

Ideal free eagles: bald eagle distribution patterns and use of kleptoparasitism on salmon rivers

by

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Abstract

During the autumn, migrating bald eagles (*Haliaeetus leucocephalus*) aggregate on coastal rivers to scavenge post-spawning salmon carcasses. In this thesis, I measured the abundance of eagles and salmon carcasses on a set of four adjacent rivers along the east coast of Vancouver Island, British Columbia. Salmon carcasses first appeared in late September, increased in abundance until mid-November, and thereafter declined. The total number of eagles tracked the temporal and spatial abundance of salmon carcasses, and generally distributed across the rivers according to the predictions of Ideal Free Distribution. I determined that the incidence of kleptoparasitism matched the distribution of eagles, and found that kleptoparasitism attempts between eagles were affected by the age of the attacker and the behavioural tactic used. Overall, my results indicate that salmon abundance affects the regional distribution patterns and use of kleptoparasitism among aggregations of foraging eagles.

Keywords: bald eagles; salmon; Ideal Free Distribution; kleptoparasitism; sociality

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Chapter 1.

General Introduction

Bald eagles (*Haliaeetus leucocephalus*) are soaring raptors that have recovered from severe population declines that were caused by the contamination of prey resources from the noxious pesticide Dichlorodiphenyl-trichloroethane (DDT) (Grier, 1982). Now widely distributed across North America, eagle populations range from northern Canada to Mexico. For the population of bald eagles distributed across the Pacific Northwest, their spatial and temporal movement patterns are largely driven by the life cycle of Pacific salmonids (Hunt et al. 1992; Elliot et al. 2011; Stalmaster, 1983; Field and Reynolds, 2013). During the fall months, eagles leave their summer breeding grounds to follow migrating salmonids as they return to their natal rivers to spawn (Knight and Knight, 1983). As post-spawning carcasses accumulate, large numbers of bald eagles aggregate on riverbanks to consume carcasses. However, as the spawning season progresses, carcass abundance begins to decline and intraspecific competition ensues, resulting in individuals using kleptoparasitism to steal carcasses from conspecifics (Bennetts and McClelland, 1991). Despite the high densities of eagles that aggregate on salmon-bearing rivers, little is known about their regional temporal and spatial distribution patterns. Thus, examining their numerical response and foraging behaviour across salmon-bearing rivers is critical for elucidating their distribution patterns on a regional spatial scale. Since eagles inhabit both pristine ecosystems and urban spaces across North America, patterns observed on regional spatial scales can then be applied to continental scales to further understand their movement patterns among resource patches.

While the regional-scale migration of bald eagles from northern latitudes to coastal rivers in British Columbia is driven by the spawning cycle of Pacific salmonids, their temporal distribution patterns among rivers are facilitated by sociality among conspecifics (Restani et al. 2000). As soaring conspecifics can be seen from a distance of 40-65 km (McClelland et al. 1982), eagles use local enhancement and visual cues from soaring eagles to locate ephemeral food patches (Knight and Knight, 1983). After locating a salmon-bearing river, eagles aggregate on riverbanks, typically arriving at the

peak of carcass availability without a time lag (Restani et al. 2000; Knight and Knight, 1983; Elliot et al. 2011). Juvenile eagles have been found to arrive on rivers earlier than adults, and also show a closer numerical synchrony to the abundance of salmon carcasses than their older conspecifics (Bennetts and McClelland, 1991; (Restani et al. 2000; Miller et al. 2006). While there may be a discrepancy between the arrival of juvenile and adult eagles on salmon-bearing rivers, the numerical response of both age classes is strongly correlated to post-spawning carcass abundance (Fitzner and Hansen, 1979; Hansen, 1986; Restani et al. 2000; Bennetts and McClelland, 1991). Consequently, the abundance of ephemeral salmon carcasses is determined to be the primary factor driving their temporal distribution patterns among resource patches (Stalmaster and Gessaman, 1984). The spatial distribution patterns of eagles among rivers has been shown to be effected by abiotic factors that are unique to each river ecosystem. Water levels and precipitation regimes during the winter months affect the amount of salmon biomass available for scavenging eagles (Stalmaster and Gessaman, 1984). Additionally, the physical features of the rivers, like position of tidal flats, affect the density of salmon carcasses that accumulate in river estuaries (Watson et al. 1991). While few studies have examined eagle spatial distribution patterns, there has yet to be a study utilizing the theory of Ideal Free Distribution to examine the distribution patterns of bald eagles in response to salmon carcass abundances across rivers.

Ideal-Free Distribution Theory

A well understood principal in behavioural ecology, the theory of Ideal-Free Distribution (IFD) examines the spatial distribution patterns of a population as a function of resource abundance in a patch and individual choices. IFD was initially proposed in 1970 by Fretwall and Lucas, and predicts that individuals will distribute to patches which leads to equal resource intake rates, even if patches vary in quality. To accomplish this state, it is assumed that individuals are fully informed on habitat quality ('ideal'), and are assumed 'free' because they can enter a patch without costs in time or energy (Fretwall and Lucas, 1970). Additionally, individuals are assumed to be of similar competitive ability so that resources are divided equally among individuals (Fretwall and Lucas, 1970). Resources are assumed to arrive at a constant rate into patches ('continuous input'), so that the proportion of individuals in a patch is proportional to the input of resources into the patch, therefore producing a 1:1 ratio. Thus, when the number of

individuals in a patch proportionally matches the amount of resources, Ideal Free Distribution occurs. While IFD has been used as the underlying theory in many studies examining animal distribution in response to the proportion of prey abundance, IFD has yet to be applied to a population of bald eagles distributed across salmon-bearing rivers. As the influx of post-spawning carcasses that become available to foraging eagles is relatively constant during the spawning season, the salmon-eagle relationship provides an ideal study system to further examine eagle spatial distribution patterns under the theoretical context of Ideal Free Distribution.

Kleptoparasitism in bald eagles

In addition to facilitating the temporal aggregations of bald eagles on rivers, sociality plays an important role in determining the type of foraging behaviour eagles implement to acquire resources (Stalmaster and Gessaman, 1984; Knight and Skagen, 1988; Bennetts et al. 1997). To acquire prey, bald eagles utilize foraging strategies best suited to their age, morphology, social dominance and the time required to learn each foraging technique (Marchetti and Price, 1989; Knight and Knight, 1983). In large aggregations of eagles with high intraspecific competition, implementing kleptoparasitism to steal food resources from conspecifics leads to higher energy gains compared to moving to another resource patch to scavenge (Fischer, 1985). The main factor that has been found to effect the outcome of kleptoparasitism attempts is the age of the individual attacking a conspecific. Indeed, several studies have determined that the age of the individual determined the frequency of attacks, the type of behavioural tactic used and the outcome of the interaction (Restani et al. 2000; Bennetts and McClelland, 1991).

As kleptoparasitism is a learned behaviour, younger birds must learn by watching older more experienced eagles in their interactions (Jorde and Lingle, 1988). Adult eagles have been shown to increase their frequency of attacks with an increase in salmon carcass abundance, while the frequency of attacks implemented by juveniles remained the same (Restani et al. 2000). In addition to the rate of attacks, there is a discrepancy in the type of behavioural tactic used by age classes in kleptoparasitism attempts. Identified as ground or aerial-based tactics, several studies have examined the use of these behaviours among juvenile and adult kleptoparasites (Restani et al. 2000; Bennetts and McClelland, 1991; Hansen, 1986; Knight and Knight, 1983). Juveniles

have been found to favour aerial-based tactics, which require more skill and experience than ground-based tactics (Bennetts and McClelland, 1991). While juveniles have been found to be more aggressive in their tactics, they have a lower successful rate than their older conspecifics (Benetts and McClelland, 1991; Knight and Knight, 1983). Conversely, adults seem to favor ground-based tactics, and experience a higher success rate in their attempts to steal (Knight and Knight, 1983, Hansen, 1986). From these studies, it is clear that the age of eagles, which drives the level of learned behaviour and foraging experience, effects the frequency of interactions, the behavioural tactic used and the outcome of the interaction.

In this thesis, I build on previous research that has examined the temporal and spatial distribution patterns of migrating eagles in response to high densities of post-spawning salmon carcasses. I accomplish this by examining the temporal movement of eagles on salmon-bearing rivers and determine if their distribution across resource patches comply to the theory of Ideal Free Distribution. To determine this, I compare the proportion of eagles to the proportion of salmon carcasses on each river to determine if they distribute according to the 1:1 ratio that is predicted under IFD. As there has yet to be a study using IFD to examine a population of eagles, this thesis provides further insight on their movement patterns at a regional spatial scale. In Chapter 3 of this thesis, I examine the effect that age has on kleptoparasitism behaviour. Specifically, I examine the relationship between the age of the target and attacker, the behavioural tactic used and the outcome of the attack. Additionally, I provide the first study that predicts the probability of a successful kleptoparasitism attack at predicted salmon abundances. Finally, in Chapter 4, I summarize the findings in the previous chapters and place my results in the context of a larger body of research. Ultimately, this thesis examines the relationship between spawning salmonids and bald eagles by examining their distribution patterns and foraging behaviour, which defines the life history of eagles distributed across the coast of British Columbia.

Chapter 2.

Bald eagle distribution in response to salmon availability on four spawning rivers

2.1. Abstract

I examined the distribution of bald eagles (*Haliaeetus leucocephalus*) across a set of rivers located on Vancouver Island, as the abundance of salmon carcasses increased and subsequently declined over the duration of the spawning season. I compared the observed distribution to the predicted distribution under Ideal Free Distribution (IFD), and determined that physical features of rivers influenced the size of eagle aggregations. I found that eagle and salmon abundances were positively correlated both temporally and spatially, and generally matched the distribution predicted by IFD. The within-river response of bald eagles to an increase in salmon abundance was strongest on the Little Qualicum river, compared to the other three rivers. I attribute this difference to the physical features of the river systems, such as sandbars and mudflats, which varied in area. These results suggest that sandbars and mudflats are important habitat characteristics which can determine the density of eagles that aggregate in river estuaries to scavenge salmon carcasses.

2.2. Introduction

A goal of behavioural ecology is to describe and predict the distribution of organisms, and determine how this may result from competitive interactions and foraging choices made by individuals (Koops and Abrahams, 2002). Scavengers in particular are an example of a meta community that assembles, competes over available resources and then re-distributes in a relatively short period of time (Kendall et al. 2014). Among the avian guild, bald eagles are opportunistic scavengers that capitalize on migrating prey species and ephemeral food patches. For the population of bald eagles found along the Pacific Northwest coast, adult salmonids returning to their natal rivers to spawn represent an ephemeral food resource that notably effects their distribution patterns.

As the relationship between eagles and spawning salmon is a relatively simple scavenger-prey system, comprised of two species occurring at high densities (Restani et al. 2000), the responses of bald eagles to salmonids has been a topic of research since the late 1970s. Numerous studies have examined the numeric responses of bald eagles to post-spawning carcasses, which determined that eagle abundance is positively correlated with the abundance of spawned out salmon, and is the primary factor influencing distribution patterns across patches (Fitzner and Hansen, 1979; McClelland et al. 1982; Stalmaster and Gessaman, 1984; Hansen, 1986; Hunt et al. 1992, Field and Reynolds, 2013). This result was further supported by Restani et al. in 2000, who concurred that carcass availability rather than environmental conditions or migration timing determined the strong numerical response of eagles to kokanee salmon. Within the age groups of bald eagles, there is a discrepancy in the timing and abundance of adult and juvenile eagles that aggregate in response to ephemeral food resources. Aggregations of juveniles have been found to peak earlier in the spawning season, showing closer synchrony with salmon abundance than adults, while older birds have been found to increase and decreased rapidly within a short period of time (Bennetts and McClelland, 1991, Restani et al. 2000). While there have been several studies that examine the numerical responses of bald eagles to ephemeral food patches, there has yet to be a study utilizing the theory of Ideal Free Distribution to examine the distribution patterns of bald eagles in response to salmon abundances across rivers.

The Ideal Free Distribution is a fundamental concept in behavioural ecology that has been used to describe and predict animal distribution patterns across landscapes. For example, IFD was used to examine the density and distribution of searching male toads in ponds, which determined that their densities were consistent with the number of arriving females and the predictions of IFD (Davies and Halliday, 1978). Similarly, IFD was used to examine the distribution of coho salmon relative to drifting prey in stream channels, which determined that their distribution patterns did not match a predicted IFD pattern (Grand, 1997). The original theory, developed by Fretwell and Lucas (1970), assumes that individuals are fully informed about habitat quality ('ideal'). Additionally, individuals are assumed 'free' to enter any patch without costs in time or energy, and are assumed to be of equal competitive ability so that the resources are divided equally (Fretwell and Lucas, 1970). Therefore, the basic model predicts that the resultant distribution of individuals is such that each individual has equal resource intake gain

even if patches vary in quality, producing the Ideal Free Distribution. The outcome is an evolutionarily stable state (ESS), at which point no (unilateral) move to another patch would be advantageous (Maynard Smith, 1982). The underlying assumptions have been modified into several variants including whether resources are continually replenished or depleted, whether the competitors are of equally competitive ability or not, or whether individuals are present or not.

In this study, I adopt a version of the IFD model that assumes 'continuous input' of resources into each patch. Each individual's intake rate is contingent on the resource input rate and the number of competitors occupying the patch. The intake rate for an individual can be expressed algebraically as:

$$W_i = Q_i / n_i, \quad (1)$$

where:

W_i = the average gain rate in patch i

Q_i = the input rate into patch i

n_i = the number of competitors in patch i

In the continuous input model, gain rates for all patches are predicted to be equal, where $W_i = Q_i / n_i$ is constant for patches i, j, k etc. (Tregenza, 1995) This process results in patches being occupied in proportion to the fraction of the total resources that enter the patch, also known as 'input matching'. If all assumptions are met and input matching occurs, an Ideal Free Distribution pattern is observed (Parker, 1978). While a continuous input of resources is a relatively uncommon scenario in nature (Tregenza, 1995), in the systems where it does occur, input matching has been supported by numerous studies. In the study by Parker (1978) male dungflies have been shown to match the input of females to a cowpat. Similarly, in pools that receive varying levels of light which results in different algal growth rates, catfish have been found to distribute proportionally to the available algae (Power, 1983). On the Pacific Northwest coast, a continuous input scenario is represented by anadromous Pacific salmonids returning to their natal rivers to spawn. After completing their spawning cycle and dying, the salmon carcasses provide scavenging eagles with a 'continuous input' of food biomass during the fall months.

Here, I investigated the distribution patterns of bald eagles within four rivers on Vancouver Island by examining their numerical responses to post-spawning salmon carcasses. To determine their temporal distribution patterns, I compared the movement of eagles in relation to salmon abundance over time. I examined their spatial distribution patterns by comparing the proportion of eagles to the proportion of salmon on each river, and compared these estimates to the predictions of IFD.

2.3. Methods

This study was conducted on four rivers on the central coast of Vancouver Island, British Columbia in the autumn of 2017. These rivers are located in the Nanaimo Lowland, which is characterized by Coastal Western Hemlock Zone and Douglas-Fir subzone habitats. The rivers used in this study include the Englishman River, the Little Qualicum River, the Big Qualicum River, and Rosewall Creek. All four rivers are managed under Salmon Escapement Programs by the Department of Fisheries and Oceans Canada for the purpose of increasing salmon abundance.

2.3.1. Description of field sites

I established two fixed field sites on each river, one located in the upper reaches of the river and the other in the estuary (Appendix A). The upper field sites were 50-100 meters in length, and were characterized by understory vegetation covered by a dense canopy, which extended from the banks of the rivers inland. In the river, there were natural obstructions like large logs, small waterfalls, and gravel bars that typically prevented carcasses from washing downstream. Stationary observation points were positioned in one location so that the entire field site was visible for censuses.

The lower field sites were located on the river estuaries, which ranged from 50-300 meters in length and were characterized by marsh vegetation with surrounding conifer forests. All estuaries had sand and gravel bars that were exposed during low tide and accumulated carcasses that were washed downstream. The observation points were positioned so the entire estuary was visible. In both upper and estuary field sites, censuses occurred on one side of the river only, as many of the rivers were accessible only from that direction.

2.3.2. Englishman river

The Englishman river is the longest system in the study, reaching 40 km in length (Appendix A, Figure A1). Due to intense logging that occurred on the Beaufort mountains, the watershed and upper reaches of the river are susceptible to flash flooding in the winter and low water flows in the summer (Brown et al. 1977). The river estuary is 129.5 ha, and was cleared in 1873 for farming and later dyked and dredged for a resort complex (Clough, 2013). In 1996 the estuary became a part of the United Nations Mount Arrowsmith Biosphere, however, despite extensive restoration projects the freshwater and estuarine habitat has yet to recover. The river supports all six species of Pacific salmonids, though escapements have been declining since 2000.

The upper field site of the Englishman river is located 7 km upriver and is characterized by deep pools and rocky river banks, which slope slightly upward until they transition to terrestrial vegetation. The field site features a dense coniferous forest which provides many options for perching eagles. While the extensive river rock bars in the river act as natural barriers, there were little to no salmon carcasses observed on the upper field site of the Englishman.

The lower field site is located in the estuary of the river, and comprises a small area within the 129 ha estuary. It is tidal influenced and is distinguished by aquatic grasses and large mud flats when the tide is out. There are several downed trees that act as perches for eagles during low tide to view and scavenge salmon carcasses. However, due to the low escapement of salmon, very few carcasses are caught by the natural obstructions and accumulate.

2.3.3. Little Qualicum river

The Little Qualicum river flows northeast and drains from Mount Arrowsmith in the Beaufort Mountains, a drainage that extends 251 km² in area, and hosts all species of Pacific salmon except for sockeye (Appendix A, Figure A2). The river has a DFO hatchery complex which is located 5 km from the mouth of the river. During the fall months the number of returning adult salmon are controlled and directed into artificial spawning channels. Some spawners are allowed to remain in the main stem of the river where gravel beds have been artificially enhanced to promote embryo survival. While the

river and artificial spawning channels aim to increase salmon production, the system is susceptible to rapid water discharge and high-water levels during periods of intense precipitation. Therefore, many spawners and post-spawning carcasses are washed downriver during fall rains.

The upper field site is located on the grounds of the hatchery complex and is characterized by a large gravel bar extending from the banks of the river. The gravel bar acts as a natural barrier and catches many post-spawning carcasses that drift downriver and provides perching space for scavenging eagles. Additionally, the numerous conifers that parallel the river provide abundant perches for scavenging eagles to view the stretch of the river.

The mouth of the river is characterized by a large estuary, which is 78 ha in size and designated as a protected National Wildlife Area. The lower field site has several large gravel and sand bars extending away from the riverbanks and shoreline which are exposed during low tide. In addition to providing large areas for eagles to perch, the gravel bars also catch many post-spawning salmon carcasses that are washed downriver. These gravel bars facilitate scavenging of post-spawning salmon carcasses by eagles as well as other bird species like gulls, ravens and crows. Beyond the gravel bars and shoreline, a large expanse of estuarine vegetation parallels the river banks, which then transitions into drier soil and sparse vegetation. Due to the physical features of the lower field site of the Little Qualicum river, there is ample space on the gravel bars for scavenging eagles to aggregate and scavenge salmon carcasses.

2.3.4. Big Qualicum river

The Big Qualicum river is 11 km long and flows out of Horne Lake at the base of the Beaufort mountains (Appendix A, Figure A3). The river hosts all species of Pacific salmon, with chum representing the highest number of spawners. A DFO hatchery complex is located 2.5 km up the main stem of the river, and features extensive artificial spawning channels. Similar to the Little Qualicum hatchery, many of the returning adult salmon are directed into artificial spawning channels to complete their life cycle. The remaining salmon are directed towards the main stem of the river, which has undergone extensive physical alterations to provide spawning habitat that enhances embryo and smolt survival. In addition to controlling the number of spawners that enter the river, the

hatchery also controls the dam at the base of Horne Lake to regulate the water levels and discharge rate.

The upper field site on the Big Qualicum river is located 4.5 km upriver from the hatchery, at roughly 6.5 km from the mouth of the river. The field site is characterized by a dense conifer forest that lines the riverbanks and features natural obstructions in the water like woody debris. A small sandbar is located in the middle of the river, which is comprised of vegetation and river rocks. Despite the natural obstruction the sandbars provides, the number of post-spawning carcasses that did accumulate in the upper field site was very low.

The lower field site is positioned on the land surrounding the mouth of the river, which is located within Qualicum First Nation territory. There is one gravel bar present in the field site which naturally catches salmon carcasses that wash downriver. During low tide, the shoreline is exposed and provides space for a variety of bird species to aggregate and forage on salmon carcasses. The habitat extending from the banks of the river is not natural, as it is used as a campground and RV park during the summer and early fall months. Extensively managed grassy fields which feature few trees and little to no understory vegetation flank the riverbanks. While the lack of forest facilitates human access, the artificial landscape and presence of humans may deter eagles from scavenging salmon in the mouth of the river.

2.3.5. Rosewall Creek

Rosewall Creek is the smallest and most natural system used in the study (Appendix A, A3). At 12 km long, the creek and its main tributary, Roaring Creek, drain out of the Beaufort mountains. Similar to the Englishman River, the forest along the lower reaches of the river was logged during the early 20th century until a provincial park was established in 1956. At the mouth of the river, there is a small DFO hatchery, although unlike the Big and Little Qualicum rivers, there are no artificial spawning channels.

The upper field site is located 1 km upriver and is defined by a steep riverbank on the West side and a gradually sloping river rock bank on the East side of the river. A dense coniferous forest lines both riverbanks, providing branches for perching eagles.

Low water levels and discharge rates characterized Rosewall creek during the field season, which delayed upriver migration by spawners until mid to late October. After completing their spawning cycle, post-spawning carcasses became wedged between rocks in the creek bed due to the low discharge rates. This facilitated access for foraging eagles, although it required individuals to stand in the creek or move them to the riverbank for consumption.

The lower field site is located at the mouth of the river, and is characterized by estuarine habitat with dense coniferous forests surrounding the estuary. The field site is tidal influenced, with the majority of the field site being submerged during high tide. During low tide the field site is comprised of mud flats and several small rock bars. Due to the flash flooding that the system was susceptible to, many carcasses that accumulated upriver were washed downriver and out into the Strait of Georgia before they could accumulate in high abundances on the tidal flats. When carcasses did accumulate, eagles would perch on the mud flats during low tide to consume them.

2.3.6. Point-Count Surveys

The data used in this study were gathered from late-September to mid-December 2017, spanning 88 days and encompassing virtually the entire duration of the salmon spawning season. The rivers were visited in a set sequence when possible (bad weather and flooding occasionally precluded this), with a visit to each river occurring in each of 13 four-day cycles. Both the upper and lower field sites were visited on each occasion. During each visit an observation period of 1.5 hours was utilized to conduct point-count surveys of bald eagles and salmon. The upper field site was surveyed in the morning as eagles are most active in the morning, while the estuary field site was surveyed during the afternoon low tide. Bald eagles present in the field sites were identified by their plumage patterns as adults typically have predominately white heads and tails, while juveniles have dark brown or mottled brown plumages.

During each visit to a field site I counted the number of spawning salmon, post-spawning carcasses, 'salmon portions', bald eagles and all other species present in the field site. Spawning salmon were classified as any live salmon that were visually identifiable in the river. 'Salmon portions' are pieces of the carcass (flesh or bone) separated from the remainder of the salmon carcass. Hereafter, the combination of

salmon carcasses and salmon portions that were present in field sites will be referred to as 'salmon'. Salmon that were located in less than 12 cm of water and were available for eagle consumption were tallied. Repeated counts of the same salmon between successive visits were prevented by documenting the species and the location within the field site. If the salmon were too decomposed or too small to identify the species, a description of its location within the field site was provided. Upon the arrival during the sequential visit, these observations were reviewed prior to conducting a count to prevent repeated measures of salmon that were previously counted.

2.3.7. Data Analysis

Temporal and spatial distribution patterns

I described the temporal distribution patterns of eagles by fitting a local polynomial regression (Loess) model to the total salmon and eagle abundances (i.e. over all four rivers) in relation to the 13 observation cycles. To examine the spatial distribution patterns of eagles on each river, I compared the mean abundance of eagles across observation cycles to the mean abundance of salmon. To test predictions of IFD, I pooled the estimates of salmon and eagle abundances from the upper and lower field sites. For all 13 observation cycles, I calculated the proportion of salmon and eagles on each river out of the total abundance on all four rivers. I completed these calculations for each river. I regressed the proportion of eagles on the proportion of salmon, and used an ANOVA to test whether the slope differed from that expected ($= 1.0$) under the IFD.

Model Analysis

To further examine the effect of salmon abundance on the numerical response of bald eagles, a statistical model approach was used to describe patterns in these data. Of the potential models to implement, I considered a Generalized Linear Model to be the most insightful because it allows for within-river comparisons of eagle abundances in response to an increase in salmon abundance. I conducted all analysis in R Studio Statistical Environment (version 3.5.1, R Core Team 2018).

Prior to running a model analysis, I screened for temporal and spatial correlation between salmon and eagle abundances. To accomplish this, I ran an Auto-Correlation Function (ACF), which determines if there is temporal autocorrelation between the

predictor and response variables at each timestep. I ran an ACF on the residuals of a simple linear regression between observation cycle and salmon ($r=0.25$), and observation cycle and eagle abundance, which determined there was no correlation between variables ($r=0.16$). Since there was no significant correlation found, it was not necessary to include the observation cycle variable in the model analysis, as the effect of time on salmon and eagle abundances is adequately captured in the those variables. In addition to a temporal ACF, a Mantel spatial autocorrelation function was performed to determine if average bald eagle abundances were correlated across field sites. This function uses a Monte Carlo approach to compare the average observed eagle abundance to the latitude and longitude gradients of the field sites (Appendix A, Table A1). The function determined that no spatial correlation was found between the average eagle abundances and field sites ($r= -0.16$, $p= 0.59$).

A global model contains a set of variables to account for the study design and are biologically relevant to the research questions (Burnham and Anderson, 2002). I performed a model competition between all possible models containing the factors salmon, river, and field site, and the salmon by river interaction. I included the field site variable to account for the study design, which had non-independent repeated measures in the upper and lower field sites.

The model selection process was based on Akaike's Information Criterion approach corrected for small sample size (AICc) to determine the most suitable model parameterization (Burnham and Anderson, 2002). I examined the Akaike weights (w_i) to determine the amount of evidence indicating the best candidate model for the data (Wagenmakers and Farrell, 2004). I validated the final GLM by plotting the Pearson's residuals against the predicted values, as well as against each explanatory variable in the model. I also calculated the generalized R^2 to assess the model fit using the methods described in Agresti (2012).

2.4. Results

2.4.1. Description of Bald Eagle Abundances and Distribution Patterns

I observed a total of 564 salmon and 944 bald eagles over 13 observation cycles spanning from September 29 to December 3, 2017 (Table 2.1). During this time there

was an average total of 43 salmon and 71 eagles per observation cycle across all rivers (Table 2.1). The abundance of salmon rose and fell over the duration of the spawning season, with the peak abundance occurring during the 8th observation cycle with 120 salmon observed. The total abundance of eagles followed a similar pattern, reaching peak abundance during the 9th observation cycle at 130 individuals. The abundance of salmon and eagles that aggregated on each river was not uniform; the highest abundance occurred on the Little Qualicum river and the lowest on the Englishman river (Table 2.1). The mean abundance on the Little Qualicum was 15 individuals per observation cycle while the mean abundance on the Englishman river per observation cycle was 1 individual (Figure 2.2). Rosewall creek and the Big Qualicum river had similar mean abundances of eagles (Figure 2.2). Summary statistics of eagle temporal and spatial distribution patterns and abundances are given in Table 2.1, Figure 2.1 and Figure 2.2.

2.4.2. Ideal-Free Distribution Analysis

From the linear model results, it is clear that the total number of eagles was correlated with the total number of salmon across all rivers ($R=0.73$, $p<0.001$; Figure 2.4). The slope of the linear model examining the proportion of eagles across the rivers is 0.66, which is shallower than the predicted slope of 1 under the IFD (ANOVA; $p<0.001$). Despite this, it is clear that eagles generally matched IFD predictions (Figure 2.4).

2.4.3. Generalized Linear Model

The results of the model competition are given in Table 2.2. The top model carries almost all the model weight, and contains the factors salmon, river and field site, with no interaction terms. Effect sizes are given in Table 2.3. The model results indicate that the intercept of the Big Qualicum river is 8 eagles ($p=0.015$; Table 2.3). On the Little Qualicum river, the expected eagle abundance is higher than the baseline by 12 individuals, resulting in an intercept of 20 eagles ($p=0.0038$; Table 2.3). In contrast, the expected eagle abundance on Rosewall creek is lower by 1 individual in relation to the baseline. This slight decrease in predicted eagle abundance results in an intercept of 7 eagles on Rosewall creek ($p=0.937$; Table 2.3). Finally, the predicted eagle abundance

on the Englishman river is lower by 2 eagles compared to the Big Qualicum, resulting in a intercept of 6 eagles ($p=0.59$; Table 2.3).

In addition to the influence of river identity, the location of field sites has a significant effect on expected eagle abundances. The model determined that on lower field sites, the predicted eagle abundance when there are no salmon is 8 eagles ($p=0.0086$; Table 2.3). Contrastingly, when there are no salmon in the upper field sites, no eagles are predicted to aggregate ($p=0.001$; Table 2.3). The final model estimate determined that eagle abundances on each river increased by 0.88 for each additional salmon, indicating there is a positive linear relationship between salmon and eagle abundances (Table 2.3, Figure 2.5).

The results of the model analysis suggest that the expected eagle abundance is higher on the Little Qualicum river in comparison to the baseline river, while the Englishman river is predicted to experience the smallest eagle abundance. Within the rivers, eagles are expected to aggregate in higher abundances on the lower field sites, which are located in estuaries and river mouths, in comparison to the more densely forested upper field sites. Although eagles are predicted to aggregate in varying abundances on each river, there is an overall linear increase in eagle abundance in response to salmon abundance across all four rivers. Further detailed results from the model analysis can be found in Table 2.3. The model performance test, which includes the generalized R^2 of 0.44, suggests that the model performed adequately well and appropriately accounts for the variance in estimates.

2.5. Discussion

Using 52 days and 13 observation cycles, this study provides new insights into the regional distribution patterns of overwintering bald eagles across salmon spawning rivers on Vancouver Island. First, I found that the total abundance of eagles across all rivers was correlated with the total abundance of salmon, which supports previous findings in the literature (Figure 2.3). Second, I determined that the proportion of eagles that aggregated on each river matched the proportion of salmon quite well, and generally distributed according to IFD (Figure 2.4). Additionally, I determined that while both the Little Qualicum and Big Qualicum rivers received similar abundances of salmon, the Little Qualicum experienced a significantly higher abundance of eagles compared to the

Big Qualicum (Table 2.1). Finally, the model analysis determined that the Little Qualicum river has the highest expected eagle abundance, whereas the Englishman river has the smallest expected eagle abundance in relation to the baseline river (Figure 2.5). Within the rivers, lower field sites experience higher predicted abundances of eagles in comparison to upper field sites, where no eagles are expected to aggregate (Table 2.3). Overall, the four rivers experience a positive increase in predicted eagle abundance with a linear increase in salmon abundance (Table 2.3, Figure 2.5). I suggest that these results are driven by the physical characteristics of rivers, such as the area of sand and gravel bars, which significantly effects the abundance of eagles that can aggregate on rivers to scavenge salmon.

2.5.1. Distribution patterns of bald eagles

The first results of the study found that the total abundance of salmon and eagles were positively correlated across all rivers (Figure 2.3). This result corroborates findings in the literature, which determined that eagle densities are correlated with varying numbers of salmon (Field and Reynolds, 2013; Restani et al. 2000; Bennetts and McClelland, 1991). I examined the temporal distribution patterns of eagles across rivers during the spawning season. Previous literature suggests that during the fall months eagles migrate from their summer breeding grounds to salmon-bearing rivers, typically arriving at the peak of spawning season without a time lag (Restani et al. 2000). The results of my study demonstrate a similar pattern, with salmon abundance peaking on November 14th (cycle 8), and both juvenile and adult eagles reaching their highest abundances on November 15th (cycle 9) (Figure 2.1). Both age groups continued to forage on salmon until December 1st, (cycle 13) when their abundances began to dissipate. Overall, bald eagles matched the temporal availability of salmon over time across all four rivers (Figure 2.1).

I determined that there was a higher average abundance of eagles aggregating on each river relative to the average abundance of salmon (Table 2.1). This result is consistent across all rivers except for the Big Qualicum river, which experienced a higher average abundance of salmon in comparison to eagles (Table 2.1). The Little Qualicum received a relatively higher mean abundance of eagles compared to the other rivers (Figure 2.2). I suggest this result is due to the physical characteristics of the rivers. The mouth of all the rivers vary significantly in the area of mudflats and sandbars, which act

as natural barriers to salmon when they are washed downriver. When exposed during low tide, eagles are able to scavenge the salmon that have accumulated on the sandbars and mudflats. Thus, due to the larger area of sandbars present on the Little Qualicum, a higher abundance of eagles aggregated relative to salmon. Since the gravel bars on the other rivers are significantly smaller, salmon accumulated to similar abundance, but there was not enough space for competing eagles to aggregate in high abundances. This result suggests that the physical attributes of rivers, mainly in the form of sandbars and mudflats, determine the abundance of eagles that aggregate on each river. This finding mirrors the study by Watson et al. (1991), which determined that eagle foraging was dependent on the spatial distribution of tidal flats and was most common at low tide. Thus, the findings of this study are a departure from many of the studies which concluded the abundance post-spawning carcass determines the number of eagles that aggregate on rivers. This deviation from the literature represents an opportunity for future studies to further examine the role that physical features of rivers play in determining the number of eagles that aggregate on salmon spawning rivers.

2.5.2. Ideal Free Distribution: Input matching

The proportion of eagles in this study matched the continuous input of salmon quite well, and generally distributed across the rivers according to IFD (Figure 2.4). An underlying assumption of IFD is that individuals are fully informed of resource quality among patches (Fretwell and Lucas, 1970). Eagles may conform to this assumption by soaring among rivers, which allows their excellent eyesight and identification of conspecifics to inform them of resource patches. As in vulture food-finding (Jackson et al. 2008), they may be able to judge the quality of resource concentrations from the movements of conspecifics to (or from) the sites. Thus, the results of this study support previous field studies which have observed IFD distribution patterns under continuous input scenarios. Examples of these studies include mate searching with one immobilized sex (Parker, 1978) and drift feeding in fish (Milinski, 1979). However, despite the distribution patterns of eagles generally matching IFD, there was a slight deviation from the predicted 1:1 scavenger to prey ratio (Figure 2.4). This deviation may have been caused by variations in competitive abilities among eagles. Sutherland and Parker (1986) argue that in continuous input scenarios if individuals are not of equal competitive ability, the distribution of individuals will not necessarily conform to IFD. Therefore, as

competitive abilities and use of foraging tactics differ among age classes of eagles (Bennetts et al. 1997) I suggest that the slight departure from the IFD ratio may be due to the variation in competitive ability of bald eagles. Additionally, as intraspecific competition has been found to effect the number of eagles that aggregate in resource patches (Hansen, 1986), this inherent sociality may have caused some individuals to depart the rivers and re-distribute. Considering this, I suggest that examining the effect of varying competitive ability and use of sociality on eagle distribution patterns would further illuminate eagles ability to spatially track a continuous input of salmon under IFD.

2.5.3. River physical features

In this study, the number of eagles that distributed across rivers in relation to salmon abundance was not equal. I found that the expected abundance of eagles on the Little Qualicum river was notably higher than the other rivers (Table 2.3, Figure 2.5). I suggest that this result is due to the area of sandbars that are exposed during low tide, which simultaneously catch salmon that are washed downriver while allowing large numbers of scavenging eagles to aggregate. The Big Qualicum river experienced a lower predicted abundance of eagles than the Little Qualicum river, despite the high number of salmon that accumulated in the river. I suggest that although there was an adequately large number of salmon in the Big Qualicum, eagles could not aggregate in high abundances due to the small river mouth and lack of sandbars. Similarly, Rosewall creek experienced a slightly lower predicted abundance of eagles, which I attribute to the dense forest, lack of sand bars, and natural obstructions present in the creek. In contrast to the Big Qualicum and Rosewall creek, the Englishman river does have large sandbar and tidal flat areas that could support dense aggregations of foraging eagles. However, the Englishman attracts very few eagles to the river due to the very low number of salmon that accumulate on the tidal flats and sandbars. Due to this, I suggest that eagles re-distributed to the nearby Little Qualicum river, which experienced a higher abundance of salmon over the spawning season and features large sandbars that facilitate scavenging.

Considering these results, I suggest that while the abundance of eagles that aggregated on each river was in response to salmon, the area of sandbars and exposed tidal flats in the lower field sites ultimately determined the number of eagles that could gather on each river. Overall, this result helps inform our understanding of scavenger-

prey conformity to IFD by inferring that physical features may affect the ability of individuals to input match prey abundances across resource patches. I suggest that future studies examine this effect by incorporating spatial data into their examination of scavenger distribution patterns in response to prey densities under Ideal Free Distribution.

2.6. Conclusions

The life history of bald eagles distributed across the Pacific Northwest coast is inextricably connected to Pacific salmonids, as post-spawning salmon carcasses represent the majority of their diet during the fall and winter months. In this study, eagles temporally matched the input of salmon well, with no delay in their arrival on the rivers. Spatially, eagles matched the proportion of salmon on each river and generally distributed according to IFD. Furthermore, this study determined that river and field site identity, which capture tidal flat and sand bar areas, have a significant effect on the abundance of eagles that aggregate on rivers. This result supports the finding by Field and Reynolds (2013), who determined that estuary area was among the top predictor of avian scavenger abundances. Other environmental factors that may have affected eagle abundances include water flow and water levels. As there was intense flooding events during the spawning season in this study, many carcasses were washed downriver and into the Strait of Georgia. I suggest that future studies examining the distribution patterns of eagles take into consideration the effect of flooding on carcass availability, and incorporate relevant data into the analysis.

Overall, the results of this study indicate that eagles temporally and spatially matched the input of salmon, and generally distributed according to IFD. As this is the first study to examine eagle distribution patterns under the predictions of IFD, it elucidates the response of a migratory scavenger species to ephemeral food patches. Furthermore, it provides a foundation for future studies to examine their spatial movements under IFD at varying spatial gradients. Lastly, this study determined that the physical features of rivers, such as the area of sandbars, affected the abundance of eagles that could aggregate on each river. Ultimately, this study fills a gap in our knowledge of the regional temporal and spatial distribution patterns of foraging bald eagles in response to spawning salmonids.

2.6.1. Tables

Table 2.1. Total abundance of eagles and salmon on the four study rivers over 13 observation cycles. The average abundance of eagles and salmon was calculated by dividing the total estimate by 13, for the average number of eagles and salmon per observation cycle. N = 13

	Total		Average		N
	Eagles	Salmon	Eagles	Salmon	
All rivers	944	564	71.5	43.3	13
Big Qualicum	165	229	12.5	17.6	13
Little Qualicum	606	240	45.07	18.4	13
Englishman	31	7	3	0.46	13
Rosewall	142	88	10.9	6.7	13

Table 2.2. Model competition for eagle abundance in relation to salmon abundance, river identity and field site. N= 13 observation cycles, on each of 4 rivers, with 2 field sites per river, for a total sample of 104 observations. DF= degrees of freedom, LogLik= log-likelihood, AICc = corrected Akaike's Information Criterion for small sample size, Δ AICc = the differences between the AICc of each model and the model with the lowest AICc score, weight = likelihood of each model relative to all other models in the candidate set.

Rank	Model	DF	logLik	AICc	Δ AIC	Weight
1	Salmon + river + field site	7	-416.55	848.3	0.00	0.895
2	Salmon + river + field site + salmon*river	10	-415.65	853.7	5.4	0.060
3	Salmon*river	6	-418.73	853.8	5.5	0.045
4	Salmon + field site	4	-423.22	854.8	6.5	0.034
5	Salmon + river	6	-422.16	857.2	8.9	0.026
6	Salmon + river + salmon*river	9	-421.95	863.8	15.5	0.015
7	Salmon + salmon *river	7	-423.65	864.6	16.3	0.013
8	Salmon + field site + salmon *river	9	-428.96	866.2	17.9	0.000
9	Salmon	3	-428.84	865.9	15.6	0.000
10	River + field site + salmon*river	9	-429.10	867.6	19.3	0.000
11	Field site + river	6	-429.64	870.2	21.88	0.000
12	River + salmon*river	7	-430.50	871.3	23.0	0.000
13	Field site + salmon*river	7	-430.89	873.4	25.1	0.000
14	River	5	-431.86	874.4	26.07	0.000
15	Field site	3	-443.63	893.5	45.24	0.000
16	Null	2	-446.25	896.6	48.34	0.000

Table 2.3. Intercept and effect sizes estimated from the generalized linear model, which analyzed eagle abundance on each river in relation to river identity, field site identity and salmon abundance. N=13 observation cycles sampled on each of the 4 rivers with 2 field sites per river, for a total sample of 104 observations. The lower field site on the Big Qualicum river is the intercept of estimated eagle abundance, and acts as a baseline to compare effect sizes. 95% CI = confidence intervals of the estimate.

Variables	Effect size, relative to BQ Lower	95% CI
Big Qualicum lower field site (intercept)	8	1.58 - 14.14
Little Qualicum	+ 12	4.12 - 20.31
Rosewall	-1	-8.06 - 7.34
Englishman	-2	-10.06 - 5.74
Upper field site	-8	-14.95 - - 3.90
Salmon abundance (slope)	0.88	0.543 - 1.22

2.6.2. Figures

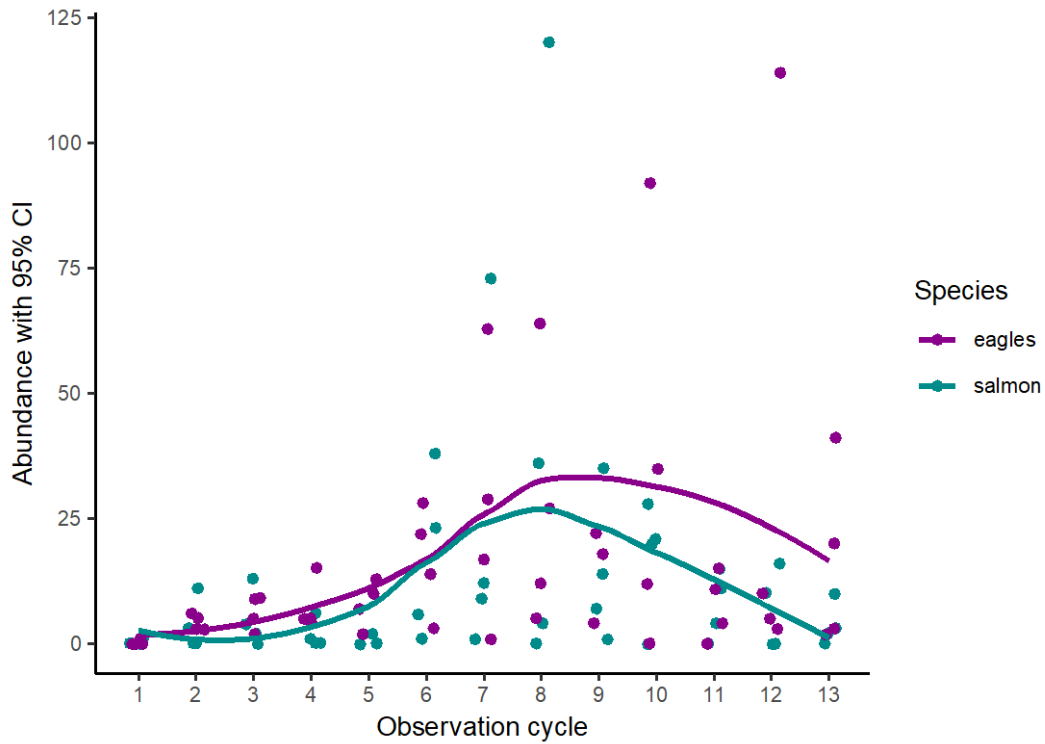


Figure 2.1. Abundance of eagles and salmon over 13 observation cycles with 95% CI. Each point is the pooled count from the upper and lower field sites on each of the four rivers, representing one estimate of eagle and salmon abundance per river, per observation cycle. Points are jittered for clarity. N=52.

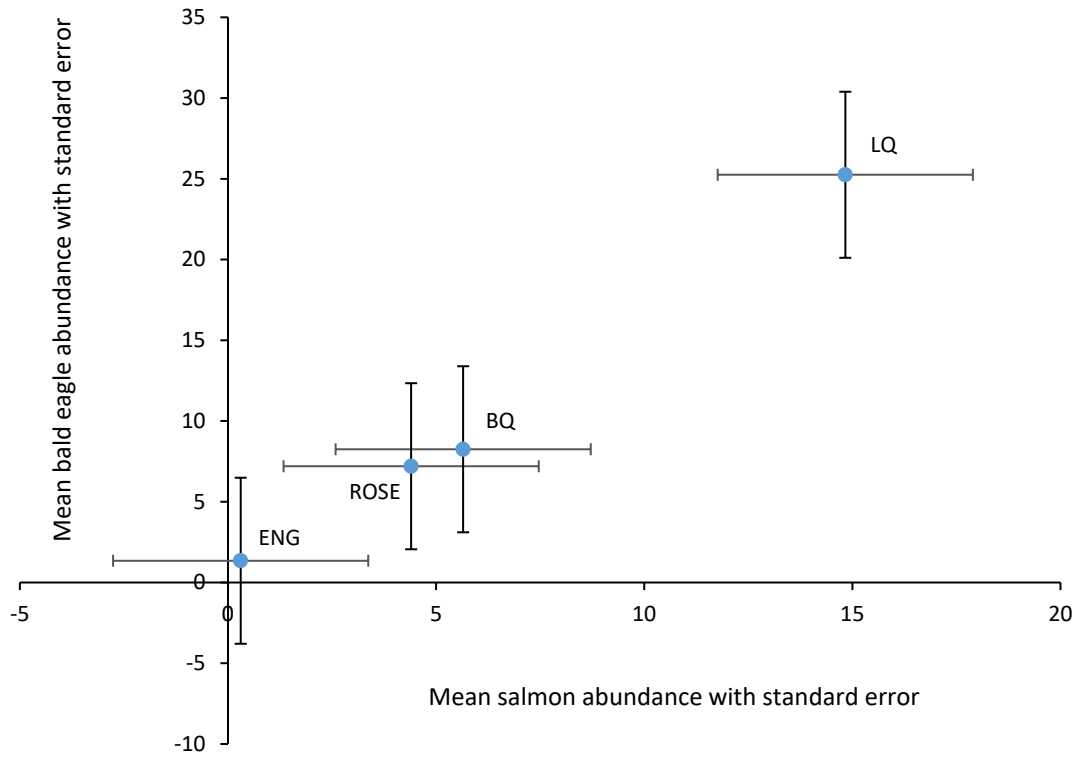


Figure 2.2. Mean bald eagle abundance in relation to mean salmon abundance on the Englishman, Big Qualicum, Little Qualicum rivers and Rosewall creek, summarizing the spatial distribution of eagles. The error bars show standard error. Mean eagle and salmon abundances were calculated by dividing the pooled abundances from both field sites by the number of observations. N= 26 observations on each of 4 rivers, with 2 field sites per river for a total sample size of 104 observations.

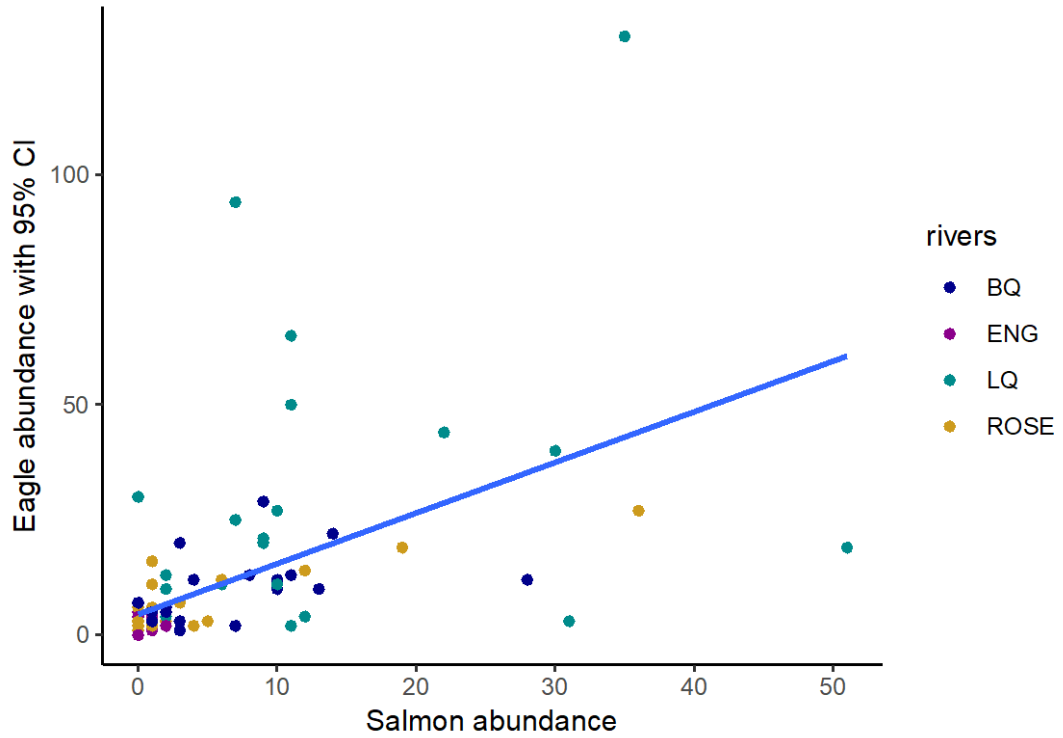


Figure 2.3. Observed eagle abundance in relation to to observed salmon abundance across all four rivers with 95% CI. N= 13 observation cycles, on each of 4 rivers, with 2 field sites per river, for a total sample size of 104 observations. Points are jittered for clarity. R= 0.73, $p < 0.001$.

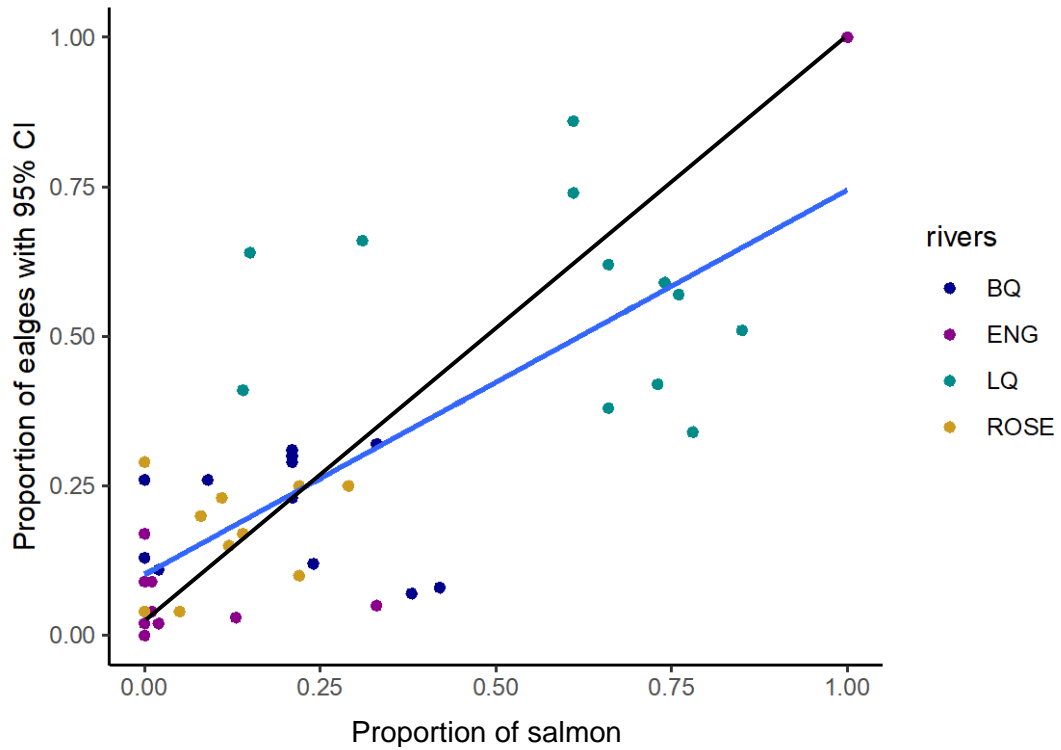


Figure 2.4. Linear model of proportion of salmon to proportion of eagles across four rivers, with 95% confidence intervals. Each point represents one estimate per river (field site counts were pooled to calculate the proportion of eagles that were located on each river out of the total across all four rivers). The black line is the 1:1 ratio of scavenger to prey that is predicted under IFD. $N=52$, $R^2= 0.56$, $p<0.001$.

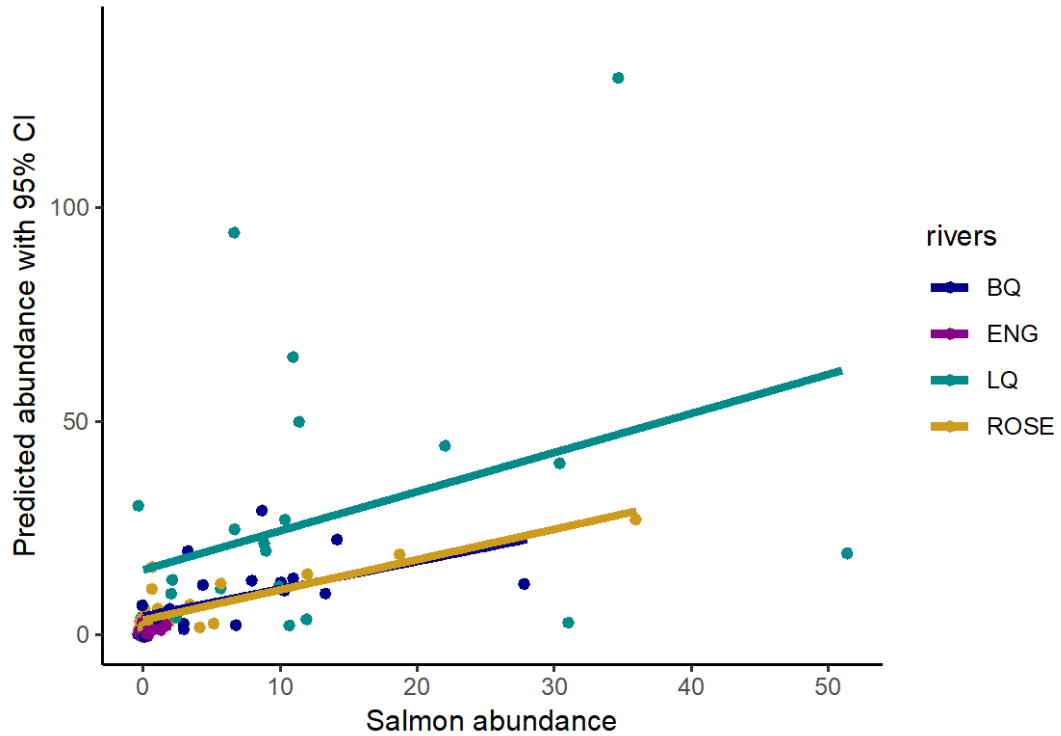


Figure 2.5. Output of the additive Generalized Linear Model showing expected eagle abundance as a function of salmon abundance and river identity. N= 13 observation cycles, on each of 4 rivers, with 2 field sites per river, for a total sample size of 104 observations. Slopes per river indicate the expected eagle abundance on each river with a linear increase in 1 salmon. Slopes are shown with 95% CI. Points are jittered for clarity. N=104. $R^2= 0.44$.

Chapter 3.

Kleptoparasitism among eagles scavenging on salmon on a set of four rivers

3.1. Abstract

During the fall months along coastal British Columbia, high densities of scavenging bald eagles aggregate on salmon-bearing rivers, often competing for salmon carcasses. Individuals attempt to steal food from conspecifics using the foraging tactic kleptoparasitism. Here, I examine the spatial distribution and rate of kleptoparasitism, the age of attackers and target individuals, the behavioural tactic used and the outcome of attempts. I observed eagle behaviour on a set of four rivers along the east coast of Vancouver Island. I observed kleptoparasitism only in estuaries and river mouths, and not on the upper reaches of each river. The proportion and rate of kleptoparasitism attempts occurred in correspondence to the proportion of eagles on each river. Both juvenile and adult eagles preferentially attacked individuals of their own age group. I determined that the behaviour 'swoop and steal' was the most successful tactic, and that juvenile attackers had more successful outcomes than adults. Finally, I determined that the success of kleptoparasitism attempts was higher when more salmon carcasses were present. Both the use and outcome of kleptoparasitism attempts are driven by the age of individuals involved in the attempts, which indicates the importance of age-related sociality in bald eagle foraging behaviour.

3.2. Introduction

Bald eagles are primarily solitary foragers that typically employ scavenging or hunting foraging techniques to acquire food resources. However, variations in ecological conditions can affect competitive behaviour and foraging tactics used to obtain prey, often resulting in the implementation of kleptoparasitism (Broom and Ruxton, 2003). Kleptoparasitism is a foraging behaviour in which individuals steal food items from inter- and intraspecific individuals (Brockmann and Barnard, 1979). These competitive interactions occur during the searching and handling of prey, with the rate of kleptoparasitism increasing as scavenger density increases (Miller et al. 2006). The

success of these interactions is influenced by various factors, which include: prey abundance and availability, differences in competitive ability, and age of foragers (Hamilton, 2002). Typically, the ecological conditions that facilitate kleptoparasitism occur when there is a decrease in prey abundance and increase in the density of scavengers competing for food resources (Hansen, 1986). This ecological condition is epitomized by the annual return of spawning salmonids to their natal rivers on the coast of British Columbia, which draws high densities of bald eagles to aggregate on rivers to forage post-spawning salmon carcasses.

After the initial pulse of carcasses that become available following the peak die-off of spawners, carcass abundance gradually declines, prompting eagles to use kleptoparasitism to obtain the remaining carcasses. To engage in kleptoparasitism, an individual targets a conspecific and attacks in an attempt to steal salmon. Despite the costs of kleptoparasitism, which include potential for injury from retaliating conspecifics, kleptoparasitism is the most energy-efficient foraging method during periods of low food abundance (Stalmaster and Gessaman, 1984). Factors that affect the outcome of kleptoparasitism attempts include salmon abundance, the age of individuals engaged in the attempt and the behavioural tactic used. The success rate of kleptoparasitism attempts have been found to be higher when there is high carcass density compared to periods of low carcass abundance (Hansen, 1986; Knight and Skagen, 1988). A study by Fischer (1985) found that adults were more likely to steal from other adults in comparison to younger birds, while juveniles did not show a preference for stealing from a specific age class. Once engaged in kleptoparasitism, the behavioural tactic used in the attempt has also been found to be dependent on the age of the attacker. These behaviours have been described as 'ground piracy' and 'aerial piracy', which are identified according to whether the behaviour originates on the ground or in the air. Adult attackers have been found to preferentially implement ground-based tactics, while juveniles often choose to implement aerial-steal (Restani et al. 2000; Stalmaster and Gessaman, 1984).

The choice to implement a ground-based tactic or an aerial-tactic in a kleptoparasitism attempt has been found to affect the outcome of the attempt (Bennetts et al. 1997, Knight and Skagen, 1988). In a study by Bennetts et al. (1997), ground-piracy had the highest success rate per attempt, while aerial piracy had the lowest. As kleptoparasitism is a learned behaviour that requires young birds to observe and learn

from older eagles, the more experienced adult eagles have been found to have higher success rates compared to juveniles (Restani et al. 2000; Jorde and Lingle 1988; Stalmaster and Gessaman, 1984). However, this result has been disputed by several studies which have not found age-specific differences in the ability to successfully steal from conspecifics (Fischer, 1985, Griffin, 1981; Bennetts et al. 1997). Thus, despite several studies examining the effect of age and behavioural tactic on the outcome of kleptoparasitic events, there doesn't seem to be a clear consensus on the role age plays in the probability of successfully stealing salmon.

Here, I address the inconsistency in the literature by investigating the effect that the age of attackers and targets, abundance of salmon, and behavioural tactic used has on the outcome of kleptoparasitism attempts. To accomplish this, I examined the temporal and spatial distribution of eagles involved in scavenging groups across rivers and over observation cycles. Second, I examined the relationship between the age of attackers and targets, and the behavioural tactics that each age group preferentially implemented in attempts to steal. Third, I examined the proportion of kleptoparasitism attempts that occurred on each river in relation to the proportion of eagles on each river. I used a statistical model to determine the predicted probability of a successful attempt considering the age of the attacker, the behaviour tactic used, and the abundance of salmon present in a scavenging group. I predicted that juveniles will have a lower probability of successfully stealing compared to adults. I also predicted that the behaviour tactic used in an attempt will affect the probability of success, with swoop and steal (aerial tactic) having a more successful outcome than flap and hop (ground tactic). Finally, I predicted that salmon abundance will affect the predicted outcome of attempts, with the probability of success increasing as the abundance of salmon increased.

3.3. Methods

The observations of kleptoparasitism used in this study were collected over 13 observation cycles, spanning from September 19 to December 3, 2018. A visit to the upper and lower field sites in each river occurred once per 4-day observation cycle. These rivers include the Little Qualicum, Big Qualicum, Englishman rivers and Rosewall creek. Maps and latitude and longitude locations of the field sites can be seen in Appendix A.

Upon arrival at each field site, I first counted the number of 'scavenging groups' present. Scavenging groups are defined as groups of bald eagles consisting of at least 2 individuals that are present at a single location around salmon. I counted the number of adult and juvenile eagles that were involved in each group, using the plumage pattern of individuals to identify their age. Individuals with a predominately white head and tail were considered adults, while individuals with a mottled brown plumage were considered juveniles. The number of adult and juvenile eagles that comprised each group will be referred to as 'group composition'.

I counted the number of salmon, post-spawning carcasses, and 'salmon portions' that were 'involved' in scavenging groups. 'Salmon portions' are pieces of carcasses (flesh or bone) that are separated from the remainder of the salmon carcass. Subsequently, the combination of salmon carcasses and salmon portions that were involved in kleptoparasitism attempts will be referred to as 'salmon'. I define being 'involved' in scavenging groups as being fought over by at least two eagles present in the groups.

On each visit I used focal sampling to watch and record kleptoparasitism that occurred within the scavenging groups. A kleptoparasitism attempt is defined as 'an attempt made by either a juvenile or adult eagle present in the scavenging group to steal salmon from a conspecific'. I termed the individual starting a kleptoparasitism attempt the 'attacker' and the individual who was being stolen from the 'target'. Each focal sample lasted 1.5 hours, during which I documented kleptoparasitism attempts between eagles in the scavenging groups.

When kleptoparasitism ensued, I noted the age of the attacker and the age of the target. Additionally, I noted the number of individuals involved, as there were occasionally more than two individuals involved in an attempt. I documented the type of behavioural tactic used to steal salmon which are identified as 'flap and hop', 'swoop and steal' and 'aerial steal'. A flap and hop is defined as 'a hopping movement across the ground while flapping their wings and moving in the direction of the target'. A swoop and steal is defined as 'an airborne swoop with exposed talons, which results in the attacker landing near the target', and an aerial steal is defined as 'a mid-air ambush to steal salmon from the target'. Flap and hop is considered a ground-based tactic, as it originates on the ground, while swoop and steal and aerial steal are considered aerial

tactics, as both behaviours begin in the air. The descriptions of these behaviours are based on definitions that have been used in previous studies which examine kleptoparasitism in eagles. At the end of a kleptoparasitism attempt the age of the winner was identified. Winning an attempt was defined as successfully stealing salmon from the target individual. Outcomes were scored as 0 or 1, with 0 being 'attempt' and 1 representing 'success'. More detailed descriptions of these behaviours, and their use in other studies can be found in Appendix B.

In the previous chapter, I estimated the number of salmon and eagles that were located on each river. These estimates are referred to as the 'background' abundances. I compared the number of eagles involved in scavenging groups relative to the background abundance for each river to determine the number of individuals engaging in kleptoparasitism.

3.3.1. Description of field sites

Although both the upper and lower field sites were sampled during each visit to a river, kleptoparasitism was never observed in the upper field site of any river. Due to this, no description of upper field sites is included in the methods. A full description of upper field sites can be found in Chapter 2.

The estuary of the Englishman river is a designated Parksville-Qualicum Beach Wildlife Management Area, and is characterized by abundant marsh grasses and aquatic plants. The lower field site is located in this estuary, where the main stem of the Englishman river flows out into the Strait of Georgia. There is a small sand spit that extends towards the Strait with several large logs that have been previously swept downriver, which are only exposed during low tide. Despite the Englishman river experiencing all salmonid species except sockeye, there were little to no salmon observed in the lower field site of the river.

The lower field site of the Big Qualicum river is characterized by a relatively small river mouth that drains into the Strait of Georgia. The physical characteristics of the field site include a small river rock bank which is only exposed during low tide. Salmon that were washed downriver accumulated on this bank, which provided a small area for eagles to aggregate to scavenge salmon. Extending from the banks of the river, there is

a semi-natural forest that features large conifers which provide ideal perch trees for eagles. The understory of the forest is characterized by dry beach vegetation and is dominated by Nootka Rose (*Rosa nutkana*) bushes.

The Little Qualicum river lower field site is located in an estuary that is a protected wildlife area. The physical features of the river are characterized by large sand bars extending from the mouth of the river which are exposed during low tide. These sandbars extend ~100 metres from the banks of the river into the bay and act as natural barriers to salmon that were washed downstream. Extending from the riverbanks, the estuary is characterized by dense marsh grasses which transition to dry vegetation along the beaches. Dense coniferous forests surround the estuary, which provide abundant perches for eagles. The physical attributes of this field site provide optimal space for eagles to aggregate and compete over salmon.

The lower field site of Rosewall creek is located at the mouth of the system, and is characterized by narrow banks and low water levels. The low water levels and slow water discharge rates were caused by an unseasonably dry fall, which prevented spawners from upstream travel until mid-October. Additional obstructions to upstream movement included downed trees which formed natural barriers to salmon. Due to the consistently low water levels, post-spawning salmon carcasses became wedged in the river rocks, as the water was not flowing fast enough to wash them into the Strait of Georgia. In response to this, eagles would perch in the creek bed to scavenge accessible salmon carcasses.

3.3.2. Data Analysis

Temporal and spatial distribution of salmon and eagles involved in scavenging groups

Using a local polynomial regression (Loess) model, I described the temporal distribution of salmon and eagles involved in scavenging groups (i.e. over all four rivers) in relation to the 13 observation cycles. I compared the number of salmon and eagles involved in scavenging groups to the background abundances (estimated in Chapter 2) on each river using a Pearson's correlation coefficient. I completed the spatial description of scavenging groups by calculating the average group composition per river.

I compared the proportion of kleptoparasitism attempts that occurred on each river to the proportion of eagles that were involved in scavenging groups per river. This was followed by an estimation of the rate of kleptoparasitism attempts that transpired per observation cycle on each river, which was calculated by dividing the number of attempts by the total observation hours (19.5 per river).

To further explore the role of age in kleptoparasitism, I calculated the number of times adult and juvenile attackers targeted conspecifics of each age group. I then used a Pearson's Chi-Square test to determine if the age of the attacker was dependent on the age of the target. Finally, to examine the relationship between attacker age and the behavioural tactic used, I calculated the total number of kleptoparasitism attempts per behaviour by each age group, and estimated the percent of those attempts that were successful.

Model Analysis

In the model analysis, I aimed to determine if the age of attackers and targets, the behavioural tactic used, and the abundance of salmon involved in scavenging groups affected the predicted probability of a successful outcome. Of the candidate models to implement, I considered a Logistic Mixed Effects Model with a binary response to be the most appropriate, as it determines the probability of an event occurring considering the predictor variables (Zuur et al. 2007). I conducted all analysis in R Studio Statistical Environment (version 3.5.1, R Core Team 2018).

Prior to running the model analysis, I screened for correlation between predictor and response variables. I accomplished this by using a Pearson's Chi-squared test to determine if the categorical predictor variables were significantly associated. The test determined that the attacker and target variables were highly correlated ($X^2 = 87.99$, $p = <0.0001$), therefore, the target variable was excluded from subsequent analyses. The other categorical variables, behavioural tactic and attacker age, were not found to be correlated ($X^2 = 4.93$, $p = 0.084$). I screened for correlation between interaction effects of the predictor variables using a Variance Inflation Factor (VIF), which determines whether factors are correlated in a regression analysis. I used a VIF test on linear models with interaction terms between attacker and behaviour, attacker and salmon and behaviour and salmon. The VIF found that the interactions between attacker and behaviour

(VIF=10.25) and behaviour and salmon (VIF=20.53) were highly collinear. Thus, due to the collinearity between these interactions, they were not included in the global model. The interaction between attacker and salmon was not found to be collinear (VIF < 6.0), and was included in the global model.

To screen for temporal correlation between observation cycles and the number of salmon involved in scavenging groups, I used an Auto-Correlation Function (ACF) test. An ACF test determines if there is temporal autocorrelation between the predictor and response variables at each timestep, which is a 4-day observation cycle. Thus, I used an ACF test on the residuals of a linear model between the salmon ~ observation cycle variables, which determined that there was no temporal autocorrelation found between the variables (ACF=0.27). In addition to a temporal ACF, a Mantel spatial autocorrelation function was performed to determine if the average outcome of kleptoparasitism attempts were correlated across lower field sites. This function uses a Monte Carlo approach to compare the average attempt outcome to the latitude and longitude gradients of the lower field sites. The function determined that no spatial correlation was found between the average outcome and lower field sites ($r = -0.52$, $p = 1.0$).

A global model contains a set of variables to account for the study design and are biologically relevant to the research questions (Burnham and Anderson, 2002). I performed a model competition between all possible models containing the factors attacker, behaviour, and salmon, and the attacker by salmon interaction. The behavioural tactic variable has three levels labeled as 'flap and hop', 'swoop and steal' and 'aerial steal', which identify the three different behavioural tactics used in kleptoparasitism. The attacker variable has two levels, which are labeled as 'A' and 'J' for adult and juvenile attackers. I included the river and observation cycle variables as random effects to account for the study design, which had repeated measures in each river and during observation cycles. The response of the model is the outcome of kleptoparasitism, which is graded on a 0 to 1 scale, with 0 being attempt and 1 representing success.

The model selection process was based on Akaike's Information Criterion approach corrected for small sample size (AICc) to determine the most suitable model parameterization (Burnham and Anderson, 2002). I examined the Akaike weights (w_i) to

determine the amount of evidence indicating the best candidate model for the data (Wagenmakers and Farrell, 2004). I validated the final model by plotting the Pearson's residuals against the predicted values, as well as against each explanatory variable in the model (Zuur et al. 2007). I also calculated the generalized R^2 to assess the model fit using the methods described in Nakagawa and Schielzeth (2012). The results of the binomial model have been transformed from the log-odds scale to the probability scale for interpretation purposes.

3.4. Results

3.4.1. Temporal and spatial distribution of salmon and eagles in scavenging groups

As reported in Chapter 2, the background salmon abundance across four rivers was 563, while the number involved in scavenging groups was 164 (Table 3.1) The background eagle abundance across four rivers included a total of 956 individuals, while the number of eagles involved in scavenging groups was 122 individuals (Table 3.1). To determine if these estimates are correlated, I used a Pearson's correlation coefficient test, which determined that the background abundance of salmon and the number of salmon involved in scavenging groups are correlated ($R=0.63$, $p<0.0001$). Similarly, a Pearson's correlation coefficient test determined that the background eagle abundance is correlated with the number of eagles that involved in scavenging groups ($R=0.72$, $p<0.0001$). The number of background salmon and eagles relative to the number involved in scavenging groups per river can be seen in Table 3.1.

I examined the temporal and spatial distribution of salmon and eagles involved in scavenging groups over 13 observation cycles. The number of salmon involved in groups was highest during the 10th observation cycle, while the number of adult and juvenile eagles involved in groups peaked during the 7th cycle (Figure 3.1). The highest average abundance of salmon involved in scavenging groups was located on the Big Qualicum river, while the lowest was on the Englishman (Figure 3.2). The highest average abundance of juvenile and adult eagles involved in scavenging groups was highest on both the Big and Little Qualicum rivers and lowest on the Englishman river (Figure 3.2). Finally, I determined that 122 individuals comprised 42 scavenging groups consisting of 60 adults and 62 juveniles. These individuals engaged in 134

kleptoparasitism attempts, with an average of 10 attempts per observation cycle (Table 3.2). Additional summary statistics can be found in Table 3.2.

3.4.2. Kleptoparasitism and behavioural tactics according to age group

I only observed kleptoparasitism attempts on the lower field site of each river. This finding is likely due to the large area of sand bars that are present in the estuaries, which allows eagles to aggregate and engage in kleptoparasitism. I determined that the proportion of kleptoparasitism attempts on each river occurred in correspondence with the proportion of eagles, which was highest on the Little Qualicum river and was lowest on the Englishman (Table 3.3). I also examined the rate of kleptoparasitism attempts on each river, which are consistent with the proportion of eagles located on each river. The highest kleptoparasitism rate occurred on the Little Qualicum river, with 4.2 attempts per observation hour, while on the Englishman river there was less than 1 attempt per observation hour. The proportion and rate of attempts among eagles in relation to the proportion of eagles on each river can be found in Table 3.3.

Of the 134 kleptoparasitism attempts observed, adults acted as the attacker in 85 attempts, while juveniles acted as the attacker in 49 attempts. In these attempts, adult and juvenile eagles almost entirely attacked conspecifics of the same age group, indicating that there is a strong age bias among attackers and targets (Table 3.4). This is supported by a Pearson's Chi-Square test, which determined that the age of attackers and targets are associated at a highly significant level ($p < 0.0001$).

Out of the total kleptoparasitism attempts, 70% of the attempts made by juvenile and adult eagles were successful in stealing salmon from their target (Table 3.5). The most successful behavioural tactic for adult attackers was flap and hop, which was successful in 79% of the attempts. Conversely, swoop and steal was the more successful tactic for juvenile attackers, which was successful in 94% of the attempts (Table 3.5). Aerial steal was the least successful tactic for both adult and juvenile attackers. Overall, the percent of attempts made by juvenile attackers that had a successful outcome was higher than adults, although adults made more attempts to steal than their younger conspecifics. Further details on the use of behavioural tactics according to age group and the outcome of attempts can be seen in Table 3.5

3.4.3. Model Results

The results of the model competition are given in Table 3.6. The top model carries the most weight, and contains the factors attacker, behaviour and salmon, with no interaction terms. Effect sizes are given in Table 3.7. To further examine the effect of attacker age on the outcome of attempts, I determined the predicted probability of success according to whether the attacker was a juvenile or adult eagle. The model treated adult attackers as the intercept and baseline estimate to facilitate comparison of effect sizes. Thus, the predicted probability of success for adult attackers is 25%, holding all other parameters constant (Table 3.7, Figure 3.3). Juvenile attackers have a 41% predicted probability of successfully stealing from conspecifics, holding all other parameters constant (Table 3.7, Figure 3.3). This results in a 16% higher probability of success than adults. These results are the predictions of kleptoparasitism outcomes after the variance in random effects, specifically river and observation cycle, have been accounted for in the model analysis.

I examined the predicted probability of a successful outcome according to the behavioural tactic implemented in an attempt. These results apply to both juvenile and adult attackers. The model treated aerial steal as the baseline behaviour to facilitate comparisons of effect sizes. Accordingly, individuals that implement aerial steal in a kleptoparasitism attempt have a 25% predicted probability of success, holding all other parameters constant (Table 3.7, Figure 3.3). Swoop and steal, the other aerial based tactic, has a 74% predicted probability of success, holding all other parameters constant (Table 3.7, Figure 3.3). According to this estimate, swoop and steal has a higher predicted probability of success by 49% in comparison to aerial steal. Flap and hop, which is the ground-based tactic, has a 67% predicted probability of success, holding all other parameters constant (Table 3.7, Figure 3.3). Based on this estimate, flap and hop has a higher predicted probability of success by 42% compared to aerial steal. Considering these results, swoop and steal is the behavioural tactic with the highest predicted probability of success for individuals who implement it in kleptoparasitism attempts.

To determine the predicted outcome of kleptoparasitism attempts based on a certain number of salmon present in scavenging groups, I used the following equation to determine the probability of success:

$$Y = \text{Inverselogit}(-1.11485 + 0.07223 * \text{salmon abundance})$$

This equation was used to calculate the predicted probability of success at varying levels of salmon abundance. The model determined that at 3 salmon, which was the average abundance in an scavenging group, the predicted probability of success was 28%, holding all other parameters constant (Figure 3.3). At 12 salmon, which was the average number of salmon present on a lower field site per observation cycle, the predicted probability of success is 43% (Figure 3.3). At 17 salmon, the predicted probability of success is 51%, which indicates that above this abundance, the predicted probability of success increases with increasing salmon abundance (Table 3.7, Figure 3.3). The highest observed abundance of salmon was 28, which results in a 70% predicted probability of success, holding all other parameters constant (Figure 3.3). Considering these results, it is clear that above a threshold of 17 salmon in a scavenging group, the predicted probability of a successfully outcome increases (Table 3.7, Figure 3.3).

Model performance tests, which includes the marginal and conditional R^2 , suggest that the fixed effects explain 14% of the response, while both the fixed and random effects explain 40% of the variance in the model response. Despite the model analysis providing further insight on the effect that age, behavioural tactic and salmon abundance has on the outcome of kleptoparasitism attempts, based on the R^2 values the model did not perform very well.

3.5. Discussion

Kleptoparasitism is a foraging strategy that involves competitive individuals stealing from others that have previously procured food (Brockman and Barnard, 1979). To investigate the role of kleptoparasitism in aggregations of eagles, I examined the effect of age, behavioural tactic and salmon abundance on the initiation and outcome of kleptoparasitism attempts across four salmon rivers. First, I determined that the proportion and rate of kleptoparasitism attempts occurred in correspondence with the proportion of eagles located on each river (Table 3.3). Second, I found that there was an age bias among attackers and targets; both adult and juvenile eagles almost only targeted conspecifics of the same age group (Table 3.4). Third, I determined that the percent of successful attempts for adult and juvenile attackers differed among

behavioural tactics (Table 3.5). I found that juveniles experienced more successful outcomes than adults, in both the observed attempts and the model analysis (Table 3.5, Table 3.7, Figure 3.3). I determined that swoop and steal has the highest predicted probability of success for individuals that implement it, regardless of age (Table 3.7, Figure 3.3). Finally, I found that above a threshold of 17 salmon present in an scavenging group, the predicted probability of success increases with increasing salmon abundance.

In this study, the occurrence of kleptoparasitism among aggregations of eagles did not occur until the 3rd observation cycle, as there were very few salmon present in field sites prior to this time. As the spawning season progressed, an increase in salmon abundance encouraged individuals to engage in kleptoparasitism to steal salmon from conspecifics. As a result, the number of salmon fought over in scavenging groups increased and peaked during the 9th observation cycle. The number of adult and juvenile eagles involved in scavenging groups followed a similar pattern, although their abundances peaked slightly earlier during the 7th observation cycle (Figure 3.1).

Interestingly, kleptoparasitism attempts were only observed on the lower field sites of all four rivers. The average number of salmon involved in a scavenging group was highest on the Big Qualicum river, while the average number of adult and juvenile eagles that were involved in a scavenging group was highest on both the Big and Little Qualicum rivers (Figure 3.2). Furthermore, I found that the proportion of kleptoparasitism attempts occurred in correspondence with the proportion of eagles that were distributed on each river (Table 3.3). The rate of kleptoparasitism attempts on each river followed a similar pattern, suggesting that on rivers with a higher proportion of eagles, individuals engage in more kleptoparasitism attempts at a higher rate (Table 3.3). I suggest this result is due to the large area of sandbars and riverbanks present in the estuaries of rivers, which provide adequate space for competing eagles to engage in kleptoparasitism over salmon. This is in contrast to the upper field sites, which are densely forested and do not feature physical features that facilitate the accumulation of salmon or kleptoparasitism among eagles.

3.5.1. Initiation of kleptoparasitism according to age

Kleptoparasitism in bald eagles is a social behaviour that is learned over time by watching older birds (Jorde and Lingle, 1988). Due to this, the age of an individual can determine their ability to compete with conspecifics and has been found to influence the initiation and outcome of kleptoparasitism attempts (Knight and Skagen, 1988). In this study, the individuals that engaged in kleptoparasitism attempts consisted of 60 adults and 62 juveniles, which formed 42 scavenging groups (Table 3.2). The average group composition included one adult and one juvenile, indicating that on average an equal number of adults and juveniles were involved in scavenging groups. I found that the adults in these groups initiated 85 attempts while juveniles only instigated 49, indicating that adults were more aggressive in their attempts to steal from conspecifics (Table 3.4). These findings are a departure from previous results, which found that juveniles comprised a significantly greater proportion of eagles involved in scavenging groups and were more aggressive in their attempts to steal (Fischer, 1985; Bennetts and McClelland, 1991).

The initiation of kleptoparasitism with conspecifics over salmon is driven by several factors, including the age and size of the attacker and the target. My results determined that there was a clear age bias among attempts, with each age group attacking conspecifics of the same age at a statistically significant level (Table 3.4). These results support a finding by Fischer (1985) who determined that adults were more likely to attack other adults than juvenile eagles. However, it has also been found that juveniles show a strong preference to initiate kleptoparasitism attempts with adults instead of individuals their own age (Hansen, 1986). The discrepancy in the age of individuals targeted may be explained by the use of 'sequential assessment', where individuals assess the fighting ability of competitors through a series of escalated displays (Rohwer, 1977). In each display, individuals convey subtle behaviours to communicate their social dominance and experience prior to engaging in a kleptoparasitism attempt (Enquist and Leimar, 1983). In bald eagles, the foraging experience, age and size of an eagle is indicated by their plumage pattern, which acts as a visual signal of their fighting ability (Hansen, 1986). A similar behaviour, called 'displaying' is performed by the target to convey their ability to fight off a defender. A target communicates this by rapidly flapping their wings and showing their talons prior to a perceived attack (Stalmaster and Gessaman, 1984).

My results demonstrate that juveniles attacked conspecifics of their own age group because their plumage conveyed they were less experienced, smaller and more likely to yield their salmon than a larger adult. According to the study by Stalmaster and Gessaman, (1984) adult eagles should attack juveniles due to their lower social ranking and inexperience, however, my results indicate that adults preferentially attacked older conspecifics. I suggest this is due to the context of each kleptoparasitism attempt; based on signals communicated prior to an attack, an individual targeted a conspecific that was most likely to yield their prey item. Thus, adult targets yielded their prey quite readily, which didn't require attackers to target younger individuals that are more likely to retaliate from an attempt. It is also possible that some of the adult eagles that targeted other adults in attacks may have been female birds. As female eagles are 24% larger than males and have been shown to be more dominant in kleptoparasitism attempts (Hansen, 1986), it is possible that the female birds were dominant over all adult eagles in attacks. Overall, I suggest that because individuals differ in terms of size, age, sex, experience and dominance, eagles choose to attack others in which they have the highest likelihood of winning. Ultimately, I infer that these social factors resulted in the clear age bias I observed among attackers and targets.

3.5.2. Outcome of kleptoparasitism and behavioural tactics used

In kleptoparasitizing eagles, age has also been found to influence the outcome of attempts and the behavioural tactic used to steal (Knight and Knight, 1983). In my study I found that juvenile eagles had a higher predicted probability of success (41%) in their attempts compared to adults (25%)(Table 3.7, Figure 3.3). Furthermore, I found that the most successful behavioural tactic for juveniles was swoop and steal, while flap and hop resulted in more successful outcomes for adult eagles (Table 3.5). This result supports a previous finding which found that ground-based tactics result in more successful outcomes for adult eagles, while younger birds experience more success using aerial-based tactics in their attempts (Bennetts et al. 1997).

I explored the relationship between behavioural tactics and the outcome of kleptoparasitism further by predicting the probability of success for each tactic. I determined that aerial steal is the behavioural tactic with the lowest predicted probability of success at just 25% (Table 3.7, Figure 3.3). Flap and hop, the ground-based tactic, experienced a 67% predicted probability of success (Table 3.7, Figure 3.3). Although

most studies have found ground-based tactics to be the most successful behaviour (Knight and Skagen, 1988, Hansen, 1986, Bennetts et al. 1997), my findings do not support this result. Instead I found that swoop and steal, an aerial-based tactic, was the most successful tactic with a 74% predicted probability of success (Table 3.7, Figure 3.3). Overall, I infer these results to indicate that eagles implemented the most appropriate behavioural tactic according to the kleptoparasitism situation. For example, if an individual is perched in a conifer, using swoop and steal to take salmon from an unexpected eagle on a sandbar may be deemed as the most advantageous tactic by the individual implementing it. If an eagle is already scavenging on a sandbar, using flap and hop to displace a nearby conspecific may be the most energy-efficient tactic and have the highest probability of success. Further research into the underlying factors that determine the use of each behavioural tactic will clarify the relationship between attacker age and the tactics they implement.

Lastly, to determine if the number of salmon present in scavenging groups affects the outcome of kleptoparasitism attempts, I predicted the probability of success for an individual at varying abundances of salmon. I determined that below a threshold of 17 salmon, the predicted probability of success was less than 50% (Figure 3.3). However, if the number of salmon present in a scavenging group was higher than 17 salmon, the predicted probability of success increased with increasing salmon abundance (Table 3.7, Figure 3.3). This result corroborates previous findings, which determined that individuals are more likely to be successful in their attempts when there are more salmon (Hansen, 1986, Knight and Skagen, 1988). I suggest that my result indicates that as salmon abundance increases, the intraspecific competition among eagles in a scavenging group decreases, resulting in individuals yielding their prey item more readily compared to attempts that occur when there is a smaller prey abundance.

While this study illuminates the role of attacker age, behaviour tactic used and salmon abundance on the outcome of kleptoparasitism attempts, there are some limitations to these results. First, considering the subtle forms of communication that transpire among scavenging groups, either through sequential assessment or displaying, this study is limited to making inferences only on the factors that I could observe. I suggest there were many behaviours that were too subtle for me to observe, which likely effected the initiation and outcome of kleptoparasitism attempts. Accordingly, I suggest that future studies attempt to address these subtleties by determining the sex of

individuals engaged in kleptoparasitism and observe attempts at a closer range to further tease apart the subtle forms of communication among kleptoparasitizing eagles. Second, I did not account for the number of eagles involved in scavenging groups in the model analysis. As the outcome of attempts are likely impacted by the number of eagles present in a group, the results and interpretation of the model analysis may be limited due to this shortcoming. To address this, I recommend that future studies incorporate the number of eagles present in scavenging groups in model analyses to determine if this affects the probability of successful outcomes.

3.6. Conclusions

In this study I demonstrate that foraging bald eagles that engage in kleptoparasitism are effected by the abundance of salmon present, the age of their competitors, and the behaviour tactic used. I determined that the number of eagles comprising scavenging groups peaked prior to the highest abundance of salmon, and occurred in the highest density on the Little Qualicum river. I determined that there was an equal number of adults and juveniles that comprised the scavenging groups, although each age group only targeted conspecifics of the same age. I found that the proportion of kleptoparasitism attempts occurred in correspondence with the proportion of eagles located on each river. Swoop and steal was the most successful behaviour for juvenile attackers, while flap and hop resulted in more successful attacks for adults. The model analysis determined that juveniles have a higher predicted probability of successfully stealing compared to adults, which deviates from previous findings in the literature. Finally, the model results determined that an increase in salmon abundance in scavenging groups results in an increase in the predicted probability of success. From these results, I conclude that both adult and juvenile eagles implemented kleptoparasitism to acquire previously procured salmon from conspecifics, and were differentially successful according to their age, behavioural tactic used and the number of salmon present in the groups. Ultimately, these results illuminate the role of sociality within groups of foraging eagles that utilize kleptoparasitism to acquire food resources.

3.6.1. Tables

Table 3.1. The background abundance of salmon and bald eagles (reported in Chapter 2) in relation to the abundance of salmon and eagles that were involved in scavenging groups per river. N =52 (one estimate of salmon and eagle abundances per river, per cycle) for both background and scavenging group estimates.

Rivers	Background salmon	Scavenging group salmon	Background eagles	Scavenging group eagles
Little Qualicum	240	72	606	62
Big Qualicum	229	82	169	38
Rosewall	88	8	142	20
Englishman	6	2	39	2
Total	563	164	956	122

Table 3.2. Data summary. Total and average abundance of eagles, salmon, scavenging groups and kleptoparasitism attempts across four rivers over 13 observation cycles. N = 13 observation cycles.

Salmon, eagles and kleptoparasitism	Total	Average per cycle	N
Salmon	164	12.6	13
Adults	60	4.6	13
Juveniles	62	4.8	13
Total eagles	122	9.3	13
Scavenging groups	42	3.2	13
Kleptoparasitism attempts	134	10.3	13

Table 3.3. Proportion of kleptoparasitism attempts and average kleptoparasitism rate on each river in relation to the proportion of eagles. Number of eagles = number of eagles involved in scavenging groups on each river, and the total across all rivers. Proportion of eagles = proportion of eagles out of the total located on each river. Number of attempts = number of kleptoparasitism attempts that occurred on each river, and the total across all rivers. Proportion of attempts = proportion of total attempts that occurred on each river. Kleptoparasitism rate = average kleptoparasitism rate per observation cycle per river, and across all rivers (19.5 hours per observation cycle). N= 13 observation cycles, on each of 4 rivers, with 1 field site per river, for a total sample of 134 observations of kleptoparasitism.

River	Number of eagles	Proportion of eagles	Number of attempts	Proportion of attempts	Kleptoparasitism rate ^{h-1}
Little Qualicum	62	0.51	82	0.61	4.2
Big Qualicum	38	0.31	30	0.22	1.5
Rosewall	20	0.16	21	0.16	1.07
Englishman	2	0.02	1	0.01	0.05
All rivers	122	1.00	134	1.00	6.82

Table 3.4. Number of kleptoparasitism attempts that adult and juvenile eagles acted as the attacker in relation to the age group they targeted. N= 13 observation cycles, on each of 4 rivers, with 1 field site per river, for a total sample of 134 observations of kleptoparasitism attempts.

		Attacker	
		A	J
Target	A	78	4
	J	7	45

Table 3.5. The number of kleptoparasitism attempts initiated by juveniles and adults eagles per behavioural tactic. Tactic = the three types of behavioural tactics which include: flap and hop, swoop and steal, and aerial steal. Number initiated = the number of kleptoparasitism attempts initiated by age group per behavioural tactic. Number successful = the number of initiated kleptoparasitism attempts that had a successful outcome, percent successful = the percent of initiated kleptoparasitism attempts that had a successful outcome, N= 13 observation cycles, on each of 4 rivers, with 1 field site per river, for a total sample of 134 observations of kleptoparasitism attempts.

Tactic	Adults				Juveniles				Total attempts
	Flap	Swoop	Aerial	Total	Flap	Swoop	Aerial	Total	
Number initiated	49	26	10	85	20	17	12	49	134
Number Successful	39	17	3	59	16	16	4	36	95
Percent successful	79%	65%	30%	69%	80%	94%	33%	73%	70%

Table 3.6. Model competition for the predicted probability of a successful outcome in relation to attacker age, behavioural tactic and salmon abundance. N= 13 observation cycles, on each of 4 rivers, with 1 field site per river, for a total sample of 134 observations of kleptoparasitism attempts. DF= degrees of freedom, LogLik= log-likelihood, AICc = corrected Akaike's Information Criterion for small sample size, Δ AICc = the differences between the AICc of each model and the model with the lowest AICc score, wt = likelihood of each model relative to all other models in the candidate set.

Rank	Model	DF	LogLik	AICc	Δ AIC	Weight
1	Attacker + behaviour + salmon	7	-139.76	291.8	0.00	0.414
2	Attacker + behaviour	6	-138.94	292.3	0.47	0.326
3	Behaviour	5	-141.71	293.7	1.82	0.167
4	Attacker + behaviour + salmon + attacker * salmon	8	-138.935	294.4	2.58	0.102
5	Behaviour + salmon	6	-141.25	294.8	2.98	0.084
6	Behaviour + attacker * salmon	6	-142.76	305.3	13.5	0.053
7	Attacker + behaviour + attacker * salmon	7	-145.32	307.3	15.5	0.012
8	Attacker + salmon	5	-149.29	308.8	16.9	0.00
9	Salmon	4	-150.961	310.1	18.2	0.000
10	Attacker + salmon + attacker * salmon	6	-149.142	310.6	18.7	0.000
11	Attacker + attacker * salmon	6	-149.723	310.8	19.0	0.000
12	Salmon + behaviour + attacker *salmon	7	-150.023	310.9	19.1	0.000
13	Salmon + attacker *salmon	6	-150.762	311.2	19.4	0.000
14	Attacker * salmon	5	-151.438	311.3	19.5	0.000
15	Attacker	5	-151.619	311.4	19.6	0.000
16	Null	3	-152.665	311.4	19.6	0.000

Table 3.7. Intercept and effect sizes estimated from the binomial logistic mixed effects model analyzing the predicted probability of kleptoparasitism success in relation to attacker age, behavioural tactic and salmon abundance. N= 13 observation cycles sampled on each of the 4 rivers with 1 field site per river, for a total sample of 134 observations. Adult attackers and aerial steal are treated as the intercepts and baselines for comparison of effect sizes. 95% CI = confidence intervals of the estimate.

Variables	Effect sizes, relative to adult attacker & aerial steal	95% CI
Adult attacker, aerial steal (Intercepts)	25%	0.05 - 0.78
Juvenile attacker	+ 16%	0.51 - 0.82
Swoop and steal	+ 45%	0.76 - 0.96
Flap and hop	+ 42%	0.71 - 0.94
Salmon (slope)	51%	0.49 - 0.54

3.6.2. Figures

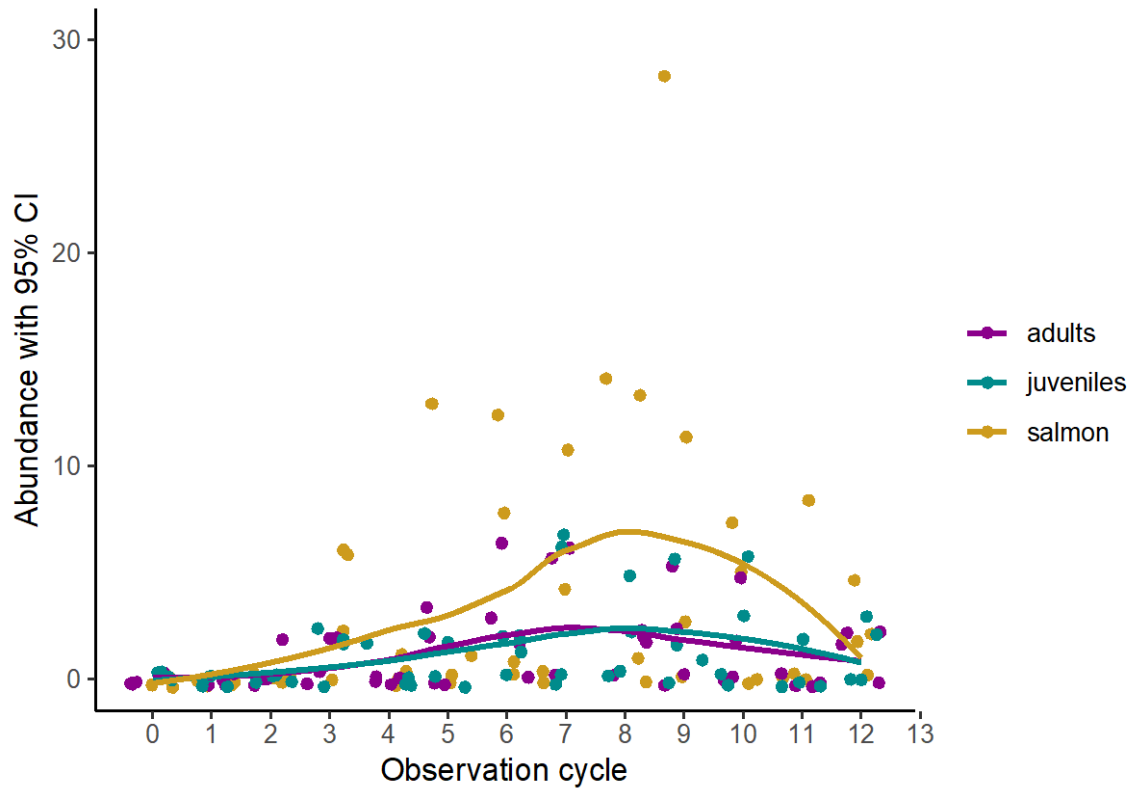


Figure 3.1. Abundance of eagles and salmon involved in scavenging groups across four rivers over 13 observation cycles with 95% CI. Each point represents one estimate for each salmon and eagle abundances per river, per observation cycle, for a total of $N = 52$ for each of adults, juveniles and salmon. Points jittered for clarity.

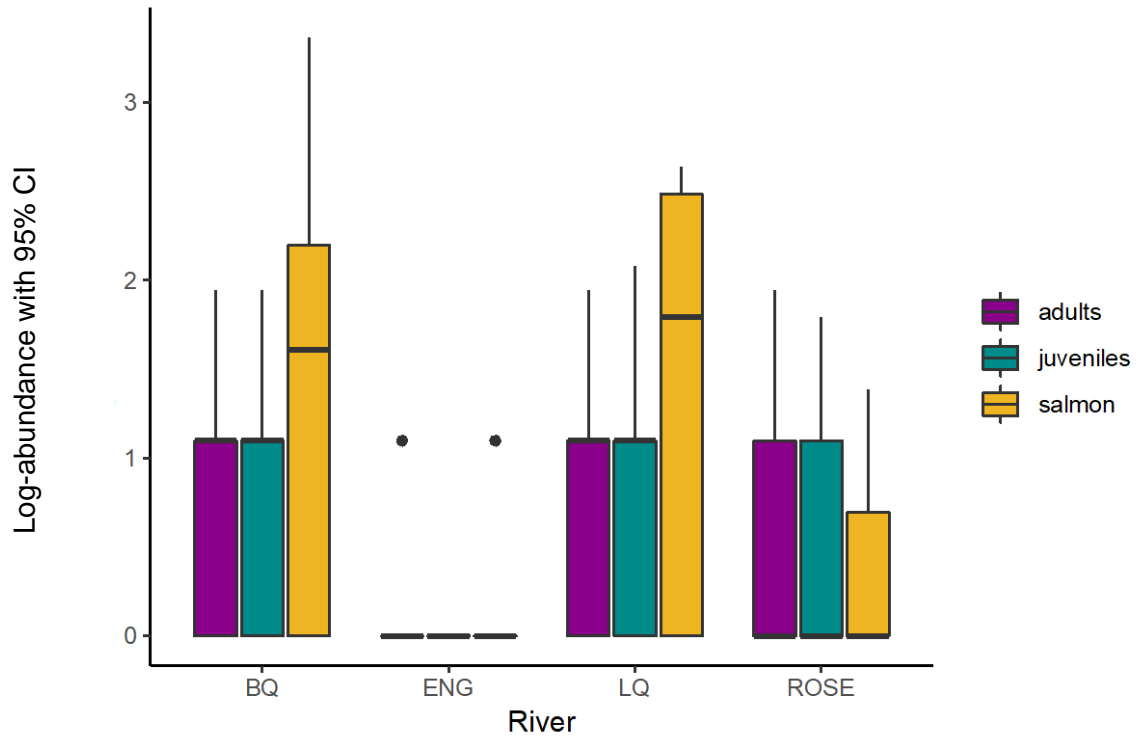


Figure 3.2. The average abundance of eagles and salmon involved in scavenging groups over 13 observation cycles per river (natural log-scale on the Y-axis). N = 13 for each bar.

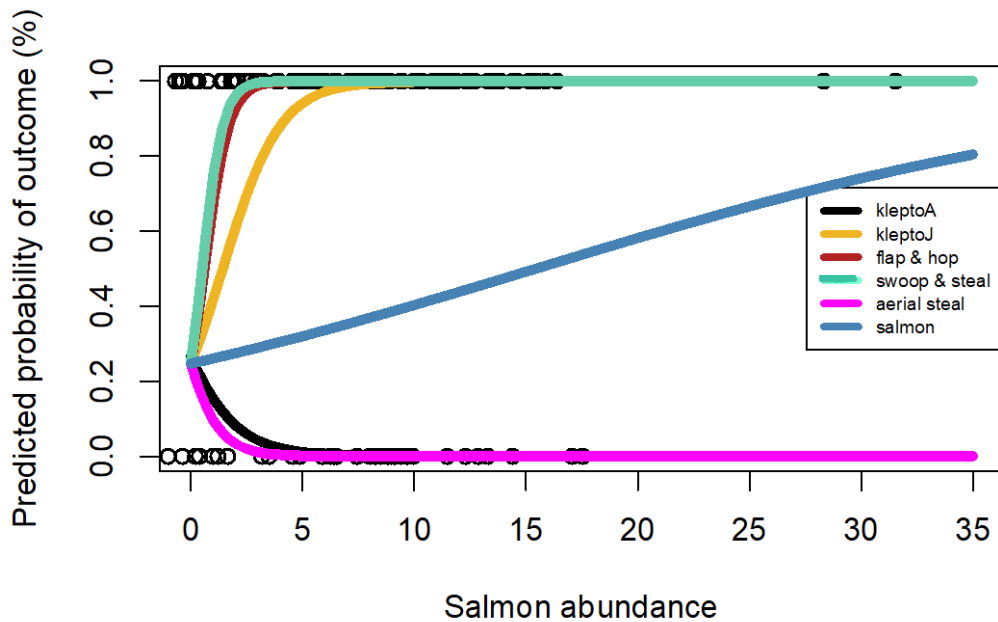


Figure 3.3. Output of binomial logistic mixed effects model showing predicted probability of a successful outcome in relation to attacker age, behavioural tactic used and salmon abundance in scavenging groups. N= 13 observation cycles, on each of 4 rivers, with 1 field site per river, for a total sample of 134 observations of kleptoparasitism attempts. Lines indicate the predicted probability of successfully stealing per attempt: adult kleptoparasite = 25%, juvenile kleptoparasite= 41%, aerial steal = 29%, flap and hop= 67%, swoop and steal= 74%, and salmon abundance =50%. $R^2= 0.40$.

Chapter 4.

General Conclusions

Understanding the effect that ephemeral salmon carcasses have on the numerical response and use of kleptoparasitism among aggregations of eagles is essential to discerning their distribution patterns and use of sociality at a regional spatial scale. In this thesis, I examined the temporal and spatial distribution patterns of migratory eagles in response to varying abundances of salmon, and observed their use of kleptoparasitism as a foraging strategy to acquire food from conspecifics. In Chapter 2, I examined the temporal distribution of eagles across four salmon-bearing rivers, and assessed their spatial distribution patterns using Ideal Free Distribution. In Chapter 3, I determined the effect that age, behavioural tactic and the abundance of salmon in scavenging groups has on the outcome of kleptoparasitism attempts.

Using 102 estimates of salmon and eagle abundances over 13 observation cycles, Chapter 2 provides insights on the temporal and spatial distribution patterns of eagles in response to fluctuating salmon abundances. First, I examined the temporal distribution of eagles by examining their peak abundance date across the rivers. I determined that the density of eagles was highest during the observation cycle following the peak in salmon abundance across all four rivers. This result corroborates previous findings which found that eagles arrive on salmon bearing rivers during the height of consumable salmon abundance without a time lag (Restani et al. 2000, Knight and Knight, 1983; Elliot et al. 2011). To investigate the spatial distribution patterns of eagles, I first examined the abundance of eagles on each river in relation to the abundance of salmon. I determined that the number of eagles that aggregated on all four rivers was highly correlated to salmon abundance. This result supports several previous findings which conclude that the numerical response of migratory eagles on rivers occurs in correspondence with salmon abundance (Stalmaster and Gessaman, 1984, Restani et al. 2000; Bennetts and McClelland, 1991). I investigated this relationship further by examining the response of eagles to the continuous input of salmon under the predictions of Ideal Free Distribution.

Ideal Free Distribution has been used in several previous studies to examine the use of patches of varying quality by unequal competitors (Hamilton, 2002; Parker and Sutherland, 1986). These studies found that when there are kleptoparasites present in a population, the distribution of individuals under-matched the distribution of resource inputs (Hamilton, 2002). Similarly, this study determined that the proportion of eagles across all four rivers under-matched the 1:1 scavenger to prey ratio. This deviation could be caused by high intraspecific competition that occurred over salmon carcasses, which may have forced less dominant individuals to nearby rivers where they could exploit available carcasses. Thus, while this study found that eagles generally matched the proportion of salmon carcasses and predictions of IFD, the use of kleptoparasitism among aggregations of eagles may be the underlying cause for a deviation from a perfect Ideal Free distribution.

Next, in my examination of eagle distribution patterns, I determined that the physical features of rivers, namely the area of sandbars, notably affected the abundance of eagles that could aggregate on each system. The Little Qualicum river, which has very large expanses of sandbars, experienced significantly more eagles in comparison to the Big Qualicum river, Englishman river and Rosewall creek. This interesting and unexpected result adds to previous evidence which suggests that eagle abundances are dependent on the spatial distribution of sandbars and tidal flats within river ecosystems (Watson et al. 1991). In response to this finding, there is an opportunity to further explore the effect that sandbar area has on the numerical response of eagles by collecting fine-scale physical data to examine this relationship in a quantitative manner. Overall, the results of Chapter 2 provide novel insights on the temporal and spatial distribution patterns of bald eagles on a regional spatial scale, and provide a foundation for future studies to examine eagle distribution patterns on continental scales.

In the third chapter of this thesis, I examined the temporal and spatial occurrence of kleptoparasitism over 13 observation cycles across four salmon-bearing rivers. I determined that the highest number of adult and juvenile eagles that were involved in scavenging groups occurred during the 7th observation cycle, while the highest number of salmon that were fought over in scavenging groups occurred during the 9th cycle. I found that the proportion of kleptoparasitism attempts on each river occurred in correspondence with the proportion of eagles. The rate of attempts followed a similar pattern, which was exemplified by the Little Qualicum river, where the proportion and

rate of attempts was highest. This is in contrast to the Englishman river, which had the lowest proportion and rate of attempts. This result corroborates a previous finding in the literature which also determined that the frequency of attempts among conspecifics increased with higher numbers of salmon and eagles (Restani et al. 2000).

After exploring the temporal and spatial occurrence of kleptoparasitism, I examined the influence that age, behavioural tactic, and salmon abundance had on the outcome of attempts. I found that 60 adult eagles and 62 juveniles comprised 42 scavenging groups, which indicates that an equal number of adult and juvenile eagles comprised the groups. This result deviates from a previous study which determined that juveniles make up a greater proportion of individuals involved in scavenging groups (Fischer, 1985). Interestingly, the adults and juveniles that comprised scavenging groups almost only targeted conspecifics of a similar age in their attempts to steal. This result supports a previous study by Bennetts and McClelland (1991) who determined that eagles attacked conspecifics of a similar age. To further examine this age bias, I proposed that individuals used sequential assessment to assess the fighting ability of contestants through a series of subtle behaviours prior to engaging in a kleptoparasitism attempt (Enquist and Leimar, 1983). As the age, size, social dominance and foraging experience of bald eagles is indicated by their plumage pattern, it is likely that individuals assessed plumage and then attacked others that were most likely to yield their prey without an escalation into a fight (Hansen, 1986). For juvenile attackers, I suggest that they did not target the larger and more experienced adults as there is a low probability of success. For adult attackers, it is possible that many of the individuals that attacked other adults were females, as they are larger and more socially dominant than males of either age group (Hansen, 1986). Thus, large female birds could attack other experienced adults without much resistance from the target. Overall, considering the sociality present among foraging eagles, I suggest that individuals attacked conspecifics that were least likely to retaliate from an attack.

In addition to affecting the dynamic between attackers and targets in kleptoparasitism attempts, the age of eagles also influenced the behavioural tactic used in kleptoparasitism. Juveniles preferentially used the aerial-based tactic swoop and steal, while adults implemented the ground-based tactic flap and hop. Interestingly, juvenile eagles that initiated kleptoparasitism attempts experienced more successful outcomes than adults. This result was confirmed in the model analysis, which

determined that juvenile attackers have a higher predicted probability of success compared to adults by 16% percent. This novel finding deviates from previous studies which determined that juveniles are less successful in their attempts to steal compared to adults (Bennetts et al. 1997). Thus, despite the equal number of adult and juvenile eagles involved in scavenging groups, juveniles demonstrated that they were more successful in stealing from conspecifics in both observed attempts and the model predictions. Lastly, I examined the effect that varying numbers of salmon in scavenging groups have on the predicted probability of success. I determined that at 29 salmon, which was the highest observed salmon abundance in scavenging groups, the predicted probability of success was 70%. However, at 3 salmon, which was the average salmon abundance per scavenging group, the predicted probability of success was 28%. Thus I determined that above a threshold of 17 salmon in an scavenging group, the predicted probability of success increased with an increase in salmon abundance. I inferred this result to indicate that intraspecific competition decreased above this threshold, which facilitated a successful outcome. Overall, the results of Chapter 3 indicate that the age of attackers affects the age of individuals they target, the behavioural tactic used, and the outcome of kleptoparasitism. Thus, further understanding the role that sociality plays in the occurrence and outcome of attempts is important to understanding kleptoparasitism, which is one of the primary foraging strategies among aggregations of eagles on salmon-bearing rivers.

Ultimately, this thesis examines the relationship between spawning salmonids and bald eagles by examining their distribution patterns and foraging behaviour across four unique river ecosystems. The results of this study provide detailed insight into the influence that varying salmon abundances have on the temporal and spatial distribution patterns of eagles at a fine spatial scale. As the physical features of the individual rivers influenced the abundance of eagles that aggregated on each river, I recommend that this pattern is further explored by incorporating physical data that pertains to each river, such as area of sand bars and water levels. I also suggest that these data are used when examining the proportion of kleptoparasitism attempts that occur on each river, as the area of sand bars may affect the number of salmon involved in kleptoparasitism and the behavioural tactic used to steal from conspecifics. Overall, I recommend that these results be built upon at varying spatial scales, which may be used to infer larger continental-scale distribution patterns of migrating bald eagles.

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Appendix A.

Supplementary Material for Chapter 2

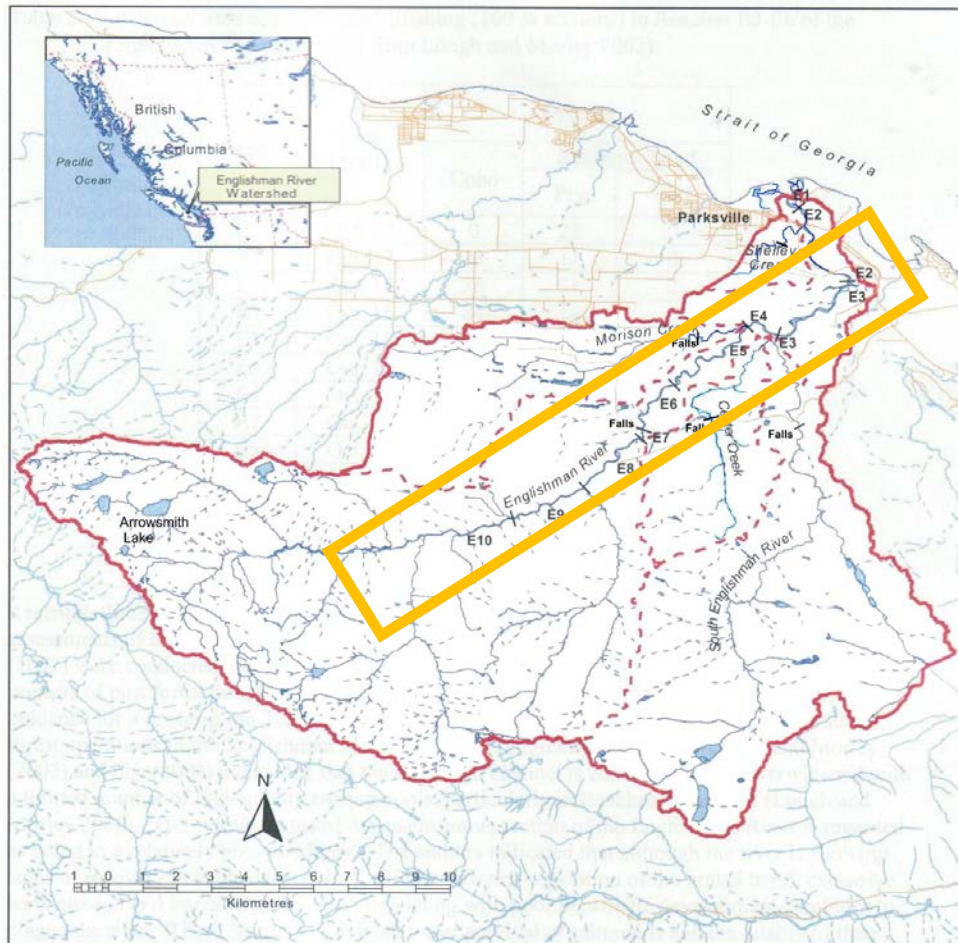


Figure A1. Map of the Englishman River, Vancouver Island, BC. The Englishman river is shown in the yellow box. Sourced from the Regional District of Nanaimo.

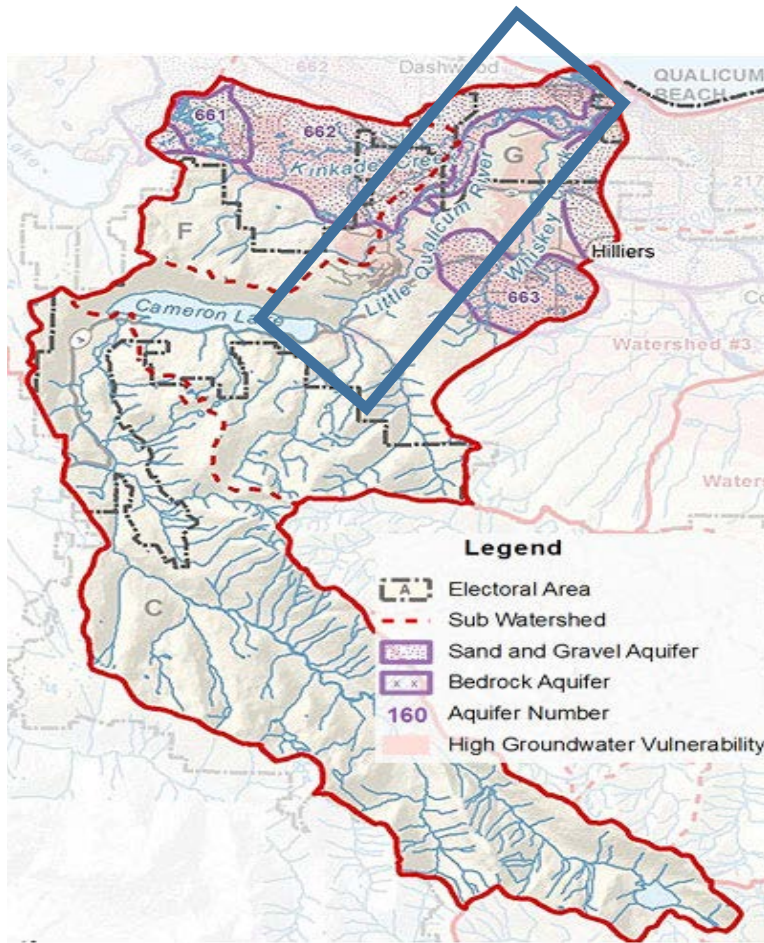


Figure A2. Map of the Little Qualicum River, Vancouver Island, BC. The Little Qualicum river is shown in the blue box. Sourced from the Regional District of Nanaimo.

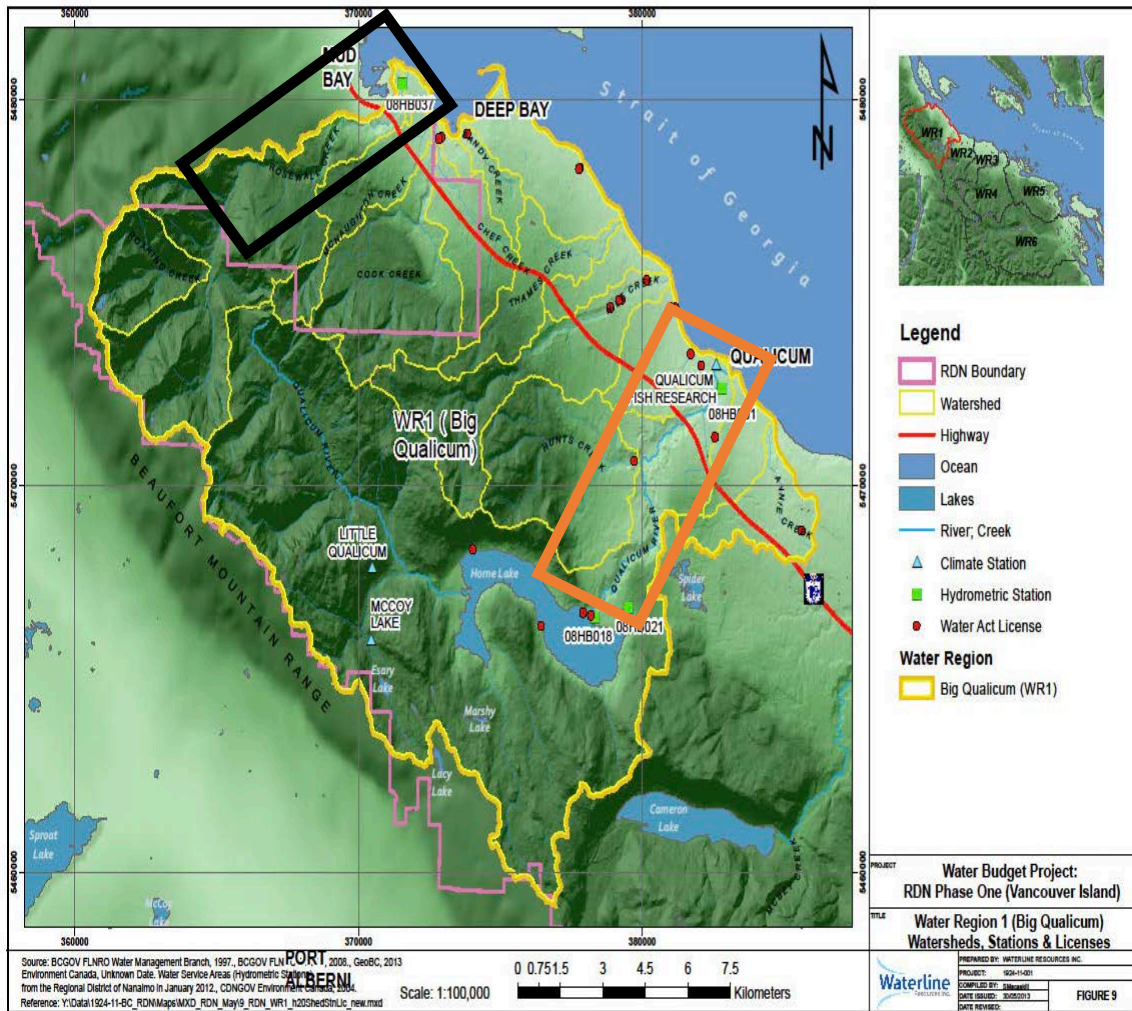


Figure A3. Map of the Big Qualicum River and Rosewall creek, Vancouver Island, BC. The Big Qualicum river is shown in the orange box. Rosewall creek is shown in the black box. Sourced from the Regional District of Nanaimo.

Table A1. Latitude and longitude of the upper and lower field sites on each study river.

River	Latitude	Longitude
Little Qualicum-L	49.2158	124.2959
Little Qualicum-U	49.2043	124.2926
Big Qualicum-L	49.2353	124.3624
Big Qualicum-U	49.2335	124.3702
Rosewall- L	49.2757	124.4716
Rosewall- U	49.2756	124.4637
Englishman -L	49.1952	124.1727
Englishman-U	49.1703	124.181

Appendix B.

Supplementary Material for Chapter 3

Table B1. Summary of terms used to describe kleptoparasitism among groups of eagles.

Terms	Definition
Scavenging group	Scavenging groups are defined as groups of bald eagles consisting of at least 2 individuals that are present at a single location around salmon
Kleptoparasitism attempt	An attempt made by either a juvenile or adult eagle present in the scavenging group to steal salmon from another eagle in the scavenging group. Outcomes of kleptoparasitism attempts were graded on a 0 to 1 scale, with 0 being 'attempt' and 1 representing 'success'.
Attacker	Eagle that initiates a kleptoparasitism attempt to steal salmon from a conspecific.
Target	A eagle that has previously procured salmon stolen by an attacker in a kleptoparasitism attempt.
Group composition	The number of adult and juvenile eagles that comprised each scavenging group. The plumage pattern of individuals to identify their age. Individuals with a predominately white head and tail were considered adults, while individuals with a mottled brown plumage were considered juveniles.
Behavioural tactics	Swoop and steal: an airborne swoop with exposed talons, which results in the attacker landing near the target. Considered an aerial-based tactic as the behaviour originates in the air. Flap and hop: a hopping movement across the ground while flapping their wings repeatedly while moving in the direction of the target. Considered a ground-based tactic, as the behaviour originates on the ground. Aerial steal: mid-air ambush in an attempt to salmon from the target. Considered an aerial-based tactic as the behaviour originates in the air.

Table B2. Descriptions of kleptoparasitism and behavioural tactics that have been used in previous studies.

Study	Terms	Definitions
Bennetts and McClelland (1997)	Foraging tactic	<p>Stooping: an eagle comes within 1 m of the water surface during a dive that was initiated from either a perch or the air. Stooping was directed at live or floating salmon.</p> <p>Scavenging: an eagle walked or waded to an unattended dead salmon. When scavenging an eagle walked or waded to an unattended dead salmon</p> <p>Aerial piracy: a pursuing eagle came within 1 m of a flying eagle carrying a salmon</p> <p>Ground piracy: eagle attempted to steal from another eagle on the ground. Initiations of this foraging behaviour was from the air, ground or perch.</p>
Fischer (1985)	Piracy opportunity	An aerial pursuit or attempted displacement of a bird that possessed prey
Hansen (1986)	Contest	Competitive interaction over food that is initiated when a pirate acts to displace a food owner and is concluded when one bird yields.
Hansen (1986)	Behaviour patterns	<p>Aerial (pirate): fly towards feeder and descends upon it with feet and talons outstretched</p> <p>Leap (pirate): jump from the ground to a height of a few meters and drops towards feeder with talons extended</p> <p>Walk (pirate): trot towards feeder with slow deliberate steps while staring intently at feeder; neck is extended and neck and beak are held horizontally; if feeder does not retreat, actor strikes with talons or beak.</p>
Knight and Skagen (1988)	Feeding attempt	A feeding attempt was considered successful either when a bird began feeding on an unoccupied carcass or when a bird supplanted an eagle at a carcass and began to feed.
Restani et al. (2000)	Foraging attempt	<p>Stooping: any flight during which an eagle circled low over the water and dropped its legs, regardless of whether a salmon was struck or captured.</p> <p>Scavenging: an eagle landed on the ground and approached a salmon carcass washed ashore</p> <p>Pirating: any approach, whether on the ground or in flight where an attacking eagle came within 1 meter of an eagle with a salmon.</p>
Stalmaster and Gessaman (1984)	Supplanting attempts	<p>Aerial attacks: aerial attacks by a flying eagle against a feeding eagle on the ground. Attacks originated at least 25m away from the feeding area.</p> <p>Ground attacks: ground attacks by eagles walking, running or flying on the ground. Attacks originated from a point <25m from the feeding bird.</p>