North America. This suggests the distribution of *laingi* is restricted to Haida Gwaii, and that the population under consideration in my thesis may not be a part of this subspecies. However, my results suggest a strong ecological similarity between goshawks on the south coast and Vancouver Island with the Haida Gwaii population, which is also highly reliant on tree squirrels. The diet of these populations stand in contrast to that of other populations currently considered part of *laingi*, such as northwest Washington and Southeast Alaska, where goshawks consume primarily birds, especially grouse. It also stands in contrast to the diet of populations elsewhere in North America, where goshawks do consume mainly mammals, but primarily hare or ground squirrels. This suggests that while goshawks in coastal British Columbia may be genetically dissimilar to those in Haida Gwaii, they may be ecologically similar and unique relative to other population, potentially supporting a status as a designatable unit. However, it does not indicate a single management strategy for all goshawk populations in coastal British Columbia. Red squirrels are native to Vancouver Island and douglas's squirrels to the coastal mainland, but red squirrels are introduced to Haida Gwaii. These ecosystems must therefore be managed differently. This highlights the importance of the type of population-specific ecological information my thesis provides.