Dietary Variation in the Northern Goshawk (Accipiter gentilis) in British Columbia

# Introduction

Effective wildlife conservation often requires understanding diet composition and its consequences for population demographics. Specialist predators selectively consume a narrow range of prey species regardless of their abundance, whereas generalists opportunistically consume a wider range and readily switch between species in response to changes in prey abundance (Steenhof and Kochert 1988; Terraube and Arroyo 2011). Specialization increases foraging efficiency on the preferred prey at the potential cost of decreased reproductive success for the specialist when that prey is scarce (Newton 1998). However, even in a generalist predator a single key prey species can be a major driver of reproductive success (Elmhagen et al. 2000; Resano‐Mayor et al. 2016). For at-risk predators, increasing the abundance of key prey species may be a useful conservation tool (Ferrer and Negro 2004; Forsman et al. 2004; Resano‐Mayor et al. 2016).

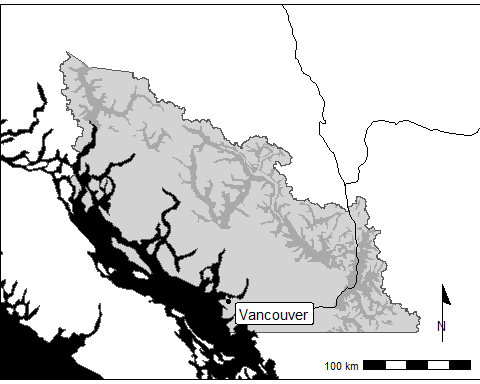
The northern goshawk (*Accipiter gentilis*) is a large forest-dwelling raptor with a Holarctic distribution. A generalist predator, the goshawk hunts a variety of small- and medium-sized mammals and birds, including squirrels, rabbits and hares, grouse, jays and crows, and pigeons (Squires et al. 2020). Despite this diverse diet, a single prey species or narrow suite of species has a strong effect on the demographics of many goshawk populations. In the Yukon, goshawks depend on snowshoe hare (*Lepus americanus*) and show strong variation in productivity, mortality, and space use in response to cyclical changes in hare abundance (Doyle and Smith 1994). Goshawks in Scandinavia likewise rely on a single prey taxon and show changes in productivity and occupancy based on the annual abundance of four grouse species (subfamily Tetraoninae) (Tornberg et al. 2005). In contrast, goshawks in the American Southwest have a wide prey base and regularly take some fourteen different species (Clint W. Boal and Mannan 1994). Fluctuations in goshawk productivity in this region are small and driven by total prey abundance, though the most influential single species is red squirrel (*Tamiasciurus hudsonicus*) (Salafsky et al. 2007). These examples suggest the identity and influence of key prey species in such an adaptable predator may be specific to each region.

In British Columbia, Canada, the coastal population of northern goshawks is the subject of federal and provincial management which focuses on the protection of breeding habitat to increase nest site availability (COSEWIC 2013). Like many raptors, goshawk populations are generally considered to be limited by both nest site availability and prey abundance (Reynolds, Wiens, and Salafsky 2006; Rutz et al. 2006). However, current management plans do not include protections for foraging habitat or actions to increase prey populations, in part due to a lack of knowledge regarding goshawk diet and foraging behavior in this region. Goshawk diet in the coastal Pacific Northwest is variable, with hawks on Vancouver Island, British Columbia, consuming primarily red squirrels (Ethier 1999), whereas hawks in nearby southeast Alaska (Lewis, Titus, and Fuller 2006) and western Washington (Bloxton 2002) take mostly medium and large birds. Even within British Columbia, a gradient of forest types from wet coastal to dry interior may produce dietary variation at smaller scales (NGRT 2008). Detailed, local information on goshawk diet and its effect on reproductive success is necessary if limiting factors beyond nest site availability are to be included in management plans.

Here we describe the breeding season diet of northern goshawks in coastal British Columbia over a two-year period. We assess whether goshawk diet differs within this region between the wetter *coastal* zone and the drier *transition* zone. We further evaluate whether dietary variables (composition, diversity) influence goshawk reproductive success.

# Methods

### Study Area and Species



In North America, the northern goshawk ranges from boreal forests of the Yukon south to high-elevation forests of Arizona and New Mexico. Two subspecies are recognized: the widespread *atricapillus* and the limited *laingi* (Squires et al. 2020). The *laingi* subspecies was first described on the Haida Gwaii archipelago in British Columbia and is smaller and darker than the *atricapillus* subspecies found elsewhere on the continent (Taverner 1940). The range of this subspecies is limited to the west coast of North America from southeast Alaska through mainland British Columbia and Vancouver Island, possibly as far south as Washington’s Olympic Peninsula (COSEWIC 2013). *A. g. laingi* is considered a species at risk in British Columbia by both the federal and provincial governments due to significant habitat loss from industrial timber harvest (NGRT 2008; COSEWIC 2013).

We studied goshawks in southwestern British Columbia, a region characterized by rugged mountains interspersed with coastal fjords and low-lying valleys. The maritime climate supports temperate rainforest dominated by Douglas-fir (*Pseudotsuga menziesii*), western redcedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) (Meidinger and Pojar 1991). The goshawk population in southwestern British Columbia is currently classified as *A. g. laingi*, though new genetic evidence may lead to future reclassification (Geraldes et al. 2018). Within this region, goshawk managers have delineated a *transition zone* comprised of low-elevation valleys connecting the wet forests of the *coast zone* with the dry interior forests east of the Coast Mountains. This narrow transition zone contains forest types intermediate between the western and eastern forests and likely represents an area of overlap between the coastal *laingi* population and the interior *atricapillus* population (NGRT 2008).

### Data Collection

We assessed goshawk diet during the 2019 and 2020 breeding seasons through a combination of egested pellets, prey remains, and nest camera photos. Active goshawk nests were located as part of long-term population monitoring conducted by the British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development (FLNRO) (for detailed survey methodology see McClaren (2005)). Some sites contained active nests in both years of the study.

Prey remains and egested pellets were collected from 33 nests (2019 *n* = 18, 2020 *n* = 15). Pellets and remains were gathered from beneath active nests, from within nests after juveniles had fledged, and from plucking posts located within the territory. For most sites, pellets and remains were collected once during the breeding season, but some sites were visited multiple times. All prey remains and all pellets from a collection location (i.e., one nest or one plucking post) were combined into a single sample for each visit to that location.

At a subset of these nests (2019 *n* = 6, 2020 *n* = 7), cameras were installed to record prey delivered to goshawk chicks. Nest cameras are an effective and relatively unbiased method of measuring avian diet (García-Salgado et al. 2015 ; Harrison et al. 2019). However, cameras may overestimate prey deliveries because goshawks cache prey items for redelivery to the nest at a later time, creating a risk of double-counting items. Due to the discrete nature of our data, we were unable to differentiate cached, re-delivered items from new items and did not attempt to account for caching in our analysis. We also did not attempt to differentiate between prey consumed by the female at the nest and prey consumed by the chicks.

Nest cameras were digital trail cameras (Reconyx brand, UltraFire and HyperFire models) mounted 2-5 meters distant from and slightly above the nest, usually in an adjacent tree. Cameras in 2019 were programmed to take three photos one second apart when triggered by motion, and an additional one photo every thirty minutes. In 2020, cameras were programmed to take five photos one second apart when triggered by motion, and an additional one photo every twenty minutes. Installation took place during the early nestling phase (between 4 June and 18 July) and cameras were left in place until after juveniles dispersed in the fall. Camera site selection was not random but constrained by topography, access, and timing of discovery.

Breeding chronology was not available for most sites. At 12 of the nests with cameras (2019 *n* = 6, 2020 *n* = 6), chicks were aged from photos taken shortly after camera installation using a pictorial guide (Clint W Boal 1994). Productivity was defined as the number of chicks to reach 32 days age (Clint W Boal 1994; McClaren, Kennedy, and Dewey 2002).

### Diet Quantification

We reconstructed prey from pellets and prey remains following a modification of the protocol used by Lewis, Fuller, and Titus (2004). Within each sample, remains were identified to the lowest possible taxonomic category and the minimum number of individuals counted (i.e. 3 hare femurs = 2 *Lepus americanus*). Intact pellets and broken but reassembled pellets were analyzed individually within each sample, while fragmented pellets were combined within each sample. Pellets were dissected and feathers, fur, and hard parts (bones, teeth, claws) were identified to the lowest taxonomic level. We counted the minimum number of individuals represented within the pellet or pellet collection. Prey items from pellets and remains were additionally categorized by size (small = sparrow- or vole-sized, medium = jay- or squirrel-sized, and large = grouse- or hare-sized).

Prey items identified to species were assigned mass using data from the literature. We assigned mass to mammals from Nagorsen (2002) and to birds from Billerman et al. (2020), using the geographically closest estimates available and averaging the mass of males and females. We treated some relatively homogenous genera (such as *Eutamias* and *Myotis*) as a single species. For these genera, we assigned mass by averaging the masses of all possible species, based on range maps. Red squirrels (*Tamiasciurus hudsonicus*) were present at a single site within out study area; when unable to distinguish between the two members of the genus *Tamiasciurus* we assigned the item to the more common *T. douglasii*. Unidentified grouse were common among remains; these were assigned the mean mass of the two grouse species present in our study area. Unidentified items were assigned mass by averaging the masses of the identified species in that size category and taxonomic class. Juveniles were assigned 50% of adult mass.

Data from prey remains and egested pellets are known to be biased indices of diet. Some authors have found combining data from both sources to produce relatively unbiased results that can serve as a helpful supplement to nest camera data (Lewis, Fuller, and Titus 2004; Simmons, Avery, and Avery 1991). However, after testing for differences between pooled pellets-and-remains data and camera data we found significant differences between these two sources. We therefore report results from pellets, pooled pellets-and-remains, and cameras separately. We do not report results from prey remains alone, as diet composition estimates from prey remains are highly biased and infrequently used in raptor diet studies.

Nest camera photos were reviewed and each new prey item delivered to the nest was recorded and identified to species when possible. When items could not be identified to species, they were identified to the lowest possible taxonomic level. Prey items identified from photos were assigned a size category and biomass by the same method used for remains and pellets. Partial items were assigned the average mass for that size category and taxonomic class.

For the overall study area, we quantified goshawk diet in several ways using data from pellets, pooled pellets-and-remains, and nest cameras. For ease of comparison, we simplified prey items into eight broad categories: tree squirrels (genus *Tamiasciurus*), hares (genus *Lepus*), all other mammals, grouse (subfamily Tetraoninae), thrushes (family Turdidae), corvids (family Corvidae), all other birds, and unidentified items. We calculated the relative proportion of avian and mammalian biomass delivered to nests. We also calculated the relative proportion of biomass composed of tree squirrels (genus *Tamiasciurus*), which are known to be an important source of prey for goshawks in British Columbia (Ethier 1999). For nests with cameras, we additionally quantified diet at the level of the individual nest and further calculated diet diversity with Simpson’s Diversity Index (Simpson 1949) using counts of items identified to genus or better. We report all diet quantification as percent of biomass or mean percent biomass the standard deviation except where counts or percent of items is explicitly specified.

### Statistical Analysis

Sites were classified as either coastal or transition based on whether the site centroid fell within the transition zone defined by NGRT (2008). We determined the site centroid by locating the central point between all known nests within each site. To assess differences in goshawk diet between the coastal and transition zones we used counts of items assigned to the eight broad prey categories. We combined all data within each source (pellets, pooled pellets-and-remains, and cameras) and within each zone (coastal and transition). We then tested each data source separately using a chi-squared test with simulated Monte Carlo *p*-values (2000 permutations) due to small sample sizes (Hope 1968). For nests with cameras, we also calculated the proportion of squirrel biomass and diet diversity at the individual nest level and compared these between the zones using a two-sided *t*-test. Finally, we tested for differences in productivity between the two zones using a two-sided *t*-test.

To determine the potential reproductive consequences of dietary variation, we examined how two aspects of diet, diet diversity and proportion of biomass composed of tree squirrels, influenced productivity. We used linear regressions in R (Team 2020) with productivity as the response variable and diet as the explanatory variable. Only one site included in the analysis had an active nest in both years; after confirming the removal of one or the other nest had no significant impact on the results, we included both nests from that site but did not include site as a random factor. Because productivity data were available only from sites with nest cameras and nest-level diet data from pellets and prey remains were sparse, we performed this analysis using only diet data from nest cameras. We used a significance level of *P* = 0.05 for all tests.

# Results

## Goshawk Diet

We identified a total of 135 prey items from pellets collected at 25 nests. Of these, 58% could be identified to genus or better, and no item could not be identified at least to class. From pellets alone, only 9 unique prey species were identified. Another 121 items were identified from prey remains collected at 30 nests, of which 51% were identified to genus or better and none could not be identified to class. From the pooled pellets-and-remains sample a total of 21 unique prey species were identified.

The majority of prey items (75%) identified from pellets were mammals. Squirrels made up 61% of biomass, while other birds (neither grouse, corvids, nor thrushes) made up 21% and other mammals (neither tree squirrels nor hares) made up another 15%. The remaining 4% of biomass was made up of corvids and thrushes.

The combined pellets-and-remains sample showed a very different composition, with only 37% of the diet made up of mammals and the majority made up of birds. The largest prey group was grouse (37%), followed by other birds (23%). Squirrels made up only 14% of the pooled sample

We recorded a total of 518 prey item deliveries on nest cameras, though camera effectiveness varied between sites: an average of 35 items were recorded per site, but one site had only one item recorded while another recorded 69 items. This variability was due to differences in camera placement and sensitivity settings. Some deliveries were obscured from the camera during delivery and consumption and were entirely removed from the analysis. Of the remaining 450 visible items we were able to identify 78% to class and 60% to genus or better. Small and medium birds were disproportionately represented among items only identified to class, frequently arriving at the nest already plucked and decapitated.

We identified 22 different prey species on nest cameras. Mammals made up the largest proportion of prey (73%, mean = 71 12), which was driven by the overwhelming dominance of tree squirrels (*Tamiasciurus* spp.). Birds accounted for only 15% of biomass (mean = 16 10), and the remaining 11% could not be identified to class (mean = 20 27). The largest prey categories were squirrels (49%, mean = 50 14), other mammals (16%, mean = 17 12), unidentified items (11%, mean = 20 27), and thrushes (3% , mean = 4 3). Based on items identified to genus or better, overall diet diversity for the study area was moderate (0.56). Diet diversity of individual nests was highly variable, ranging from 0 to 0.72 with a mean of 0.46 0.21.

## Difference between ecological regions

A chi-squared test of pellet data alone did not show a significant difference between goshawk diet in the coastal and transition zones (2 = 7.53, *P* = 0.1). However, a chi-squared test of the pooled pellet-and-remains data did show a significant difference (2 = 41.75, *P* << 0.05), as did a test of the camera data (2 = 23.84, *P* = 0.003).

Based on data from cameras, nests in the transition zone (*n* = 8) received a slightly higher mean proportion of biomass from tree squirrels than did nests in the coastal zone (*n* = 5; 47% and 57%, respectively), but this difference was not significant (*t*-test3.75 = 1, *P* = 0.38). However, mean diet diversity was significantly higher in the transition zone (0.54) than the coastal zone (0.29, *t*-test10 = -2.26, *P* = 0.047).

## Productivity

We observed no nest abandonment following camera installation. One nest in 2019 failed 9 days after installation when two chicks succumbed to siblicide and the third appeared to fledge prematurely. Two cameras’ memory cards filled prior to fledging, and no productivity data are available for these sites. The remaining 12 nests all fledged at least one chick. Successful nests fledged 1 (*n* = 6), 2 (*n* = 4), or 3 (*n* = 1) chicks. Siblicide was also observed in four other nests, which lost one chick each.

We found no affect on goshawk productivity of either the proportion of diet composed of squirrel biomass (*P* = 0.44) or diet diversity (*P* = 0.28). There was also no significant difference in goshawk productivity between the coastal and transitional zones (*t*-test4.71 = 0.93, *P* = 0.4).

# Discussion

Northern goshawks are generalist predators which consume a broad range of prey species, but not all prey are of equal importance. A single key prey species often contributes disproportionately to goshawk diet, and the identity of this species may be specific to each goshawk population. In coastal British Columbia we found goshawks consumed 29 different species during the breeding season, but the majority of their diet was composed of tree squirrels of the genus *Tamiasciurus*. Across the entire study area this single taxa made up 49% of the total biomass recorded, with the proportion at individual nests ranging from 26% to 86%. Despite the clear importance of tree squirrels in the diet, the proportion of squirrel biomass did not influence goshawk productivity, nor did dietary diversity.

Across much of North America, the key goshawk prey species is usually mammalian, often from the family Leporidae or Sciuridae (Clint W. Boal and Mannan 1994; Doyle and Smith 1994; DeStefano et al. 2006; Miller, Carlisle, and Bechard 2014). However, in the coastal temperate rainforests of the Pacific Northwest goshawk diet generally contains more birds than mammals and the key prey is usually a species of grouse (subfamily Tetraoninae) (Watson et al. 1998; Thraikill, Andrews, and Claremont 2000; Bloxton 2002; Lewis, Titus, and Fuller 2006). Despite inhabiting coastal rainforests, goshawks on Vancouver Island, British Columbia, consume primarily red squirrels (*T. hudsonicus*), with this single species making up 69% of the diet (Ethier 1999). Our results from the coastal mainland of British Columbia are consistent with findings from Vancouver Island and more broadly with results from the interior of North America, but stand in contrast to findings from elsewhere in the Pacific Northwest.

The variation in key prey species between goshawk populations reflects the diversity of habitats which goshawks inhabit. Within our study area, low-elevation mountain valleys bridge the wet forests of the coast and the dry forests of the interior, creating a narrow region of intermediate habitat types where coastal and interior goshawk populations may overlap (NGRT 2008). At this smaller scale, we found evidence of a difference in diet composition and diversity between the coastal and transition zones. However, the identity of the key prey, tree squirrels, was the same in both zones and comprised an equally large proportion of the diet in each. This suggests that, while transition zone habitats give hawks access to a wider range of prey species than coastal zone habitats, these alternate prey fail to replace tree squirrels in importance.

Multiple studies have found a link between the abundance of a key prey species and goshawk demographics, including reproductive success. Following the assumption that a generalist predator consumes prey species relative to their abundance, diet composition may be used as proxy for prey abundance, although this assumption has rarely been made in raptors (but see Resano‐Mayor et al. (2016)) and never in goshawks. Under this assumption, if tree squirrel abundance influences goshawk productivity then the proportion of squirrel biomass delivered to a nest should be related to the number of young fledged. Alternatively, a diverse diet may indicate a wide prey base which buffers against fluctuations in the abundance of any single prey species. Our study found no support for either hypothesis. There is evidence that goshawks select prey in proportion to their abundance, but also that goshawks can be highly specialized. Without data on prey abundance within our study sites it is difficult to draw any strong conclusions regarding goshawk selectivity and its reproductive consequences; however, it is notable that the only nest in our study to experience a complete breeding failure received the smallest proportion of squirrel biomass out of any nest.

Our conclusions are complicated by the multiple methods of collecting and measuring diet data used in our and other studies. We used three methods to collect data on goshawk diet–egested pellets, prey remains, and nest cameras–and found significant differences between the results they produced. Cameras are widely considered one of the least biased methods for measuring diet at the nest in raptors (Tornberg and Reif 2007; García-Salgado et al. 2015; Harrison et al. 2019). We therefore consider our results from nest cameras to be the truest approximation of goshawk diet, although we acknowledge that cameras are not entirely free of bias. Compared to cameras, prey remains were the most biased, grossly overestimating the proportion of avian biomass in the diet. For this reasons we did not analyze prey remains separately; however, the pooled pellets-and-remains sample was also biased toward avian prey. Pellets alone were the least biased in coarse composition, but severely underestimated species richness. Measuring diet composition by counts or biomass adds further uncertainty, with counts overestimating avian prey relative to biomass. These complex results highlight the importance of clearly reporting the source and measurement of raptor diet data. Because all of these methods have been used in past studies we believe there is value in reporting the results of each for ease of comparison. However, we recommend future diet studies prioritize collecting data via cameras, either video or still images, rather than physical specimens.

Our study addresses a fundamental question regarding the basic ecology of an at-risk population of northern goshawks, but many more remain unanswered. While nest cameras are an effective way to measure prey delivered to the nest they cannot record prey consumed by adults away from the nest, prey consumed by juveniles after they have fledged, or prey consumed during the winter. As a result, we captured an incomplete picture of breeding season diet and have no insight into nonbreeding season diet. Additionally, we collected no data on prey abundance and so cannot draw conclusions regarding goshawk prey selection or individual specialization. These limitations are not exclusive to our work: few studies have successfully combined prey abundance with both goshawk diet and reproductive success, and no North American study has comprehensively addressed goshawk diet away from the nest (Rutz et al. 2006; Squires and Kennedy 2006). Filling these gaps represents an important step for future studies which seek to improve goshawk management in British Columbia and elsewhere in the species’ range.

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