

INDIVIDUAL VARIABILITY IN FORAGING SUCCESS OF HARBOR SEALS (*PHOCA*
VITULINA) PREYING ON PACIFIC SALMON (*ONCORHYNCHUS SPP.*) INFORMS
PREDATOR MANAGEMENT

By

Grace Freeman

Accepted in Partial Completion
of the requirements for the Degree
Master of Science

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MASTER'S THESIS

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A Thesis

Presented to

The Faculty of

Western Washington University

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Of the Requirements for the Degree

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Abstract

The complexities of trophic dynamics complicate the management of predator populations. In some cases, targeted culling campaigns are meant to control predator populations. In these campaigns, predators are considered ‘rogue individuals’ based on visitation rates to a site. This definition carries the underlying assumption that all predators impact prey equally, however, individual variability in foraging success may compromise such an assumption. Thus, to test the hypothesis that foraging success varies among individual predators, I studied harbor seals preying on adult Pacific Salmon during the 2014-2019 fall salmon runs. I analyzed individual harbor seal visitation rate and foraging success based on photographs and field observations, and I employed Generalized Linear Mixed-Effects Models to determine individual variability in metrics of foraging success. Individual harbor seal identity better explained both total foraging success and the odds of success of a given foraging event when compared to models based on visitation rate alone. My data suggest that considering intraspecific variability and classifying ‘rogue individuals’ based on foraging success is a more accurate protocol for managing predator populations than relying solely on visitation rate of the predators.

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Introduction

The complexities of trophic dynamics represent a fundamental aspect of conservation biology. Predators are often the focus of ecosystem-based conservation efforts not only because they affect their communities in ways disproportionate to their biomass, but also because predators are often charismatic to the public (Krause & Robins, 2017; Marshall, Stier, Samhouri, Kelly, & Ward, 2016; Sergio et al., 2008). Moreover, the impacts of predators go beyond the direct mortality of prey species and extend to all trophic levels in the of a predator's community (Polis & Strong, 1996). For example, the reintroduction of an apex predator, the gray wolf (*Canis lupus*), to Yellowstone National Park in 1995 triggered a top-down trophic cascade that affected prey species abundances, riparian vegetation, and even stream hydrology (Smith, Peterson, & Houston, 2003). As in this famous example of top-down ecosystem control, predator populations are often treated as a homogenous group in which each individual carries the same potential to impact their communities through direct prey mortality (Linnell et al., 1999). This assumption, however, is largely untested, and a number of studies across a variety of taxa present evidence to the contrary (Estes, Riedman, Staedler, Tinker, & Lyon, 2003; Guillemette & Brousseau, 2001; Svanbäck & Persson, 2004). Hence, a better understanding of variability in the trophic impacts among individual predators in a population could foster greater understanding of trophic ecology and allow for more efficient management of predators, their prey, and ecosystems as a whole.

Due in part to their sizable impact on their communities, the management of predator populations is both critical and highly nuanced. General culling and bounty campaigns in which predators are killed or hunted at large have long been employed to control predator populations in both terrestrial and marine settings (Bearzi, Holcer, & Di Sciara, 2004; Lavigne, 2003). These

general campaigns target a predator population as a whole with the goal of decreasing predator abundance and as a means of reducing prey mortality (Bowen & Lidgard, 2013). Such management approaches have historically been based on the assumption that predator populations consist entirely of generalists; that is, individuals that forage opportunistically rather than seeking out one type of prey or specializing in a given foraging behavior (Svanbäck & Persson, 2004). Some recent culling campaigns have taken more targeted approaches by seeking to remove individual predators thought to have the largest impact on prey species of concern (Bowen & Lidgard, 2013). The targeted predators are known as ‘rogue’ or ‘problem’ individuals and are thought to be the predators consuming a disproportionately large amount of prey relative to others in the same population (Butler et al., 2008; Graham, Harris, Matejusová, & Middlemas, 2011; Linnell et al., 1999). An underlying assumption in the rogue individual paradigm is that a small number of individuals in a predator population are responsible for most of the depletion of the prey population (Linnell et al., 1999). Under this assumption, directed culling campaigns have been used in which presumed rogue individual predators are targeted for removal to reduce prey mortality while simultaneously maintaining stability of the predator population (Bowen & Lidgard, 2013; Tidwell, van der Leeuw, Magill, Carrothers, & Wertheimer, 2017). Targeting rogue individuals addresses the flawed assumption that all predators impact the prey population to an equal degree, however, there is a dearth of research and scientific data for use in culling campaigns, especially in marine environments (Bowen & Lidgard, 2013; Guillemette & Brousseau, 2001). Furthermore, few programs have measurable objectives, and their success is often not evaluated (Bowen & Lidgard, 2013).

Intraspecific variation in prey consumption and resource use by predators can significantly influence prey community structure across a variety of predator taxa (Harmon et al.,

2009; Rudolf & Rasmussen, 2013). For example, in California sea lions (*Zalophus californianus*), males tend to forage on large pelagic species such as adult salmon and females target juvenile fish and benthic prey (Adams et al., 2016; Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, Hanson, Scordino, Jeffries, Marshall, et al., 2017; Jones et al., 1997). In sea birds and polar bears (*Ursus maritimus*), males forage at different times of day from their female counterparts and typically consume prey at a higher trophic level (Bearhop et al., 2006; Thiemann, Iverson, Stirling, & Obbard, 2011). There are even reports of male grey seals (*Halichoerus grypus*) that specialize in raiding human-placed salmon traps (Königson, Fjälling, Berglind, & Lunneryd, 2013). Moreover, individuals can differ in how well they perform adaptive behavior for reasons not attributed to sex or visitation such as variances in either physical or behavioral skill (Sih, Sinn, & Patricelli, 2019). For example, individual foraging variability in sea otters (*Enhydra lutris*) and harbor seals (*Phoca vitulina*) has been attributed to differences in dive behavior (Bjorkland et al., 2015; Schwarz et al., 2018; Tinker, Costa, Estes, & Wieringa, 2007; Voelker, Schwarz, Thomas, Nelson, & Acevedo-Gutiérrez, 2020). Alternatively, male southern sea lions (*Otaria byronia*) seem to display prey preferences given that most rarely consume fur seals (*Arctocephalus ausralis*), but others have a tendency to do so repeatedly (Bolnick et al., 2003; Harcourt, 1993). Accounting for variability among individuals of the same species — whether attributed to sex or individual differences — is an essential but often overlooked step in effectively managing predator populations. Most current management strategies assume a homogeneous predator population or account for individual variability based solely on the amount of times a predator visits a site of interest (Bowen & Lidgard, 2013; Linnell et al., 1999).

In the United States, marine mammals are protected under federal law, and special permits must be issued to undertake culling campaigns of any kind. Permits for modern, targeted campaigns are granted according to guidelines based on repeated appearance of individual predators at the site of concern (Marine Mammal Commission [MMC], 1978). Individuals are considered rogue and are thus eligible for removal based on the idea that prey consumption is determined entirely by visitation (NMFS, 2018). In one example, an individual is eligible for removal if it is observed at the site on five or more days (regardless of timing) or is observed preying on a species of concern at least once (NMFS, 2018). In 2019, these guidelines were changed from “and” to “or” to capture more individuals that managers deemed problem animals, but who hadn’t been observed often enough or captured the prey item required to be eligible for removal under the original definition (Steingass, Jeffries, Hatch, & Dupont, 2020). This model is more targeted than historical bounty campaigns and addresses the assumption that all individuals within a predator population have the same impact on prey abundance. Such protocols could still be biased, however, in that they continue to operate under the untested assumption that all predators are equally likely to affect prey during each visit or foraging attempt. In that way, the current guidelines fail to account for potential variability of foraging behaviors and success of individual predators not attributed to their visitation rate at the site of concern (Bowen & Lidgard, 2013).

Harbor seals in the Salish Sea (the inland waters of Washington State, USA and British Columbia, Canada) are an ideal study system to examine the assumption that visitation rate is the sole driver of variability in the consumption of prey. During the early 1900s, a state-sponsored population control program led to a stark decline in Washington’s harbor seal population as an estimated 17,000 harbor seals were lethally removed from state waters (Newby, 1973). The

program ended in 1960, and harbor seals gained federal protections in 1972 with the passage of the Marine Mammal Protection Act (MMPA) (Jeffries, Huber, Calambokidis, & Laake, 2003). Under the MMPA, the intentional ‘take’ of marine mammals is a federal offense in the United States, and ‘take’ is defined broadly as, “to harass, hunt, capture, or kill, or attempt to harass, hunt, capture, or kill any marine mammal” (MMC, 1978). Since the implementation of the MMPA, pinniped abundance has increased with many populations reaching or approaching carrying capacity (Wright, Riemer, Brown, Ougzin, & Bucklin, 2007). Harbor seal populations in California, Oregon, and Washington, for example, have been growing at an estimated rate of 5-7% annually since the 1970s (Jones et al., 1997), a recovery which has shifted trophic dynamics and dramatically increased predation pressures on salmonids (Adams et al., 2016; Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, Hanson, Scordino, Jeffries, Pearson, et al., 2017; Jeffries et al., 2003; Thomas, Lance, Jeffries, Miner, & Acevedo-Gutiérrez, 2011). Their regional abundance allows for predictable observation of harbor seals within the Salish Sea and underscores the influence these predators can exert on the population dynamics of their prey.

Harbor seals in the Salish Sea feed on many different prey species of conservation concern, including Pacific salmon (*Oncorhynchus* spp.) (Bjorkland et al., 2015; Bromaghin et al., 2013; Jeffries et al., 2003; Lance, Chang, Jeffries, Pearson, & Acevedo-Gutiérrez, 2012; Olesiuk, 1993). Predation by harbor seals is suspected of hindering the recovery of iconic and endangered species, such as Chinook salmon (*O. tshawytscha*) (Adams et al., 2016; Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, Hanson, Scordino, Jeffries, Pearson, et al., 2017; Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, Hanson, Scordino, Jeffries, Marshall, et al., 2017). As in other parts of the world (e.g., Middlemas, Barton, Armstrong, & Thompson, 2006), harbor seals aggregate at river mouths in the Salish Sea to prey on salmon

returning to spawn. One such site is Whatcom Creek, a small creek located in downtown Bellingham, Washington State, where harbor seals congregate each fall for the annual return of spawning Pacific salmon (Farrer & Acevedo-Gutiérrez, 2010). Whatcom Creek also borders a public park and is home to a salmon hatchery with a fish ladder (Farrer & Acevedo-Gutiérrez, 2010). This unique combination offers the opportunity to estimate individual visitation rate and foraging success of a marine predator via direct observation while also allowing for a predictable temporal distribution within a relatively contained system. As a result, Whatcom Creek is an ideal site to observe harbor seal behavior in the creek as a means of examining the assumption that visitation is directly and solely responsible for levels of prey consumption among harbor seals in the Salish Sea. Specifically, I examined the hypothesis that visitation rate alone can explain foraging success and, as such, is an appropriate indicator of the impact of an individual predator. To address this hypothesis, I used a long-term dataset to estimate salmon abundance, identify individual harbor seals, and describe harbor seal occurrence and foraging success.

Methods

Study Site

I conducted my study at the mouth of Whatcom Creek where it flows into Bellingham Bay (48°45'14"N and 122°29'00"W) in downtown Bellingham, Washington State, USA. The site is approximately 215 m long, 58 m across at the widest point, 25 m at the narrowest, and covers a surface area of approximately 7,225 m², depending on tide. Harbor seals are safely observable from a path to the southeast of the creek and from a boardwalk built along the north bank of the creek.

Whatcom Creek flows east to west from Lake Whatcom about 4.5 km until it reaches Bellingham Bay. Since a pipeline rupture and subsequent fire in 1999, the creek has been the focus of restoration and monitoring efforts by multiple city programs and the Washington Department of Fish and Wildlife. Following the explosion, field staff reported more than 100,000 dead fish and concluded that all aquatic life in Whatcom Creek had been killed by the explosion itself or the subsequent fire (Madsen & Nightengale, 2009). This report sparked an effort to restore not only the aquatic wildlife but also the riparian habitat. Annual surveys conducted by the City of Bellingham have indicated a substantial drop in anadromous fish abundance with fewer than 10 Chinook or Chum (*O. keta*) salmon spotted during spawning surveys in any given year from 2000-2009 (Madsen & Nightengale, 2009). Since that time, spawning returns have increased, and the creek and its tributaries currently provide approximately 6.5 km of accessible habitat for juvenile salmon and support small wild self-sustaining runs of Coho (*O. kisutch*) and Steelhead (*O. mykiss*) (Fairbanks & Penttila, 2016). In addition, Whatcom Creek Hatchery, located on the north bank of the study site and run by Bellingham Technical College, maintains a population of chum salmon (Madsen & Nightengale, 2009). The annual return of hatchery chum salmon in the fall consistently draws fishermen and harbor seals to the area.

Salmon Occurrence

Salmon return data from 2014 to 2019 were collected from the hatchery's records of daily returns (Washington Department of Fish and Wildlife, 2020). Among these data were the number of individuals present and the species of each return. Since the vast majority of the returns (96%) were hatchery-raised Chum salmon (Washington Department of Fish and Wildlife, 2020) and this study focused on salmon predation regardless of species, I combined all species

into one metric of returns. Salmon run in Whatcom Creek between October and December; and during those months, hatchery staff collect return numbers frequently but not always daily. Due to this uncertainty, I calculated a 3-day rolling average of salmon numbers the day before, during, and after an observation. This value was then used as an indicator of the salmon abundance at the time a harbor seal was observed. To calculate the average number of salmon encountered by an individual seal, this 3-day average was averaged across the number of days on which the harbor seal was observed.

Harbor Seal Occurrence

From 2014-2019, undergraduate students from Western Washington University's Marine Mammal Ecology Lab systematically collected data on harbor seal occurrence for two-hour observations during slack tides. At the start of each observation and every 30 minutes for the remainder of the time, observers recorded the number of fishermen present. These values were averaged across the observation and the mean used to represent the number of fishermen present for the day. Additionally, harbor seal behavior was observed for the entirety of the observation period. Because a small area was monitored by at least two observers and harbor seals were typically alone or in pairs, it was possible to employ focal individual sampling (Martin & Bateson, 2007) on every seal within the site. Any seal occurrences that corresponded to the months of October, November, and December were considered 'run visits' and tallied as such in analysis. The number of seals present on each day was determined *a posteriori* via photographic analysis and identification (see below).

Individual Identification of Harbor Seals

Observers used a digital Cannon EOS 60D camera with a 75-300 mm, f/4-5.6 lens to take photos of the harbor seals' heads when they surfaced. Right, left, and front shots were taken when possible. If multiple seals were present, observers also took a photo of the creek at large to aid in cropping of individual harbor seals later. Of all photos taken of an individual seal on a given day, candidate photos were selected whenever the face was visible regardless of lighting or focus. The best candidate photo for each individual on each day was selected for identification, and selected photos were cropped to include only the individual in question. These photos were entered into a database and run through Wild.ID, an opensource photographic analysis software (Bolger, Morrison, Vance, Lee, & Farid, 2012). The program aided in analysis by comparing cropped photos to an existing database to analyze similarities in the photos and propose possible matches. If at least one proposed photo was accurate, the match was confirmed, and the new photo was given the corresponding ID and added to the existing photographic database for that individual. If Wild.ID failed to find a match for a new photo, the photo was identified manually according to standard methodology used in pinniped photo-identification (Harrison et al., 2006; Mackey, Durban, Middlemas, & Thompson, 2008; Thompson & Wheeler, 2008) by comparing distinctive spot patterns, scars, eye color, and other features to those present in the database of all individuals observed at the creek to date. For a manual match to be confirmed, at least three features on the unknown individual were matched exactly with a database photo and a second experienced researcher confirmed the match. If a selected photo was unable to be matched due to lighting or poor photo quality, it was omitted from the dataset.

Foraging Success of Individuals Harbor Seals

Prior research (Farrer & Acevedo-Gutiérrez, 2010) and field observations conducted since 2014 indicate that harbor seals visit the site to prey on returning salmon. Thus, each visit was tallied as a predation or foraging attempt. Successful foraging attempts were defined as those in which a seal captured one or more salmon during the observation period and were confirmed *a posteriori* via photo analysis. Raw, uncropped photos were analyzed to determine presence or absence of adult salmon in the seal's possession. If an individual was confirmed to have control of a salmon, that individual was identified by comparing the timestamp of the raw photo to the cropped photos in the identified database. After confirming a match, the corresponding individual ID was then credited with a successful foraging attempt for that day.

Statistical Analyses

All statistical analyses were conducted using R statistical software version 4.0.2 (R Core Team, 2020). I ran two sets of analyses to describe harbor seal foraging success: The first set of models examined the odds of a successful foraging event, for which I used a Generalized Linear Mixed-Effects Models (GLMM) with binomial distribution in the R package “lme4” to account for the binary nature of the independent variable (Bates, Mächler, Bolker, & Walker, 2015; Lloyd-Smith, 2007). The second set of models examined the total number of successful foraging attempts, for which I used a GLMM with a Poisson log link function. The data were also checked for zero-inflation, and a Poisson distribution was found to predict the appropriate number of zeros (predicted = 103, observed = 102). I checked for overdispersion using the “performance” package in R (Lüdtke et al., 2020), and no overdispersion was detected ($X^2 =$

41.5). For both sets of models, adjusted R^2 values for GLMMs were calculated using the “rsq” package in R (Zhang, 2020).

GLMMs are robust and flexible tests which can analyze non-independent (such as observations of the same individual), non-normal data (such as counts), and allow for consideration of both fixed and random effects as well as their interactions (Bolker et al., 2009; Lloyd-Smith, 2007; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Model assumptions were validated with residual plots, and multicollinearity among variables was assessed using a Variance Inflation Factor (VIF) calculated with the “performance” package in R (Lüdecke et al., 2020). If a covariate was found to be colinear with another in the model ($VIF > 10$), the factor with the highest VIF value, thus explaining the most overlapping variance, was removed and the model was run again. Once multicollinearity was addressed, the lowest Akaike Information Criteria (AIC) value was used to indicate the most parsimonious model (Bolker et al., 2009; Zuur et al., 2009). All models from step one of each model-building process are presented in the results, and the most parsimonious model from the second step is presented for each independent variable.

Odds of a Successful Foraging Event

The odds of a successful foraging attempt were modeled to determine individuals’ impact on their prey species relative to factors beyond their visitation rate alone. Specifically, modeling in the binary allowed for the inclusion of factors that could not be represented in the ‘total successes’ metric such as tide level (high or low), number of fishermen present, and number of additional seals present. To determine if individual variability (‘ID’) played a role in predicting the odds of a successful foraging attempt, the first step was to generate a set of four models with

the ‘binomial’ family to explain the binary outcome (success/no success) of an individual’s visit on any given day (Table S1). Due to the use of the ‘binomial’ family, the outcome was a log-likelihood or odds of success rather than a count value. Because it can be assumed that the presence of more salmon would result in higher odds of success for a harbor seal and no successes can be recorded on days without salmon, the null model for this set utilized Generalized Linear Models (GLM) and included only number of salmon as a fixed factor. Two candidate models added the number of visits recorded by the individual in question as fixed factors: visits throughout the year (‘total visits’) or visits during October-December (‘run visits’). Finally, the last candidate model was a GLMM with the binomial link that added ‘ID’ as a random intercept to the null model. The factor ‘ID’ encompassed the number of visits recorded by each individual as well as the variability inherent to that individual – a metric that was impossible to directly measure and describe in this study. As a result, there were issues of multicollinearity and thus ‘visits’ and ‘ID’ could not be included in the same candidate model. All three candidate models were compared to the null to determine which model – the null, or the null plus ‘run visits’, ‘total visits’, or ‘ID’ – better explained the odds of a successful foraging attempt by an individual harbor seal (Table S1).

The second step in determining which factors influence success was to build the most parsimonious model to explain the odds of a successful foraging attempt. I used a backwards-directional model selection technique with potential factors and their interactions added based on ecological knowledge of the system and tested at each step (Zuur et al., 2009). The potential factors were number of fishermen present (mean value across the observation time), tide (high or low), year, fishing season status (open or closed), number of additional harbor seals present (total for the day), and the number of salmon present (3-day-rolling average), and ‘ID’. Those factors

found to be insignificant were removed from the model, and any that did not improve the model fit as indicated by AIC was not included in the next step. If a covariate was found to be colinear with another in the model ($VIF > 10$), the factor with the highest VIF value, thus explaining the most overlapping variance, was removed, and the model was run again.

Total Number of Successful Foraging Attempts

I also analyzed the total number of successful foraging attempts to determine which factors contributed to an individual's overall impact on their prey population. The first step was to test the assumption that visitation alone can predict total number of successful foraging attempts by an individual harbor seal. To do so, I created a null and three candidate models (Table S2). The null model was based on mean number of salmon present on each day the seal was observed calculated as a three-day rolling average. Again, I used 'salmon' as the ecological null because a successful foraging attempt is only possible when a non-zero number of salmon are present, and this ecological model was the base to which all other factors were added. Two candidate models were built by adding number of visits (either 'total visits' or 'run visits'), as a fixed explanatory variable. All three fixed models (the null and the two candidates) utilized GLMs with Poisson distributions and included total number of successful foraging attempts as the independent variable. Lastly, a final candidate model was generated using a GLMM with a Poisson distribution and included the null plus 'ID' as a random intercept. All three candidate models were compared to the null to determine which factor – the null, or the null plus 'run visits', 'total visits', or 'ID' – better explained total number of successful foraging attempts by an individual harbor seal (Table S2).

The second step was to determine the model that could best predict the total number of successful foraging attempts by an individual harbor seal. To do this, I followed the aforementioned backwards-directional model selection technique testing significance of terms and improvement of fit as each potential factor and/or interaction was added. The factors considered in this model were mean number of fishermen encountered (averaged across the observation and then across days on which the individual seal was observed), the number of years during which the seal was observed ('total year' or 'run year'), and 'ID'.

Rogue Individuals

To determine which individuals would be classified as 'rogue' or 'problem individuals' in a hypothetical culling campaign, I applied current federal protocols (Steingass et al., 2020) to the studied population. Those individuals became the group classified as 'current rogue' (Table S3). Then, I developed a new protocol based only on successful foraging attempts regardless of individual visitation rate. In doing so, I sought to create criteria that would eliminate at least half of the successful foraging attempts by removing the smallest number of rogue individuals (Table S3). I also sought to use a mathematical metric that could be generalized to management settings and predator populations beyond this study. Ultimately, I proposed that those individuals that recorded a number of successful foraging attempts greater than or equal to one standard deviation above the mean could be classified as 'rogue individuals' and thus eligible for removal in a hypothetical culling campaign. I determined the 'proposed rogue' class of individuals based on these criteria (Table S3).

Results

From a total of 1151 selected photos, 1106 (96.0%) photos were positively identified yielding 170 individual harbor seals. Of these individuals, 96 (56.5%) were observed during more than one year, seven (4.1%) were observed during five of the years, and one (<1%) individual (ID0039) was observed at the creek during all six years of the study (Figure S1). A total of 156 (91.7%) identified individuals were observed at the creek only during run months (Figure 1). Four (2.4%) individuals were observed at least one time during five or more months, and one of these individuals (ID0039) appeared at least once during each month when summed over the six years of the study (Figure 1). There was no evidence of individuals employing hunting behavior outside of the 'run months' when adult salmon were not present at the site (Figure 1).



Figure 1: *Number of visits per observation by individual harbor seal ($n = 170$ seals) relative to month summed across 2014-2019.*

Salmon in Whatcom Creek ran every fall and were almost entirely hatchery-raised chum (96.9%). The run size per year was 6494 ± 6302 salmon (mean \pm SD, $n = 6$ years) with a minimum of 191 and a maximum of 14,611 returns (Figure S2). The run typically started in late October and continued into December with a peak in late November (Figure 2). The number of harbor seals observed followed the same general pattern of salmon numbers with a sharp peak in November (Figure 2). There was variability in the visitation rate of individual seals across the study: The mean number of total visits per year was 2.34 ± 2.66 visits ($n = 170$ seals) with a minimum of 1 and a maximum of 21 visits (Figure S3a). The mean number of run visits per number of runs present was 1.97 ± 1.59 ($n = 170$ seals) with a minimum of 0 and a maximum of 10.5 visits per run (Figure S3b).

Odds of a Successful Foraging Event

The rate of foraging success varied greatly across the studied population with a mean success rate of $13.9 \pm 24.0\%$ (successes per visit). The minimum rate of success for an individual harbor seal was 0% – based on a range of one to 108 attempts without success – and the max was 100% – relating to one attempt and one success. There was no relationship between visits and odds of success ($R^2 = .002$; Figure 3). The number of salmon present during an observation varied across the study and was a significant predictor of odds of success during a given observation ($p << .001$, [95% CI: 0.22, 0.50]; Table 1). However, neither visit metric (total nor run visits) was significant in their respective models ($p = .10$, [95% CI: -0.11, 0.01], $p = .51$, [95% CI: -0.01, 0.01] respectively; Table 1). The random factor, seal ID, added to the null model based on salmon present was significant ($p << .01$, [95% CI: 0.09 – 0.18]) and improved model fit over the null ($\Delta AIC = 37.7$; Table 1).

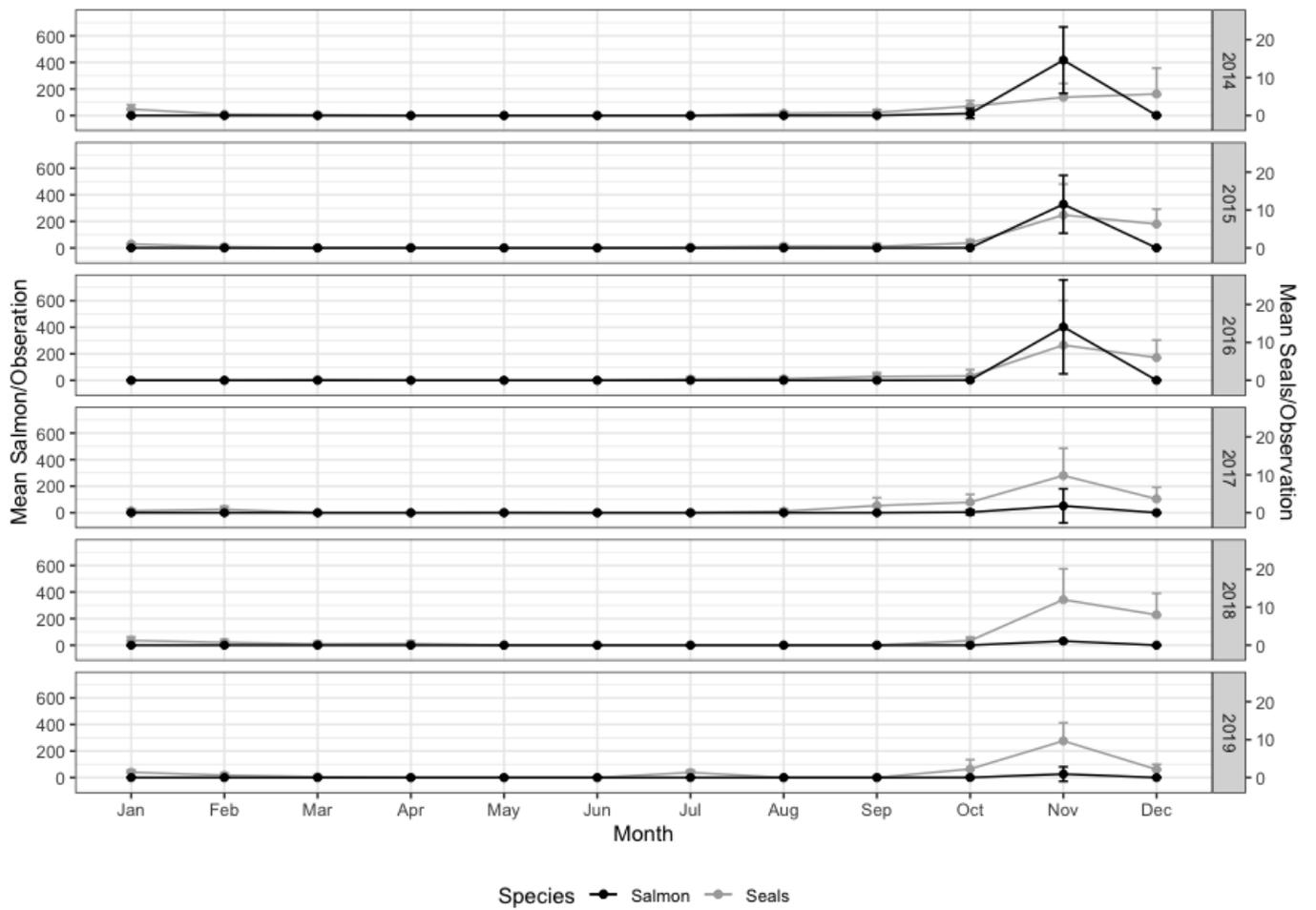


Figure 2: Mean number of salmon present per observation per month of the study calculated as the mean of a three-day rolling average corresponding to the day of observation. Mean number of harbor seals present at each observation per number of observations per month of the study. Error bars represent standard deviation.

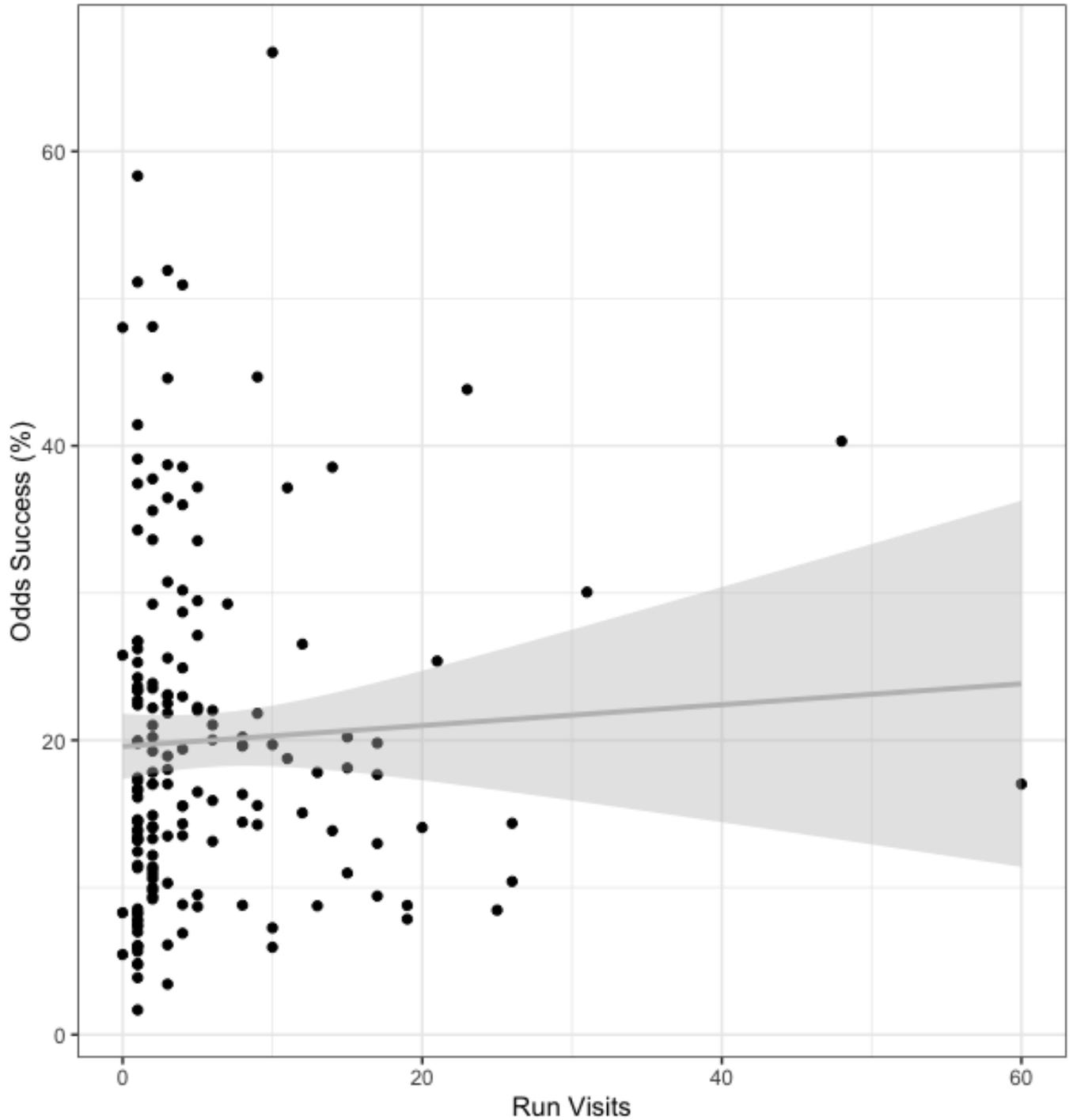


Figure 3: Predicted odds of a successful foraging attempt for each individual harbor seal by the number of run visits for that individual ($n = 170$ seals). The line represents a GLM of expected odds of success by run visits based on a visits-only model with a 95% confidence interval based on standard error ($R^2 = .002$).

Table 1: Model results predicting the odds of success of a single foraging attempt by an individual harbor seal relative to number visits for that seal as well as identity of the seal in question. The change in AIC value is that when compared to the model of best fit as determined by the lowest AIC value.

Models for Odds Success	df	AIC	ΔAIC
Nulls (GLM)			
Odds Success ~ Salmon	2	915.2	70.1
Candidates (GLM)			
Odds Success ~ Salmon + Total Visits	3	914.3	69.2
Odds Success ~ Salmon + Run Visits	3	916.7	71.6
Candidate (GLMM)			
Odds Success ~ Salmon + (1 ID)	3	877.4	32.3
Final Model (GLMM)			
Odds Success ~ Fishermen + Other Seals + Fishermen:Other Seals + (1 ID)	5	845.1	0

To determine the most parsimonious model to explain the odds of a successful foraging attempt, I built six candidate GLMMs using various fixed factors and 'ID' as a random intercept. The number of fishermen present was significant when incorporated to the model with 'ID' ($p << .001$, [95% CI: 0.02, 0.05].) Furthermore, 'tide' (high or low) was insignificant ($p = .37$, [95% CI: -0.90, 0.32] and was omitted the final model. The factor 'fishing season status' (open or closed) was colinear with number of fishermen present ($VIF = 9.08$) and thus was not included in the model. Adding the number of harbor seals present at the time of the foraging event was significant in the model as was the interaction between this term and the number of fishermen ($p << .001$, [95% CI: 0.016, 0.017], $p << .001$, [95% CI: -0.003, -0.001] respectively). Thus, the final, most parsimonious model of the six models tested included the number of fishermen present, the number of seals present, and the interaction between these two as fixed factors, as well as 'ID' as a random intercept (Table 2).

Total Number of Successful Foraging Attempts

Total foraging success varied among individual harbor seals over the course of the study. A total of 66 (38.8%) individual seals recorded one or more foraging success and 164 successful attempts were observed (Figure 4). The total number of foraging successes per individual ranged from 0 to 23 with a mean of 1.00 ± 2.28 (Figure S4). Mean number of salmon encountered was a significant predictor of total number of successful foraging attempts ($p < .01$, [95% CI: -0.43, -0.06]). Due to issues of collinearity, adding any additional term to the null model rendered the 'salmon' term insignificant. However, 'run visits' ($p << .01$, [95% CI: 0.05, 0.06]), 'total visits' ($p << .01$, [95% CI: 0.03, 0.04]), and 'ID' ($p << .01$, [95% CI: 0.96, 1.00]) were all significant in their respective candidate models. When comparing models, the candidate with 'run visits' improved model fit over the null and the 'total visits' candidate ($\Delta AIC = 153.1, 49.9$

respectively; Table 3). 'Run visits' better predicted total successes than did 'total visits' ($\Delta\text{AIC} = 49.9$; Table 3). 'Run visits' was also moderately correlated with total foraging successes (adjusted $R^2 = .36$). However, the candidate model with 'ID' as a random intercept was a better fit with an AIC significantly lower than that of the 'run visits' model ($\Delta\text{AIC} = 14.0$; Table 3). This model also explained significantly more variance than the model based on visits alone (adjusted $R^2 = .81$).

Table 2: *GLMM model output for the final, most parsimonious model describing odds of success for a given foraging event. CIs represent the 95% confidence interval for the estimate of each parameter in the model.*

Coefficient	Estimate	95% CI	Exp	Z value	P value
ID	-3.38	(-3.94, -2.81)	---	-11.8	<<.001
Fishermen	0.061	(0.041, 0.081)	1.06	5.97	<<.001
Other Seals	0.076	(0.042, 0.110)	1.08	4.37	<<.001
Fishermen:Other Seals	-0.002	(-0.004, -.001)	1.01	-3.88	<<.001

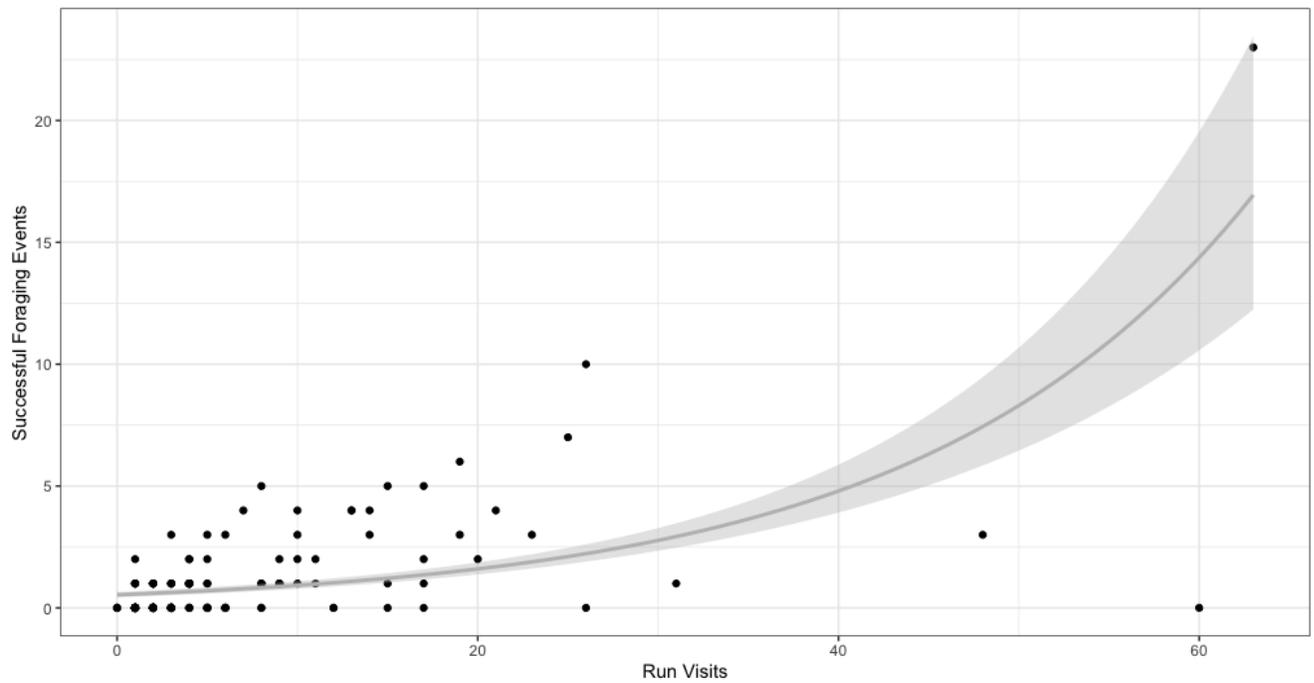


Figure 4: Number of successful foraging for each individual harbor seal by the number of run visits for that individual ($n = 170$ seals). The line represents a GLM of successes by run visits with a Poisson distribution (adjusted $R^2 = .36$) and 95% confidence interval based on standard error.

Table 3: Model results predicting the total number of successful foraging attempts recorded by individual harbor seals relative to number of run visits number of total visits and individual ID. The change in AIC value is that when compared to the model of best fit as determined by the lowest AIC value.

Models for Total Successes	df	AIC	ΔAIC
Null (GLM)			
Successes ~ Mean Salmon	2	606.0	204.1
Candidates (GLM)			
Successes ~ Mean Salmon + Total Visits	3	502.8	101.0
Successes ~ Mean Salmon + Run Visits	3	452.9	51.0
Candidate (GLMM)			
Successes ~ Mean Salmon + (1 ID)	3	438.9	36.9
Final (GLMM)			
Successes ~ Run Years + (1 ID)	3	401.9	0

When fitting the most parsimonious model for the total number of successful foraging attempts made by a given individual harbor seal, 11 candidate models were created and compared. The mean number of salmon encountered by the individual was found to be statistically insignificant when considered with 'ID' ($p = .32$, [95% CI: -0.17, 0.17]) and was thus removed from further models. The mean number of fishermen present during the observation was also insignificant and removed from further analysis ($p = .50$, [95% CI: -0.11, 0.17]). 'Run visits' was colinear with 'ID' ($VIF > 10$) and was omitted from analysis, but 'run years' was significant in the model ($p \ll .01$, [95% CI: 0.40, 0.75], Table 4). The most parsimonious model of the 11 tested included 'ID' as a random intercept and the number of years during which an individual was observed during the run ('run years') as a fixed factor explaining the total number of successful foraging attempts by an individual (Tables 3 and 4).

Rogue Individuals

When applying the current protocols used in culling campaigns (NMFS, 2018), 81 (47.6%) individuals from the studied population were deemed 'rogue' and thus, under current guidelines, would be eligible for removal in a hypothetical culling campaign. These individuals were responsible for 100% of the total successful foraging attempts observed. However, 17 (21.0%) of those individuals eligible for removal under current protocols never recorded a successful foraging attempt and 36 (44.4%) recorded only one.

When applying my proposed protocol based on successful attempts alone, 14 (8.2%) individuals would be considered rogue and thus eligible for culling. These individuals accounted for 23.6% of the total visits and 51.5% of all successful foraging attempts recorded from 2014-2019. Using these criteria would reduce the individuals eligible for removal by 82.7% while reducing the number of successful foraging attempts accounted for by 48.5%. Eighty-nine

individuals (52.4% of the studied population) recorded no captures and had fewer than five visits, so they were not classified as rogue under either protocol.

Table 4: *GLMM model output for the final, most parsimonious model describing the total number of successful attempts recorded by an individual harbor seal. CIs represent the 95% confidence interval for the estimate of each parameter in the model.*

Coefficient	Estimate	95% CI	Z value	P value
ID	-2.05	(-2.63, -1.46)	-6.82	<<.001
Run Years	0.57	(0.39, 0.74)	0.09	<<.001

Discussion

Individual harbor seals recorded varying numbers of visits and successful foraging attempts on salmon over the six years of the study (Figures S3 and S4). Most individuals were observed only during run months (Figures 1 and 2), and the number of successful foraging attempts during this time was highly variable (Figure S4). This suggests that while most of the seals that visit Whatcom Creek are targeting adult salmon, there is still strong variation among this group. There was no relationship between odds of a successful foraging event and the number of run visits recorded by each individual ($R^2 = .002$; Figure 3). Moreover, despite the correlation between number of run visits and total successes, there was significant variance left unexplained by a visits-only metric (adjusted $R^2 = .36$; Figure 4). For example, the individual with the most successful foraging attempts (ID0039) did not record the most visits, and the individual with the most visits (ID0012) recorded no successful foraging attempts. These two extremes showcase strong behavioral differences within the predator population and provide evidence against the assumption that a predator's impact on the prey population can be determined by visit frequency. Incorporating individual identity into the model for total successful foraging attempts explained 81% of the variance (adjusted $R^2 = .81$). Furthermore, under my proposed protocols based only on the success rate of each predator, removing only 14 (8.2%) individuals from the studied population would eliminate more than 51.5% of the successful foraging attempts recorded in the creek (Table S3). This discrepancy again illustrates the outsized impact of the most prolific individual predators on their prey at large regardless of visit frequency.

There are several possible explanations for the observed individual variability in foraging success. The significance of 'run year' in explaining an individual's total foraging successes

provides evidence for the importance of an individual's site-specific experience. With each additional run during which a seal was observed, the predicted number of successful foraging attempts recorded by that individual also increased (Table 3). This increase was independent of run visits, suggesting a potential behavioral or experience-based learning effect given that the individuals who return year after year are more successful hunters overall regardless of how many times they visit during those years. The significance of run year also corroborates the idea of 'habituated individuals' proposed by NMFS in the Bonneville Dam campaign (National Marine Fisheries Service, 2019; Steingass et al., 2020). Previous work on marine (Königson et al., 2013; Tidwell et al., 2017) and terrestrial (Linnell et al., 1999) predators suggested that those individuals who return to a site year after year are habituated and have a greater impact on the local prey population than those individuals who visit during only one season. Evidence from this study supports the hypotheses that repeat visitors across years are more impactful to the prey population than their non-habituated counterparts. This evidence is nuanced, however, in that those individuals who visit more often in one year are not more likely to record a success during each visit (Figure 4). Further, the impact of run years was relatively small and not independent of individual predator identity (Table 4). Hence, predator identity must still be considered in that it separates habituated individuals with high rates of success from individuals who visit the site frequently but have low predation success.

Additional variability inherent to the individual could also influence overall success of individual predators. For example, large-bodied harbor seals consume prey at a higher trophic level (Bjorkland et al., 2015). Furthermore, sex is known to play a role in harbor seal prey-preference – especially during the pupping season (Schwarz et al., 2018; Voelker et al., 2020). Given that only one type of prey item was considered in this study, the differences in success

during the salmon run could be attributed to either size or sex of the seal. Skill could also play a role in determining a predator's impact on the prey population. The most successful individual (ID0039) was consistently observed hunting in the same location within the creek: at the base of the falls upstream from the hatchery's fish ladder. Few other seals ventured high into the falls where ID0039 recorded most of its successes indicating that ID0039 may have possessed the extra strength or size required to swim against the rapids and falls. Past studies of food web theory in individual predators have indeed pointed to the connection between predator size and trophic position with a non-linear relationship between predator body size and mean body size of the prey consumed (Bolnick et al., 2011). Because the current study focused on adult chum salmon of roughly the same size, this variation could have translated to a variance in number of prey items consumed rather than size of prey consumed by individual predators.

Though impossible to directly measure in this study, differences in foraging technique employed by each individual is another possible driver of individual predator variability. Differences in hunting behavior are often attributed to diving behavior (Bowen, Boness, & Iverson, 1999; Lesage, Hammill, & Kovacs, 2011; Thomas et al., 2011), but it is possible that variation in spatial preference and foraging technique employed in the relatively shallow Whatcom Creek still had an effect on overall success of each individual. Furthermore, previous work has demonstrated that harbor seals exhibit geographic preference for hunting grounds on a regional scale (Peterson, Lance, Jeffries, & Acevedo-Gutiérrez, 2012; Thomas et al., 2011). Observations of varied hunting behavior at Whatcom Creek support this hypothesis of geographic specialization among predators at a site with microhabitats. Specifically, some individuals showed preference for hunting relatively high upstream in the falls where salmon sometimes rest on their migration. Other individual seals seemed to prefer a more passive

method of hunting termed ‘bank’ in which the individual waited in the shallow eddy near the hatchery fish ladder and opportunistically cornered fish onto the bank. Another group of individuals seemed to prefer the ‘upside down’ method of hunting in which they passively floated in the mid-channel and waited to attack fish passing by. This last method, though seemingly most common among individual harbor seals at Whatcom Creek, appeared to be the least likely to result in the capture of salmon, as noted by observers. Instead, the active method of hunting high in the falls, a tactic that likely involves more specialized skill and a larger body size, appeared to observers to be the most efficient hunting method.

Further, studies have shown certain individual pinnipeds to be river-specialists (Butler, Middlemas, Graham, Thompson, & Armstrong, 2006; Graham et al., 2011). It is likely that some of the individuals known to frequent Whatcom Creek are among the river-specialist group and are thus better able to exploit the unique qualities of a river-based foraging site. It follows that these individuals may also exhibit preference for a given hunting technique that is more advantageous in river environments. Evidence from a convergent system suggests that brown bears (*Ursus arctos*) preying on chum salmon sometimes developed alternative strategies specific to their hunting location (Gill & Helfield, 2012). At Whatcom Creek, each microhabitat lent itself to a specific hunting strategy, so it is possible that behavioral plasticity and a predator’s ability to adapt could explain the variable odds of success among individual predators. Hunting technique was not directly recorded in conjunction with successful foraging attempts, but future work should analyze behavior to determine if success rates significantly differ among strategies as suggested by anecdotal observations in this study.

Beyond behavioral variability and geographical preference of the individual seal, the number of additional seals present significantly influenced the odds of a successful foraging

attempt for each predator (Tables 1 and 2). Each additional seal on a given day contributed to an approximate 8% increase in the odds of an individual's success. Observational evidence suggests that this effect could be due to the use of cooperative hunting techniques, or at least the opportunistic use of the interactions of other seals during pursuit of prey. To my knowledge, no research has been published on cooperative hunting in harbor seals, but similar behaviors have been observed in other marine predators (Páez-Rosas et al., 2020; Pitman & Durban, 2012). Cooperative hunting is common in cetaceans and other social marine mammals (Hiruki, Schwartz, & Boveng, 1999; Páez-Rosas et al., 2020; Pitman & Durban, 2012). For example, orca whales (*Orcinus orca*), are known to use coordinated efforts and cooperation to increase the net energy intake of all involved in the hunt (Pitman & Durban, 2012). Cooperative hunting has also been documented in leopard seals (*Hydrurga leptonyx*), as adult seals are known to lure penguins (*Pygoscelis antarctica*) toward another seal waiting below the ice (Ainley, Ballard, Karl, & Dugger, 2005; Hiruki et al., 1999). In addition, one study found that adult male Galapagos Sea Lions (*Zalophus wollebaeki*) worked together to corner yellowfin tuna (*Thunnus albacares*) onto a bank before sharing the prey items between them (Páez-Rosas et al., 2020). Similar hunting behaviors were repeatedly observed at Whatcom Creek, pointing to the possibility of cooperative hunting at the site. Specifically, observers reported seeing harbor seals working together to employ a 'bank' method of hunting in which individual seals corner a fish on the bank of the creek or against rocks. The catch was then shared among the individuals involved in the hunt. The increase in seals present at the site on a given day may have contributed to an increase in the use and success of cooperative hunting techniques and thus, a rise in overall successful foraging attempts for the respective individuals present on that day.

The last factor which significantly contributed to an individual harbor seal's odds of a successful foraging attempt was the number of fishermen present during the attempt (Table 2). With each additional fisherman present at the site, the odds of a successful foraging attempt increased by 6% (Table 2). This relationship was independent of visits and likely due to changes in predator behavior that correspond to the presence of fishermen. Across the study, observers reported seeing the seals employ a 'parked' foraging behavior in which a seal waited near the fishermen and attacked the prey already captured on the fishermen's line – a behavior reported in other settings as well. One report from California found evidence of both California sea lions and harbor seals interacting with commercial fishing gear and causing damage to traps and hook and line systems (Beeson & Hanan, 1996). In fact, it was estimated that commercial troll fishermen lost 12% of the catch to predation by pinnipeds (Beeson & Hanan, 1996). Another study analyzed a similar pattern in gray seals in which they raided traps placed by fishermen and found that a few individuals were responsible for most of the prey mortality associated with the behavior (Königson et al., 2013). Individual predators at Whatcom Creek could specialize in the 'parked' technique to capture prey directly from fishermen, resulting in a negative compounding effect of fisherman abundance on salmon returns. Furthermore, the positive correlation between fishermen and foraging success of harbor seals suggests that closing the fishing season early (as in 2018 and 2019) or completely (as in 2020) may not only reduce salmon mortality due to the effects of fishing by humans but also by seals —specialized or otherwise. This impact of fishermen on the odds of a predator's success was independent of visits recorded by each predator providing further evidence for the importance of individual variability beyond visitation rate alone.

Regardless of the driver or drivers behind individual variability in foraging success among a predator population, the results of this study suggest that relying on visitation rate as a proxy for a predator's impact on the prey population is imprecise. As a result, employing a culling campaign based on visitation rate alone cannot efficiently and effectively manage predator populations. Instead, individual identity of the predator must be considered. I present evidence of the presence of rogue individual harbor seals in Whatcom Creek, and suggest that the consumption of salmon varied to a large extent with individual identity and to a small extent with visit frequency. Future studies, however, should focus on the drivers of this variability to better understand the nuanced relationship between individual predators and their impact on prey. Evidence from this study suggests that some individuals (particularly ID0039) regularly capture and consume more than one prey item during a given foraging event. As a result, examining the absolute number of captures recorded by each individual – rather than the number of successful foraging attempts – would give a clearer measure of each predator's impact. Additionally, a rolling average was used in this study to describe the number of prey individuals present at the site on a given day. Describing this value at a finer scale could help parse the effects of prey abundance on the success of predators within the system. Lastly, running molecular analysis to determine the sex of each predator could help determine to what degree – if any – sex played a role in the observed individual variability.

The results of this study suggest that addressing individual identity is necessary to fully understand each predator's impact on their prey populations. Still unknown, however, is the degree to which predators impact prey on a population-scale. The rogue individual paradigm considers all prey items of the same size and age class to carry equal weight within their population. Because fecundity of adult salmon varies greatly with sex and fitness of individual

(Helle & Hoffman, 1995), however, it is likely that variability in the composition of prey consumed by a predator would result in varied impact on the prey species. Further, it is possible that predation does not have a large effect in relation to other factors influencing prey abundance. Future studies should look at stock size estimates and forecast modeling to evaluate the true impact of collective predation on prey populations. Studies have suggested that among factors including climate change, habitat degradation, and human influence, predation may not impact prey populations to a significant degree (Li, Ainsworth, & Pitcher, 2010). Future work should build on the current study to place predator populations' impact on prey species in a broader, more comprehensive context.

Calls for culling as a technique to manage predators and their prey have long relied on the assumption that all predators are equally likely to impact the prey population and those who visit more frequently will consume more prey. However, this study presented evidence of individual variability in foraging success that challenges such an assumption. Modifying the criteria by which rogue individuals are defined could better capture the individual nuances of the rogue paradigm across environments and predator-prey systems. As a result, this study finds that a new definition of 'rogue' or 'problem individual' based solely on total foraging successes would be a more effective management tool rather than relying on visits as a flawed proxy for the same metric. Because individual variability has been identified in other predator species, the results of this study could be widely applicable. Though more logistically difficult to measure, managers must consider intraspecific variability to most efficiently and effectively manage predator populations through culling.

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Appendix

Table S1: *Candidate models for predicting the log odds of a successful foraging attempt for a given individual harbor seal based on the number of salmon present, the number of visits recorded by the individual, and the individual ID.*

Candidate Models for Odds Success
Null (GLM) Odds Success ~ Salmon
Candidates (GLM) Odds Success ~ Salmon + Total Visits Odds Success ~ Salmon + Run Visits
Candidate (GLMM) Odds Success ~ Salmon + (1 ID)

Table S2: *Candidate models for predicting the total number of successful foraging attempts for a given individual harbor seal based on the mean number of salmon encountered by the individual, the number of visits recorded by the individual, and the individual ID.*

Candidate Models for Total Successes
Null (GLM) Successes ~ Mean Salmon
Candidates (GLM) Successes ~ Mean Salmon + Total Visits Successes ~ Mean Salmon + Run Visits
Candidate (GLMM) Successes ~ Mean Salmon + (1 ID)

Table S3: *Relative impact (ratio of percent of successes to number of individuals) for classes of the most successful predators. Classes are not mutually exclusive, and, based on inclusion criteria, each includes those individuals in the classes in the rows above. ‘Proposed Rogue’ indicates the class of individuals which would be categorized as rogue under proposed protocols whereas ‘Current Rogue’ refers to the class of individuals classified as rogue under current protocols. The ‘Proposed Rogue’ group was so delineated because it accounts for more than half of the successful foraging attempts of the studied population and uses criteria that could be applied in any setting. Specifically, those individuals in the ‘Proposed Rogue’ category have each recorded a number of foraging successes greater than the mean plus the standard deviation of successful foraging attempts for the studied population.*

Class	Class Criteria (# of Successful Foraging Attempts)	Class Size (# of Individuals)	% of Studied Population	% of Successful Foraging Attempts in Studied Population	Relative impact (% Successes: Class Size)
Extreme Impact	≥ 10	2	1.2	20.0	10
High Impact	≥ 5	7	4.1	37.0	5.3
Proposed Rogue	≥ 4 (mean + SD)	14	8.2	51.5	3.7
Moderate Impact	≥ 3	21	12.4	67.1	3.2
Current Rogue	≥ 1 or 5+ visits	81	45.9	100	1.2



Figure S1: *Number visits per observation per year by individual harbor seal ($n = 170$ seals).*

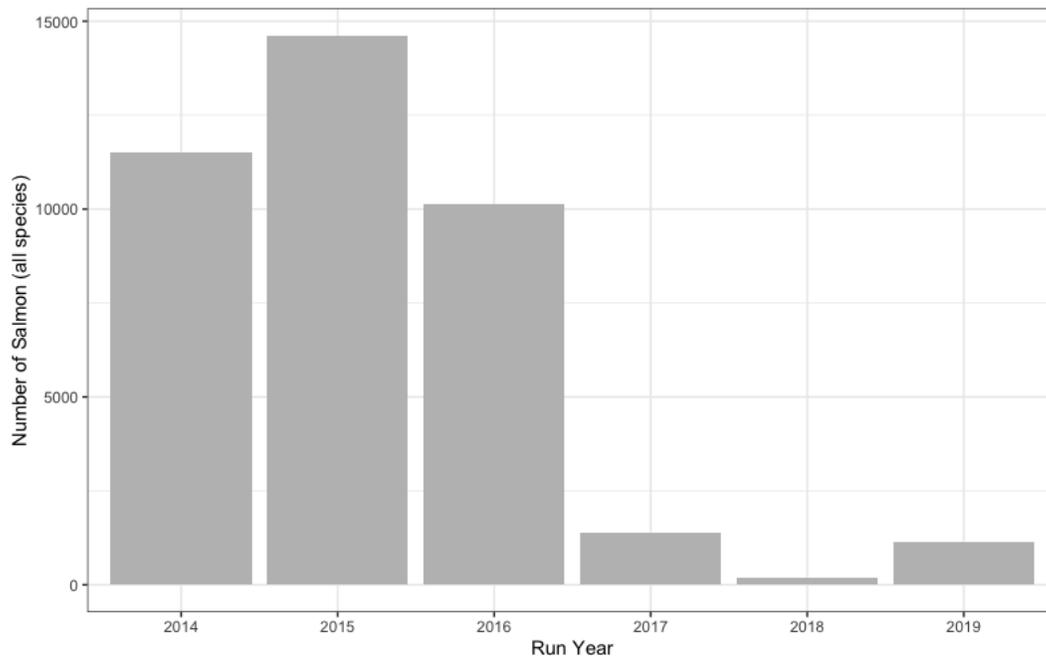


Figure S2: *Number of salmon of all species observed during the salmon run each year. Year indicates that in which the run event started.*

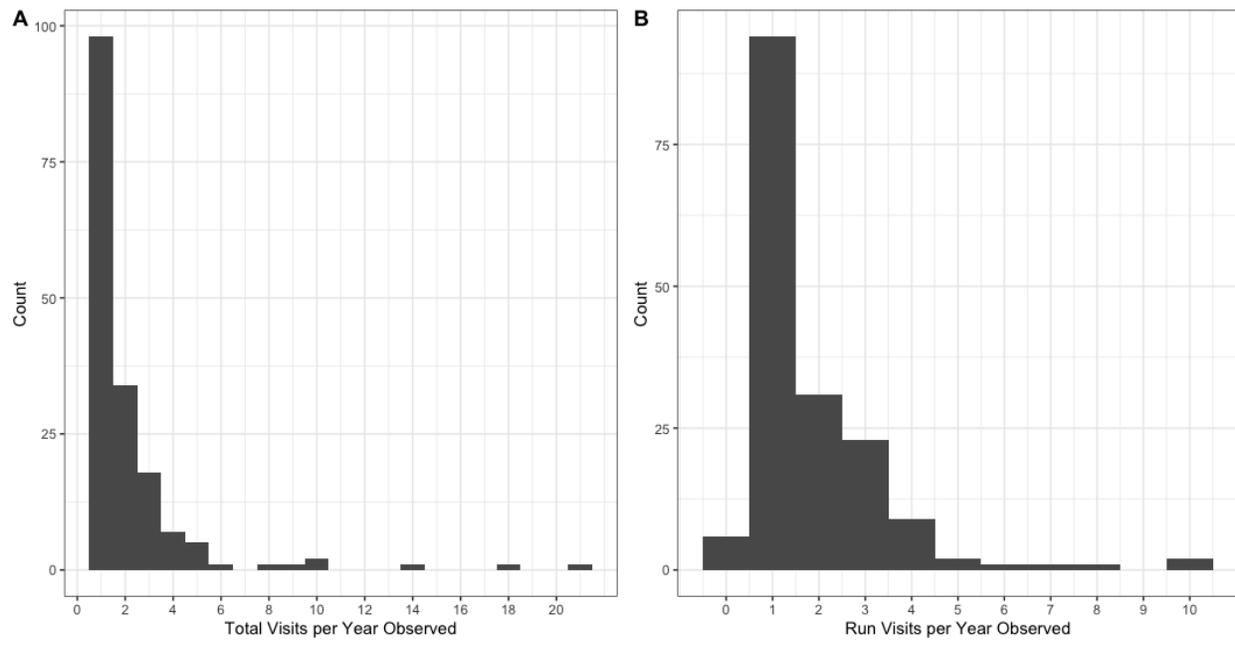


Figure S3: *Frequency histogram of total visits (a) and run visits (b) per year observed for each individual harbor seal.*

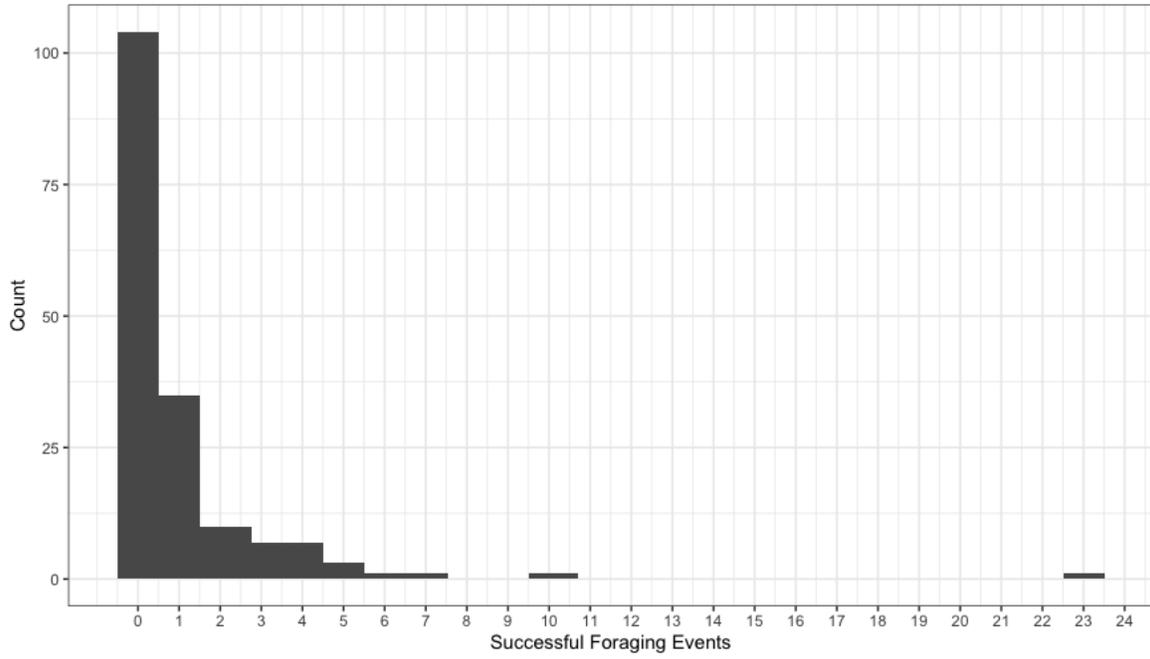


Figure S4: *Frequency histogram of successful foraging attempts for each individual harbor seal.*