Bookends 0.4

# 1 Conclusion

**Overview**

Specialist and generalist predators differ in their degree of dependence on prey species with cascading consequences for many aspects of their life history (Korpimaki & Norrdhal 1991, Resano-Mayor et al. 2016). Specialist predators are efficient hunters of their main prey at the cost of poor success when hunting other species, whereas generalist predators hunt many species with equal skill (Terraube et al. 2011). A specialist predator may struggle to compensate with other prey when its main prey becomes scarce, but generalist predators readily switch to alternate prey (Steenhof & Kochert 1988, Terrabue & Arroyo 2011). As a result, specialist predators depend on a single species and their demographic parameters–such as migration, reproductive success, and survival–vary in synchrony with its abundance (Korpimaki & Norrdhal 1991, Terraube et al. 2011). In contrast, generalist predators make use of many species and their populations are relatively stable (Hanski et al. 1991, Andersson & Erlinge 1977).

The familiar dichotomy between specialist and generalist predators is, of course, an oversimplification. The abundance of a single prey species can be a major driver of demographic parameters, such as reproductive success, for a generalist predator as well as a specialist one (Elmhagen et al. 2000, Resano-Mayor et al. 2006). Furthermore, within 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. A single individual may also become more specialized over its lifetime as a result of age and experience (Rutz 2006). Correctly identifying the degree of specialization and understanding its effect on demographic parameters is more than a matter of theory or curiosity: the consequences of specialization can scale up from individuals through populations to entire species, with profound implications for conservation (Ferrer & Negro 2004, 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 (Gutiérrez & Carey 1985). The association appears to be driven, in part, 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 holds true across the subspecies’ range, although the relative contribution of each taxa varies with geographic region and forest type in response to local 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 smaller portion of the diet and woodrats, which are more abundant, dominate (Ward et al. 1998). Even within a single spotted owl population some individuals specialize 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 (Carey at al. 1992), and where both taxa are present owls which consume primarily flying squirrels have larger home ranges than those which consume mostly woodrats (Zabel et al. 1995). Evidently diet and prey abundance affect some demographic parameters, such as breeding density, which has led some to recommend increasing prey abundance as a route to increase owl abundance (Forsman et al. 2014). Yet prey abundance does not appear to affect 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).

In contrast to the spotted owl’s dependence 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, which is consistent with a generalist foraging strategy. However, 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. Some goshawk populations appear to be strongly generalist (e.g. Arizona, Salafsky et al. 2007), whereas in others a key prey species is a major driver of productivity, survival, and other demographic parameters (e.g. Yukon, Doyle & Smith 1994; and Finland, Tornberg et al. 2005). I found no affect of the degree of dietary specialization on goshawk productivity. There are several explanations for this unexpected finding. First, specialists may not be more productive than generalists. Specialist individuals may preferentially consume tree squirrels but have similar levels of fitness as generalist individuals in this population (Woo et al. 2008). Alternately, specialization may not be the result of preference. Individuals may lack strong prey preferences and take tree squirrel in proportion to their abundance. Total prey abundance, rather than tree squirrel abundance, may drive productivity (Salafsky et al. 2007). Finally, as in the spotted owl, prey abundance and diet during the breeding season may not be a lesser driver of productivity than other factors, such as weather or winter prey abundance.

Goshawk diet varies across its range in response to the regional presence and abundance of prey species (Drennan 2006). I found the key prey of goshawks in the south coast region was tree squirrels. This contrasts with studies of goshawk diet elsewhere in the Pacific Northwest where the key prey is generally grouse (Watson et al. 1998, Thrailkill et al. 2000, Bloxton 2002, Lewis et al. 2006), but is similar to work on Vancouver Island where the key prey is also tree squirrels. My results also contrast with studies from other regions of western North America where the key prey may occasionally be a species of squirrel, but is most often a species of hare or rabbit. The unexpected difference between diet in my study area and the larger Pacific Northwest may in part be due to differences in methodology. When the results from studies across temperate rainforest ecosystems are standardized (data from pooled pellets-and-remains or remains only, measured by counts), the contrast between regions within the Pacific Northwest is much less pronounced. However, the proportion of mammalian prey, particularly tree squirrels, in the diet remains markedly higher within coastal British Columbia than outside it. Tree squirrel abundance is higher in the south coast region than in other temperate rainforest ecosystems (Carey et al. 1995, Ransome & Sullivan 2003). No Pacific Northwest study has assessed goshawk diet and and absolute prey abundance simultaneously (but see Ethier 1999). Nonetheless, regional data hint at a pattern of higher dietary specialization in regions or forest types with higher tree squirrel abundance (see Figure 2.1). Across the 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. If goshawks are more specialized on tree squirrels where tree squirrels are more abundant, this would indicate a slight difference in the prey community of these two zones but a similar abundance of tree squirrels. Goshawks in my study area appear to be a generalist predator opportunistically exploiting a locally abundant prey species.

**Directions for future research**

Comparing the foraging ecology of the northern spotted owl and the northern goshawk highlights significant knowledge gaps regarding goshawk biology. The controversy surrounding spotted owl conservation, 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 likewise shrouded in controversy, has not received the same level of study. Where data are available, it is more difficult to generalize research on 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, particularly coastal British Columbia.

One knowledge gap related to the work I present here is how variation in prey abundance affects the degree of dietary specialization, productivity, and survival of individual goshawks. Dietary specialization such as goshawks in my study area exhibit may be the result of a preference for the main prey or simply an absence of other options. Data on prey abundance is necessary to understand the mechanism of goshawk specialization and whether it is the result of high selectivity for tree squirrels, high abundance of tree squirrels, or some combination of both. This information could in turn be used to evaluate how changes in key prey abundance and total prey abundance influence goshawk demographic parameters, particularly productivity. Without this knowledge it is impossible to fully understand 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 diet and prey abundance. Goshawk home range size varies across their geographic range and goshawks have been observed foraging in diverse habitat types, leading to ongoing debate 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). Variation in goshawk home range size and habitat selection may likewise be explained by diet and prey abundance. (Kenward 1982, Penteriani et al. 2013). If so, foraging habitat management could only be conducted with knowledge of goshawk diet and recommendations made for one population could be applied to others only with great caution. Filling this knowledge gap with information specific to coastal British Columbia is crucial and has been identified as a priority by goshawk managers (NGRT 2008, Parks Canada 2018).

To address this crucial knowledge gap, the British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development (FLNRORD) and I conducted a pilot study of foraging habitat use in coastal British Columbia. Between 2018-2020 we tagged and tracked 4 male and 9 female goshawks. 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 14-gram solar-powered GPS-UHF tags (Ecotone Telmetry brand, Harrier model), also containing a VHF tag, 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 from the base). Base stations were placed beneath or above nests and tags checked for proximity to the station every 15 minutes.

We were able to retrieve data from 10 out of 13 birds, collecting between 3 and 73 (mean 37.89 26.69 standard deviation) days of breeding season (20 April - 15 September) locations (see Figure 2.1). Tracked birds provided 45 - 2964 location points (mean 837.78 923) with an average of 31.03 ( 62.28) locations per bird per day. Over the study period we observed only one probable mortality. I estimated breeding season home ranges and core-use areas using 95% minimum convex polygons (MCPs) and 50% MCPs, respectively. The mean breeding season home range was 2008.89 ha but male home ranges were far larger than female home ranges (t-test). Core-use areas were more similar, but still larger for males than for females. Female home ranges and core-use areas were smaller due to the significantly higher amount of time females spent near the nest (chi-squared). Males also traveled further from the nest than females (t-test). The mean furthest distance from the nest a male traveled was 7.05 ( 1.76) km, while females on average only ventured 2.86 ( 2.02) 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. Home ranges were rarely circular, but rather shaped by geographic constraints such as coastlines or mountains peaks (see Figures 2.2 and 2.3). Within home ranges, kernel density estimates show habitat use is not even across a male’s territory. Instead, there are clusters of activity around areas which are likely high-quality foraging habitat.

We encountered several challenges over the course of the three-year pilot. First, the location data we obtained were biased toward females. Females are more aggressive near the nest than males and so are more likely to be captured when using the dho-gaza trapping method. Data from female tags downloaded more frequently onto the base stations than data from male tags because of the large amount of time females spent near the nest, where the base stations were located. Consequently, we collected far more location data on females than males, which offered relatively little insight into foraging habitat use since males provide most of the food during the breeding season. Second, we were only able to locate four of the six birds tagged in the first year using the VHF tag and could not download data from the winter or subsequent spring, and never relocated the remaining two birds. Our inability to relocate birds is likely due to a combination of the limited range of the VHF tags and the difficult topography of our study area, compounded by the birds’ failure to return to known breeding areas. Finally, technical failures resulted in no data downloads for two birds, too many location points for one birds, and too few location points for many others. Future work should consider more powerful VHF tags for easier relocation and an alternate-days duty cycle to reduce the number of missed locations.

Despite these setbacks, my results show several interesting patterns and offer promising suggestions for management. 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 and may therefore be uniquely well-suited to studies of foraging habitat selection. The high fidelity of females to the nest area confirms the importance of protected buffers around nests to prevent the disturbance of 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. Areas used extensively by males usually fall outside the nest area and are not be captured by current nesting habitat protections. Preliminary inspection of movement data indicates 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 present in the surrounding landscape, and that any timber harvest within the foraging area should prioritize the preservation of 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 the characteristics of suitable and high-quality foraging habitat.

**Management implications**

Climate change is one of the largest and most difficult to anticipate threats facing biodiversity (Bellard et al. 2012). The current understanding of how climate change will impact goshawks in coastal British Columbia is largely speculative (Parks Canada 2018). Although I found no evidence of a link between the degree of dietary specialization and goshawk productivity, the level of specialization I observed and findings from other studies suggest goshawks in my study area are highly dependent on tree squirrels for successful reproduction. Notably, Ethier (1999) found goshawk productivity on Vancouver Island to be significantly correlated with red squirrel abundance. Tree squirrels are themselves highly dependent on conifer seeds and their abundance varies with the size of the annual cone crop. (Smith 1970). Seed production is cyclical, but may be increased by higher temperatures and inhibited by drought (Boucher et al. 2020). As the climate warms and drought risk rises, climate-driven changes in seed production may cascade upward through prey abundance to impact goshawk populations in coastal British Columbia. Significantly more work is needed to understand the relationship between prey abundance, the buffering ability of alternate prey, and goshawk productivity, but my results provide an important starting point for incorporating climate change into goshawk management.

Wildlife management, whether rooted in a single-species or ecosystem-based approach, generally centers around species, subspecies, or unique populations at risk of extinction (cite). My thesis examines a single population of goshawks on the south coast of British Columbia which is currently classified as part of the subspecies *laingi*. The precise range of *laingi* has always been unclear, but recent genetic evidence calls into question the boundaries currently used in goshawk management. Geraldes et al. (2019) identified the Haida Gwaii population as highly unique and distinct from populations on Vancouver Island and the mainland coast. Their findings indicate the distribution of *laingi* may be restricted to Haida Gwaii and challenge the conservation status of goshawk populations elsewhere within the putative range of *laingi*. My results suggest a strong ecological similarity between goshawks within my study area, Vancouver Island, and Haida Gwaii, where goshawks are also highly dependent on tree squirrels (COSEWIC 2013). The diet of these populations stands in contrast to others in temperate rainforest ecosystems which are currently considered *laingi*, such as the Olympic Peninsula or Southeast Alaska, where goshawks consume mainly birds. Goshawks in coastal British Columbia are further different from populations elsewhere in western North America, where goshawks also consume primarily mammals but do not specialize on tree squirrels. Goshawks in coastal British Columbia may therefore be ecologically similar to each other, and ecologically distinct from other populations, even if they are genetically dissimilar. Ecological similarity does not indicate a single, uniform management strategy is appropriate for all goshawks in the region: red squirrels, for instance, are an introduced species on Haida Gwaii. However, it does demonstrate that management plans benefit from the type of fine-scale ecological information my thesis provides. Further, their ecological similarity suggests these goshawks may deserve special management consideration as a population unique to the temperate rainforests of coastal British Columbia.

# 2 Figures

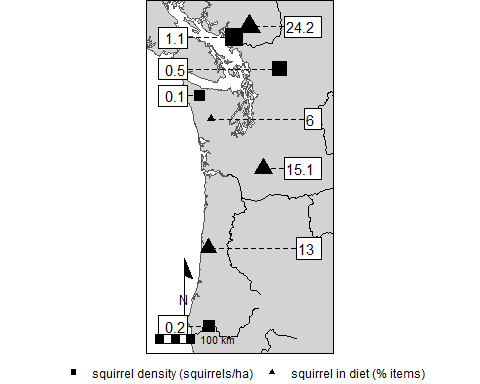


Figure 2.1: Comparison of goshawk dietary specialization and squirrel abundance in the Pacific Northwest. Size of symbol represents relative specialization or abundance. Goshawk diet estimated pellets-and-remains or remains only and measured using counts of items. Tree squirrel abundance estimated from number of individuals/ha. Adapted from Carey et al. (1992), Watson et al. (1998), Thrailkill et al. (2000), Bloxton (2002), Ransome and Sullivan (2003), and this study.

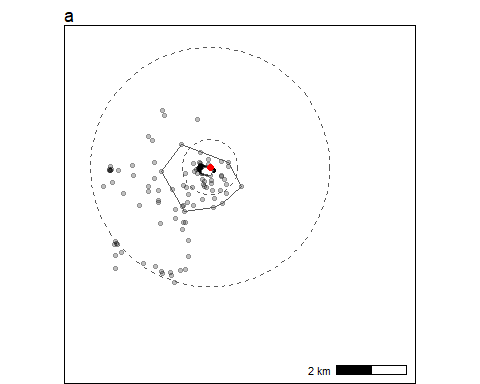


Figure 2.2: Breeding season home range and core-use area of one tagged female goshawk in 2020.

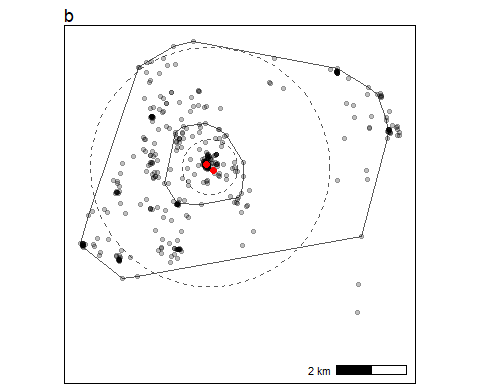


Figure 2.3: Breeding season home range and core-use area of one tagged male goshawk in 2019

Table 2.1: Summary of telemetry data from pilot study

|  | | Days of data collected | | | Relation to nest | | | Home range (ha) | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| ID | Site | first | last | N. days | N. points | Max. distance from nest (m) | % points taken at nest | 50% MCP | 95% MCP | 50% KDE | 95% KDE |
| HAR12 | FMT | 2020-06-25 | 2020-06-28 | 3 | 104 | 2.3 | 3.9 | 0.7 | 103.7 | 13 | 152.1 |
| HAR03 | GRV | 2020-06-08 | 2020-06-28 | 20 | 2964 | 2.4 | 95.9 | 0 | 0 | 0 | 0 |
| HAR10 | MTC | 2019-05-02 | 2019-06-29 | 58 | 315 | 5.5 | 78.4 | 0.3 | 58.9 | 8.7 | 113.4 |
| HAR02 | RLK | 2020-06-13 | 2020-07-08 | 25 | 977 | 4 | 72.1 | 5.4 | 280.6 | 12.7 | 267.4 |
| HAR08 | TCR | 2019-06-10 | 2019-06-27 | 17 | 45 | 0.1 | 82.2 | 0 | 0.2 | 0 | 0.4 |
| AVERAGE | - | - | - | 25 | - | 2.9 | 66.5 | 1.3 | 88.7 | 6.9 | 106.7 |
| HAR09 | MTC | 2019-05-02 | 2019-07-02 | 61 | 409 | 4.4 | 2.4 | 530.1 | 2611.2 | 636.3 | 3032.8 |
| HAR04 | RLK | 2019-06-22 | 2019-07-08 | 16 | 532 | 7.8 | 9 | 423 | 4441.1 | 662.3 | 4407.6 |
| HAR05 | SKA | 2019-06-23 | 2019-09-04 | 73 | 1557 | 8 | 0 | 1548.2 | 6052.9 | 1642.2 | 6674.7 |
| HAR07 | TCR | 2018-07-08 | 2018-09-14 | 68 | 637 | 8 | 0 | 904.8 | 4531.4 | 850.6 | 5263.1 |
| AVERAGE | - | - | - | 54 | - | 7 | 2.9 | 851.5 | 4409.2 | 947.9 | 4844.5 |