Factors Influencing Avian Predation of Juvenile Upriver Bright Chinook Salmon

Prepared for: Pacific Salmon Commission Chinook Technical Committee

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Summary

To investigate the effects of piscivorous colonial waterbird (avian) predation on juvenile salmonids (smolts; *Oncorhynchus* spp.) and to determine what proportion of all sources of smolt mortality (1 – survival) were due to avian predation, we conducted a retrospective analysis on Upriver Bright (URB) fall Chinook Salmon (*O. tshawytscha)* that were marked with Passive Integrated Transponder (PIT) tags and released into the middle Columbia River, USA. We used a state-space Bayesian model that incorporated live detections of tagged fish and recoveries of dead tagged fish on up to 13 different avian colonies to jointly estimate predation and survival probabilities over multiple river-reaches and years (2008 – 2019). Predator species included Caspian Terns (*Hydroprogne caspia,* hereafter "CATE"*)*, Double-Crested Cormorants (*Nannopterum auritum,* hereafter "DCCO"), California Gulls (*Larus californicus)* and Ring-billed Gulls (*L. delawarensis,* collectively hereafter "LAXX"*)*, and American White Pelicans (*Pelecanus erythrorhynchos,* hereafter "AWPE"). River-reaches included (1) capture/release from the Hanford Reach for wild-origin smolts or downstream of Priest Rapids Dam for hatchery-origin smolts to McNary Dam, (2) McNary Dam to John Day Dam, (3) John Day Dam to Bonneville Dam, and (4) Bonneville Dam to the Pacific Ocean.

The accuracy of PIT-tag based predation probabilities (proportion of available tagged fish consumed) rely on estimates of PIT tag deposition and detection probabilities, parameters that account for the fraction of consumed tags deposited by birds on their breeding colony (i.e. deposition probabilities) and the fraction of deposited tags subsequently recovered by researchers following the breeding season (i.e. detection probabilities). Previously published studies provided estimates of detection probabilities for all 13 colonies included in this study and estimates of deposition probabilities were available for CATE, DCCO, and LAXX. However, deposition estimates were not previously available for AWPE, a principle avian predator species of URB Chinook smolts. To address this critical uncertainty, we conducted a field study in 2020 in which we fed AWPE PIT-tagged juvenile salmonids and then recovered tags following the breeding season to estimate deposition probabilities. Results indicated that AWPE deposition estimates were 0.47 (95% credible interval = 0.36 – 0.60), indicating that for every 100 PIT tags consumed, on average, 47 were deposited by AWPE on their breeding colony. This compares to previously published deposition estimates of 0.71 (0.51 – 0.89), 0.51 (0.34 – 0.70), and 0.15 (0.11 – 0.21) for CATE, DCCO, and LAXX, respectively. American White Pelican deposition estimates derived from this field study were then incorporated into the state-space Bayesian model to generate more accurate estimates of URB Chinook predation probabilities.

Estimates of predation probabilities on PIT-tagged URB Chinook smolts were highly variable depending on the year, the avian predator species, the location of the colony, and the fish's rearing-type (hatchery, wild). Estimates of cumulative predation (predation by all 13 colonies combined) indicated birds annually consumed 0.066 (95% credible interval = 0.049 – 0.089) to 0.133 (0.107 – 0.179) of all available tagged hatchery smolts during out-migration to the Pacific Ocean and 0.082 (95% credible interval = 0.062 – 0.132) to 0.283 (0.210 – 0.419) of available tagged wild smolts during out-migration to the Pacific Ocean. Results indicated that avian predation annually accounted for 7.3% (4.3 – 11.9) to 16.2% (12.0 – 21.3) and 8.0% (5.5 – 12.4) to 29.1% (19.7 – 40.2) of all sources of mortality for hatchery and wild smolts, respectively, during out-migration to Bonneville Dam, the furthest downstream dam URB Chinook smolts encountered during seaward migration. Of the predator species and colonies evaluated, predation probabilities were consistently the highest by AWPE nesting on Badger Island and DCCO nesting on

Foundation Island, with estimates as high 0.068 (0.045 – 0.107) and 0.019 (0.01 – 0.035), respectively, on hatchery smolts and 0.214 (0.146 – 0.347) and 0.071 (0.043 – 0.132), respectively, on wild smolts. Predation probabilities by CATE and LAXX, however, were generally less 0.03 of available smolts annually for both hatchery and wild smolts. Of the river reaches evaluated, predation was consistently the highest in the first river reach upstream of McNary Dam, although predation occurred throughout the entire outmigration corridor to the Pacific Ocean. Results indicated that the predator-specific and cumulative effects of avian predation on URB fall Chinook smolts were substantial in some, but not all, river reaches and years, and that DCCO and AWPE posed the greatest threat to smolt survival.

Predation probabilities indicated that AWPE were responsible for the greatest impacts, with predation probabilities especially high during later part of the study (2015 – 2019). We therefore investigated what factors might explain the variation observed in AWPE predation probabilities with an analysis assessing the covariation of several abiotic and biotic factors with variations in predation levels over time. Results indicated that smolt length was found to be the most commonly included covariate among the best predictive models of predation, followed by rear-type. The best predictive models all indicated an inverse relationship between length and probabilities of predation, with smaller-sized Chinook smolts more susceptible to AWPE predation. While wild smolts were generally smaller than their hatchery counterparts, consistent with higher levels of predation, our analysis found evidence of differing predation levels for wild and hatchery smolts after accounting for differences in length. Wild smolts also have longer residence times and thus increased exposure times to predators relative to their hatchery counterparts, behavioral differences that increase their susceptible to predation. Abiotic factors were found to be relatively less predictive of variations in predation compared with biotic factors. However, water transit time, an approximate estimate of river current speed, was also identified in several of the best fitting models and thus may influence URB Chinook smolt susceptibility to avian predation. Collectively, results of this study provide a comprehensive, system-wide assessment of piscivorous colonial waterbird predation on URB Chinook smolts over the course of a 12-year study period.

Introduction

Accurate assessment of cause-specific mortality is paramount to understanding factors that affect the survival of salmonids (*Oncorhynchus spp.)* and the development of effective management plans for species of conservation concern. Numerous studies indicate that predation by piscivorous colonial waterbirds, although not the original cause of salmonid declines (Nelson 1991), is now a factor limiting the survival of some salmonid populations in the Columbia River basin, USA (Collis et al. 2001, Evans et al. 2012, Evans et al. 2016, Payton et al. 2019). Multiple waterbird species nest in the region with Caspian Terns (*Hydroprogne caspia*, hereafter "CATE*)*, Double-crested Cormorants (*Nannopterum auritum*, hereafter "DCCO"*)*, California Gulls (*Larus californicus)* and Ring-billed Gulls (*L. delawarensis*, collectively hereafter "LAXX"), and American White Pelicans (*Pelecanus erythrothynchos*, hereafter "AWPE"*)* identified as the principal avian predators of juvenile salmonids during out-migration (Evans et al. 2012, Evans et al. 2016, Payton et al. 2019). Avian breeding colonies are located on numerous nesting sites spread throughout the middle and lower Columbia rivers with the timing of the breeding season (April to September) coincident with the peak smolt out-migration period (April to August), making most anadromous salmonids susceptible to predation by colonial waterbirds (Adkins et al. 2014; Evans et al. 2016).

Recent research indicates that avian predation rates or probabilities (proportion of available fish consumed) on Upriver Bright (URB) juvenile fall Chinook Salmon (*O. tshawytscha*) originating from the Hanford Reach of the middle Columbia River were substantial in some years. For instance, Payton et al. (2020) estimated that avian predation probabilities were in excess of 0.20 (or 20%) of available URB Chinook smolts in some years. Tagging studies involving URB Chinook have been on-going since 1987 (Fryer 2019). Upriver Bright fall Chinook are one of the most productive salmon stocks in the Pacific Northwest (Langness and Reidinger 2003, Harnish et al. 2013). The stock is important to both regional and international commercial ocean fisheries and local sport and tribal fisheries (Dauble and Watson 1997). The stock is also an integral part of the culture of Columbia River Tribes that rely on salmon for ceremonial, subsistence, and economic reasons. Passive integrated transponder (PIT) tagging studies involving URB Chinook rely on capturing and releasing smolts and then using subsequent recapture and recovery events to estimate fish behavior and survival (Fryer 2019, FPC 2019). In addition to avian predation, salmonid smolts are subject to numerous other non-avian sources of mortality during out-migration (e.g., hydroelectric dam passage, predation by piscivorous fish, disease, and other factors; Ward et al. 1995; Muir et al. 2001; Dietrich et al. 2011; Harnish et al. 2014) and determining to what degree avian predation limits smolt survival relative to these other sources of mortality is critical for prioritizing management actions for URB Chinook and other salmonid stocks (Evans et al. 2016). Results from Payton et al. (2020), which jointly estimated predation and survival probabilities of PIT-tagged URB Chinook, indicated that avian predation was a relatively small component of smolt mortality in some river reaches and years (less than 10%), but accounted for large proportion (greater than 40%) of all sources of mortality (1-survival) in other river reaches and years.

A major factor influencing the accuracy of PIT-tag based predation probability estimates is the accuracy of estimates of PIT tag deposition and detection probabilities (Payton et al. 2020), model parameters which represent the fraction of consumed tags deposited by birds on their nesting colony and the fraction of deposited tags subsequently recovered by researchers following the breeding season (Hostetter et al. 2015). For example, a portion of PIT tags consumed by birds are damaged and rendered unreadable following digestion or are regurgitated off-colony at loafing, staging, or other areas used by birds during the breeding season (Hostetter et al. 2015). Estimates of PIT tag detection and deposition probabilities for CATE, DCCO, and LAXX colonies in the Columbia River basin are available in previously published literature, with datasets dating back to 2008 (Evans et al. 2012, Hostetter et al. 2015). Estimates of deposition probabilities, however, were not available for AWPE colonies (Hostetter et al. 2015, Payton et al. 2020). American White Pelicans were identified as a principal predator species of URB Chinook smolts and the number of birds breeding on Badger Island in McNary Reservoir, located just 70 river kilometers downstream of the Hanford Reach, has also significantly increased in recent years and is now the largest AWPE colony in the Columbia River basin (Cramer et al. 2021). Without empirical data on AWPE deposition probabilities, however, the amount of predation attributable to these birds is speculative (Payton et al. 2020). Breeding AWPE have also been documented foraging > 100 km away from their respective colonies (Knopf and Evans 2004) and based on the low estimates of deposition probabilities for other piscivorous waterbirds species (Hostetter et al. 2015), deposition probabilities for AWPE remain a critical uncertainty in studies of avian predation (Evans et al. 2016, Payton et al. 2020, Cramer et al. 2021).

It is well documented that biotic and abiotic conditions play an important role in the survival of juvenile salmonids during out-migration to the ocean and after ocean entry (Petrosky and Schaller 2010, Burke et

al. 2013, Peterson et al. 2014, Evans et al. 2014). While levels of avian predation on juvenile URB Chinook were high in some years, there was substantial variability in predation probabilities and predation probabilities varied significantly by predator species (AWPE, LAXX, CATE, DCCO), river reach, and year (Payton et al. 2020). Differences in predation probabilities were also observed between hatchery and wild URB Chinook smolts, with wild fish significantly more likely to be consumed compared with their hatchery counterparts. This finding was unexpected, as other studies of avian predation indicate either no difference in the relative susceptibility of fish based on rear-type or that hatchery fish are disproportionately consumed relative to their wild counterparts (Fritts et al. 2007, Hostetter et al. 2012). Research on other salmonid populations in the Columbia River indicate that fish size, run-timing, and migration behavior may all be related to a fish's susceptibility to avian predation (Ryan et al. 2003; Hostetter et al. 2012; Evans et al. 2016; Payton et al. 2016, Hostetter et at. 2021). Previous research has also demonstrated that environmental conditions, like river flows and water transit times, can influence smolt susceptibility to avian predation (Hostetter et al. 2012, Payton et al. 2016, Hostetter et al. 2021). To what degree these biotic and abiotic factors influence URB Chinook smolt susceptibility to avian predators, however, is unknown but identification of these factors could potentially be used to develop more effective management plans.

The primary objectives of this study were to (1) collect data to estimate PIT tag deposition probabilities by AWPE by conducting a field study in 2020, (2) use this information to revise and update the colony-specific and cumulative avian predation and survival probability estimates of Payton et al. (2020), and (3) investigate what biological and environmental factors influence the susceptibility of URB Chinook smolts to predation during out-migration. Collectively, results provide a comprehensive, system-wide assessment of piscivorous colonial waterbird predation on URB Chinook smolts over the course of a 12-year study period.

Methods

Study Area – We investigated predation and survival of hatchery and wild URB fall Chinook smolts marked with PIT tags during 2008 – 2019; updating the dataset used by Payton et al. (2020). Due to restrictions associated with the coronavirus outbreak, URB Chinook smolts were not marked with PIT tags in 2020, preventing inclusion of data from that year. The study area described in Payton et al. (2020) was the same used herein. In brief, hatchery fish were released at the Priest Rapids Hatchery downstream of Priest Rapids Dam at River kilometer (Rkm) 639 and wild fish were captured in the Hanford Reach between Rkm 557 and 639 and released at boat ramps between Rkm 576 and 587 (Figure 1). Following release, survival and predation were evaluated through four river reaches or sections of the Columbia River: (1) release to McNary Dam (Rkm 470), (2) McNary Dam to John Day Dam (Rkm 349), (3) John Day Dam to Bonneville Dam (Rkm 234), and (4) Bonneville Dam to the Pacific Ocean (Figure 1). River reaches were defined by the location of PIT tag detection sites and the location of bird colonies capable of foraging on tagged fish within each river reach. Smolt survival and predation through Reaches 1 – 3 were estimated based on detections of live fish passing in-river PIT tag arrays and recoveries of tags from dead fish on bird colonies. Smolt predation in Reach 4 was also based on recoveries of dead fish on bird colonies on East Sand Island in the Columbia River estuary (Rkm 8), however, survival could not be estimated in Reach 4 due to a lack of PIT tag detection sites downstream of East Sand Island at the mouth of the Columbia River (Figure 1).
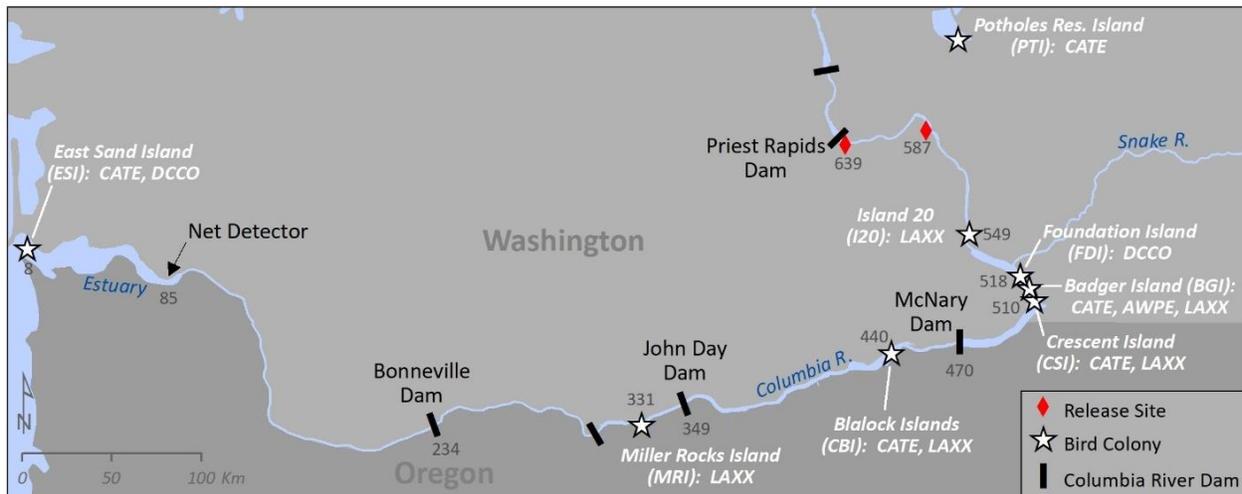
Figure 1. Mark-recapture-recovery locations of PIT-tagged hatchery and wild Chinook Salmon smolts released downstream of Priest Rapids Dam during 2008-2019. Release sites included the Priest Rapids Hatchery and the Hanford Reach section of the Columbia River. Recapture locations include McNary Dam, John Day Dam, Bonneville Dam, plus a net detection system in the lower Columbia River. Recovery locations include Caspian Tern (CATE), Double-crested Cormorant (DCCO), California Gull and Ring-billed Gull (LAXX), and American White Pelican (AWPE) colonies. Distances represents river kilometers from the Pacific Ocean.

Mark-Recapture-Recovery – The same mark-recapture-recovery dataset described in Payton et al. (2020), updated with URB Chinook PIT tag releases from 2019, were used in the present study. In brief, hatchery URB Chinook from Priest Rapids Hatchery (PRH) and wild URB Chinook captured in the Hanford Reach (HR) were PIT-tagged and released annually during 2008 – 2019. In most years (2008 – 2016), hatchery fish were released during a two-week period in the latter half of June, except for 2017 – 2019, when fish were released during a four-week period from mid-May to mid-June. Wild fish, which rear in the Hanford Reach prior to out-migration, were captured and released during a one-week period in early June in all years. Following release, a proportion of tagged URB Chinook were detected (volitionally recaptured) at downstream detection sites equipped with PIT tag arrays (a series of antennas). Arrays were located at the McNary Dam, John Day Dam, and Bonneville Dam juvenile bypass fish facilities or at a corner collector (a spill-like route; Bonneville Dam only) and at a vessel towed pair-trawl net detection system in the lower Columbia River (Rkm 75; Figure 1). Adult URB Chinook returning to the Columbia River following ocean residency were detected at arrays located in fishways at Bonneville Dam one to five years following release as a smolt (Figure 1). Recapture records were retrieved from the PIT Tag Information System (PTAGIS), a regional mark, recapture, recovery database maintained by Pacific States Marine Fisheries Commission (PSFMC 2021).

Following release, a proportion of tags implanted in URB Chinook smolts were also recovered on bird colonies (i.e., dead fish). Colonies included in the study were those previously identified as posing a potential threat to juvenile salmonids during out-migration (Evans et al. 2012, Evans et al. 2016). Bird species and colonies included CATE nesting on (1) Potholes Reservoir Islands, (2) Badger Island, (3) Crescent Island, (4) Central Blalock Islands, and (5) East Sand Island; LAXX nesting on (6) Island 20, (7) Badger Island, (8) Crescent Island, (9) Central Blalock Islands, and (10) Miller Rocks Island; DCCO nesting on (11) Foundation Island and (12) East Sand Island; AWPE nesting on (13) Badger Island (Figure 1). The methods of Evans et al. (2012) were used to recover PIT tags from each bird colony. In brief, portable PIT

tag antennas were used to detect tags after birds dispersed from their breeding colonies in August – October. The entire land area occupied by nesting birds were scanned for tags following each breeding season, with a minimum of two complete sweeps or passes of each colony site conducted each year. The land area occupied by birds during each breeding season was determined based on aerial images and/or ground surveys of the colony taken during the peak nesting season (see also Adkins et al. 2014).

Not all PIT tags ingested by avian predators were deposited on the bird's nesting colony (i.e. deposition probabilities were less than 1.0) and not all deposited tags were detected by researchers after the breeding season (i.e. detection probabilities were less than 1.0). For instance, some proportion of consumed tags were regurgitated or defecated at off-colony loafing or roasting sites, deposited tags were removed or damaged by wind or water erosion, or deposited tags were missed (not detected) by researchers during the scanning process (see also Hostetter et al. 2015). Given these known sources of tag loss, an accurate estimate of the total number of fish consumed by birds required an adjustment or correction for both PIT-tag deposition and detection probabilities on bird colonies. The methods and data of Hostetter et al. (2015) and Evans et al. (2019) were used to estimate colony-specific detection probabilities and, in the case of CATE, DCCO, and LAXX, deposition probabilities. Prior to this study, however, no estimates of deposition probabilities were available for AWPE (see PIT Tag Deposition Study below).

To estimate detection probabilities, PIT tags with known tag codes were intentionally sown on each bird colony by researchers prior to, during (when possible), and following the nesting season. Recoveries of these tags during scanning efforts after the breeding season were then used to model the probability of detecting a tag that was deposited during the breeding season (see Survival and Predation Estimation below for additional details). As part of previously published research, to estimate deposition probabilities, juvenile salmonids implanted with PIT tags of known codes were fed to nesting CATE, DCCO, and LAXX throughout the peak breeding season (April - June) at multiple colonies (see also Hostetter et al. 2015). The numbers of ingested tags subsequently found by researchers at each colony at the end of the breeding season were used to estimate tag deposition probabilities. Colony-specific PIT tag detection probabilities and predator-specific PIT tag deposition probabilities (collectively referred to as "recovery probabilities") used in this study were those previously reported by Evans et al. (2019), updated with data from 2019, and are provided in Appendix A, Table A1.

PIT Tag Deposition Study – Estimated deposition probabilities from AWPE breeding on Badger Island (the sole pelican colony included in the study) were not available in previously published literature as there have been no studies conducted to directly estimate PIT tag deposition probabilities for this species and colony. To determine what fraction of PIT tags ingested by AWPE were subsequently deposited on the Badger Island breeding site we followed the methods of Hostetter et al. (2015) by directly feeding dead juvenile salmonids implanted with PIT tags to pelicans during the smolt out-migration period and then recovered those tags following the breeding season. Deposition probabilities were estimated by feeding juvenile-sized hatchery Rainbow Trout (*O. mykiss;* fork length range = 112 – 273 mm) with known tag codes to adult AWPE on Badger Island during to May to July (*Table 1*). To account for potentially different levels of colony attendance during the breeding season, multiple feeding periods or trials were conducted based on the colony's nesting chronology, with tagged fish consumed during the nest building (May), egg incubation (June), and chick-rearing (July) stages. Fish used in deposition trials were implanted with the same PIT tag implanted in URB Chinook smolts (12-mm x 2-mm, 134 kHz, full-duplex). A

camouflaged boat and portable blind were used to approach AWPE on Badger Island and to present them with PIT-tagged fish (*Figure 2*). Only fish that were known to have been consumed by an adult pelican were included in the study. Tagged fish were consumed by adult pelicans throughout the course of each day (range = 0903 – 1907 hrs) to mimic variable foraging times and trials were designed to feed as many individual birds as possible.

Figure 2. PIT-tagged Rainbow Trout (left panel) and observation equipment (center panel) used in deposition trials at the Badger Island American White Pelican colony (right panel) in 2020.

Using these same methods, and as part of a separately funded study (Evans et al. 2021), PIT-tagged juvenile suckers (*Catostomidae*) were also fed to adult AWPE breeding on an island in Clear Lake Reservoir, CA in 2020. Clear Lake Reservoir has had one of the largest nesting colonies of AWPE in the Klamath Basin for the last two decades (Evans et al. 2016). Similar to the field study on Badger Island, PIT-tagged fish were consumed by Clear Lake Island AWPE during three discrete deposition trials that were based on the colony's nesting chronology, with tagged fish consumed throughout all daylight hours and by multiple pelicans during each trial. Results from Clear Lake Island deposition trials are reported herein to assess whether AWPE deposition probabilities varied by colony site (Badger Island, Clear Lake Island) and to bolster sample sizes of PIT-tagged fish used to estimate pelican deposition probabilities for use in this and other predation analyses.

Sample sizes of tagged fish used in deposition studies by AWPE nesting on Badger Island and Clear Lake Island in 2020 are provided below in *Table 1*. Sample sizes of tagged fish used in AWPE deposition trials (n = 401; *Table 1*) were similar to those used in CATE (n = 456) and DCCO (n = 428) deposition trials by Hostetter et al. (2015), which should result in similar levels of precision in estimates of AWPE deposition (see *Discussion* for additional details).

Table 1. Sample sizes of consumed and recovered PIT-tagged fish by American White Pelicans nesting on Badger Island and Clear Lake Island in 2020.

Colony	Trial (dates)	Consumed	Recovered
Badger Island	1 (May 17-19)	36	5
	2 (June 5-9)	95	33
	3 (July 5-10)	108	48
Clear Lake Island	1 (May 8-10)	55	16
	2 (May 29-31)	97	48
	3 (July 1-3)	10	2
ALL		**401**	**152**

The methods of Hostetter et al. (2015) were used to estimate deposition probabilities based on the number of tags consumed each week and number recovered following the breeding season. In brief, the probability of a PIT tag being deposited on each colony was inferred from the binomial process of recovering the experimental tags. That is, for each colony studied, we assumed

$$k_i \sim \text{Binomial}(n_i, \phi * \psi_i)$$

where k_i is the number of PIT tags recovered from the number of tags observed to be consumed (n_i) in week i, ϕ represents the probability a consumed tag is deposited on a colony, and ψ_i represents the probability that deposted tags were then detected following the nesting season. ψ_i was assumed to be a logistic function of week. That is:

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 * i$$

where β_0 and β_1 are both derived from non-informative priors (normal [0, 5]).

Predation and Survival Estimation – The joint mortality and survival (JMS) estimation methods of Payton et al. (2019) were used to estimate reach-specific and cumulative URB Chinook smolt predation and survival probabilities during 2008 – 2019. In brief, this hierarchal state-space Bayesian model incorporated both live and dead detections of PIT-tagged fish in space and time to simultaneously estimate predation and survival probabilities. The model used two vectors, $\boldsymbol{y}$ and $\boldsymbol{r}$, to describe each fish's recapture history following tagging and release at each of the four (4) downstream recapture sites and each of the avian recovery sites under consideration. Each vector $\boldsymbol{y}$ was a 5-length vector, where y_j was an indicator variable of a fish's recapture at recapture opportunity j, and $\boldsymbol{r}$ was a 15-length vector, where, for $d \in \{1,2,...,14\}$, r_d was an indicator variable of recovery from colony d and r_{15} indicated a fish was unrecovered. Implicitly, the model provided inference about each fish's state, represented by an unobserved 5-length vector $\boldsymbol{z}$, where z_j was an indicator variable of whether the fish was still alive at recapture opportunity j.

Parameters used in the model were:

$\boldsymbol{\Theta}$, a 15x5 matrix where $\Theta_{k,d}$ represented the probability a fish released survived to recapture opportunity k and then subsequently succumbed to mortality cause d prior to arrival at recapture opportunity $k+1$

$\boldsymbol{p}$, a 5-length vector where p_k represented the probability that a fish alive at recapture opportunity k was successfully recaptured

$\boldsymbol{\gamma}$, a 15-length vector where, for $d \in \{1,2,...,14\}$, γ_d represented the probability of recovering a fish which died due to mortality cause d, and γ_{15} = 0 represented the lack of recoveries of fish which died from all other unspecified causes. Each γ_d is the product of two colony specific parameters, ϕ_d and ψ_d, representing the probability of a consumed tag being deposited and, given deposition, redetection by researchers following the nesting season.

From the spatially explicit rates of $\boldsymbol{\Theta}$, the survival probabilities, represented by $\boldsymbol{s}$, across river reaches could be derived. Explicitly $\boldsymbol{s}$ was defined to be a 5-length vector where s_k represented the probability a

fish released at Priest Rapids Hatchery or in the Hanford Reach survives through river reach k (i.e., $s_k = 1 - \sum_{i \leq k} \sum_d \Theta_{k,d}$). It then follows that an individual fish's life can be expressed with the following state-space interpretation:

$$z_j \sim \text{bernoulli}(z_{j-1}, * \, s_j),$$
$$y_j \sim \text{bernoulli}(z_j * p_j),$$

and

$$r_d \sim \text{bernoullli}\left(\sum_j (z_{j+1} - z_j) * \theta_{j,d} * \gamma_d \right) \forall d \in \{1, \dots, .13\}.$$

Somewhat unique to this group of fish was the significant intermixing or co-nesting of AWPE and LAXX on Badger Island, with both species responsible for predation impacts on URB Chinook smolts. Additional model considerations were needed to attribute predation by AWPE versus LAXX in areas of co-nesting and model the recovery of tags from this mortality source (represented by $r_{14} = r_{MIX}$).

$$r_{MIX} \sim \text{bernoulli}\left(\sum_j (z_{j+1} - z_j) * \left(\begin{array}{c} (1 - \rho_{AWPE}) * \theta_{\,AWPE} * \phi_{AWPE} \, + \\ (1 - \rho_{LAXX}) * \theta_{\,LAXX} * \phi_{LAXX} \end{array} \right) * \psi_{MIX} \right)$$

where ρ_{AWPE} and ρ_{LAXX} represent the proportion of tags consumed by AWPE and LAXX respectively deposited in the portions of the colony inhabited by only that genus of bird (i.e., not deposited in the intermixed portion of the colony). We derived these estimates delineating predation probabilities among the intermixed and otherwise portions of Badger Island using the measured levels of predation from the "AWPE only" and "LAXX only" regions along with supplemental data describing the proportion of each genus nesting within the "mixed" area versus the "only" areas. We assumed that the odds of a tag consumed by a given species being deposited versus within the "mixed" delineation to be similar to the odds of a bird of that species nesting in the "mixed" delineation. However, we observed significant variation in the proportion of raw tags recovered from each delineation which could indicate that the proportional consumption of tags between the "mixed" and "only" colonies varied over the year. We only had one observed count of birds for each genera each year which thus we assumed each count to be a random observation of the proportion of birds nesting within each region of Badger Island. We then assumed that the seasonal average odds of a tag consumed by a given species being deposited on the "mixed" delineation to be similar to the odds of a bird of that species nesting on the "mixed" delineation (see Appendix B for full details).

Low recapture rates inhibit precision in partitioning the morality impacts of colony d among the river reaches where that colony was assumed to forage. Previous research indicates that predation impacts by individual colonies were spatially proportionate amongst river reaches and years (Evans et al. 2016; Hostetter et al. 2018). Therefore, we implemented a hierarchical "informed partitioning" method to share information among years based on the assumption that the odds of being consumed by a colony foraging among multiple river segments were similar among years. Specifically, informed partitioning involved first defining $\boldsymbol{\theta}_{\mathbf{y}}^{cumulative}$ to be a 15-sized vector where $\theta_{y_d}^{cumulative}$ represented the probability a released fish succumbed to mortality cause d, in year y. Then, for each colony d in year y, 5-length vector $\boldsymbol{\rho}_{y_d}$ defined the partitioning of $\theta_{y_d}^{cumulative}$ into $[\Theta_{y_{1,d}}, \Theta_{y_{2,d}}, \dots, \Theta_{y_{5,d}}]$. That is,

$$[\Theta_{y_{1,d}}, \Theta_{y_{2,d}}, \dots, \Theta_{y_{5,d}}] = \theta_{y_d}^{cumulative} \boldsymbol{\rho}_{y_d}$$

where

$$\boldsymbol{\rho}_d \sim dirichlet(\boldsymbol{\alpha}^d).$$

Temporal variation was assumed to be inherent to rates of mortality (Evans et al. 2014, Hostetter et al. 2015), recapture (Sandford and Smith 2002), and recovery (Ryan et al. 2003; Evans et al. 2012). Under the assumption that fish released within the same week experienced similar rates of mortality/survival, recapture, and recovery; URB Chinook were grouped into weekly release cohorts. The week specific rates were accordingly denoted $\boldsymbol{\Theta}_{y,w}$, $\mathbf{p}_{y,w}$, and $\boldsymbol{\gamma}_{y,w}$. Rates of mortality, recapture, and recovery from weeks closer in time were assumed to be more alike than those temporally further apart. Serial correlation in survival/mortality and recapture rates were assumed and accounted for with life path simplexes as described by Payton et al. (2019). Temporal variation in detection rates were estimated more directly by intentionally sown PIT tags with known tag codes on each colony before, after, and, in some instances, within each breeding season (see Hostetter et al. 2015). Estimated detection probabilities at each colony were then interpolated from the logistic curve estimated from the intentionally sown tags. In some uncommon instances, researchers were unable to sow PIT tags prior to the nesting season. In these cases, the methods of Payton et al. (2019) were used to infer an estimation of inner-seasonal variation in recovery rates using information from similar colonies in the same year or using information from the same colony in different years. These instances are denoted in Appendix A, Table A1.

Finally, not all active bird colonies were scanned for URB Chinook smolt PIT tags in all years during 2008 – 2019. Two notable examples were that of the Badger Island AWPE colony in 2013 and the Foundation Island DCCO colony during 2013 and 2015 – 2019, where large numbers of birds nested, but there were no efforts to recover fish tags following the breeding season. To address this data gap, we assumed the average annual predation probabilities observed from years when the colony was scanned were similar to those in years where the colony was not scanned (see also Payton et al. 2020). Estimates of colony size (number of breeding adults) indicated that the Foundation Island cormorant colony has remained relatively stable in size since 2008, ranging from 308 to 390 breeding pairs annually (Evans et al. 2019). The Badger Island pelican colony, however, has increased in size from a low of 1,349 breeding pairs in 2008 to high 3,330 pairs in 2018 (Cramer et al. 2021; see also Appendix A, Figure A.1). Estimates of average predation from these two colonies in these specific years represent best-guess estimates of predation, estimates which are explicitly labelled as such in tables and figures (see *Results* below).

The prior for the initial week's detection probability in each year was defined to be $uniform(0,1)$. Analogously, the prior distribution assigned for the life paths simplexes in the initial week of each year was assumed to be $\mathrm{Dirichlet}(\mathbf{1})$, where $\mathbf{1}$ was an appropriately sized vector of ones. Weakly-informative priors of $\mathrm{half-Normal}(0,5)$ were also implemented for all variance parameters. Previous testing and applications of the JMS model have demonstrated that, given sufficient data, the information provided by prior distribution assignments has negligible impacts on predation and survival estimates but is valuable for computational efficiency.

All models were implemented using the software STAN accessed through R version 4.1.0 (R Core Team 2021) using the rstan package (version 2.21.1; Stan Development Team 2020). To simulate random draws

from the joint posterior distribution we ran four Hamiltonian Monte Carlo (HMC) Markov Chain processes. Each chain contained 4,000 adaptation iterations, followed by 4,000 posterior iterations. Posterior iterations were then thinned by a factor of 4. Chain convergence was visually evaluated and verified using the Gelman-Rubin statistic (Gelman et al. 2013) and all accepted chains reported zero divergent transitions. Reported estimates represent simulated posterior medians along with 95% highest (posterior) density intervals (95% credible interval {CRI}).

Covariate Analysis – We investigated factors, or covariates, that potentially influenced URB Chinook susceptibility to avian predation, with an emphasis on factors of potential management relevance. Analyses focused on the disproportionate levels of predation observed on hatchery and wild URB Chinook by AWPE on Badger Island during the latter half of the study period (2015 – 2019), a period when the highest levels of predation occurred (see Results below). Biotic covariates included individual fish characteristics of rear-type (hatchery, wild) and length (fork-length, mm). Length was measured, on average, 20 days (range = 13 and 53 days) prior to release for hatchery fish and just one day prior to release for wild fish, so hatchery fish were larger at release than depicted by their length at the time of tagging. It should also be noted that hatchery fish had longer to recover from potential handling and tagged effects than wild fish but both groups were held for at least 24 hours prior to release. Abiotic covariates assessed included measures of (1) release-date, (2) water temperature at the Pasco monitoring station, (3) flow at the Pasco monitoring station, (4) discharge at McNary Dam, (5) spill percentage at McNary Dam, and (4) water transit time through the Hanford Reach. Flow conditions from release to McNary Dam were represented by average daily measurements of flow (kilo cubic feet per second [kcfs]) at Pasco monitoring station, discharge at McNary dam, spill percentage at McNary Dam, and an approximation of water transit time (hereafter "WTT") from the tailrace at Priest Rapids Dam to the forebay of McNary Dam. WTT indices are calculated as the ratio between discharge and reservoir elevation. Values of WTT were generated with the COMPASS water velocity model (data provided by J. Faulkner, NOAA). Water temperature (°C) was measured daily at the Pasco monitoring station. Data relating to temperature, flow, discharge, and spill percentage were obtained from the Data Access in Real Time website (DART 2021). The size (number of adults) of the AWPE on Badger Island was also likely a factor associated with variation in predation levels but intra-annual (e.g., weekly) estimate of colony size were not available, nor were there dramatic changes in annual estimates of colony size during the latter half of the study period (see Appendix A, Figure A.1). Finally, we also tested for the usefulness of the inclusion of a random effect for day, assumed to be autocorrelated among days, to account for all additional unmeasured or accounted for sources variability.

We used a modified version of the predation rate model (Hostetter et al. 2015) allowing for the consideration of biotic and abiotic factors as covariates via logistic regression. However, as discussed above, the intermixing of the AWPE and LAXX colonies necessitated the simultaneous modelling of LAXX predation from BGI as well to estimate the proportion of tags recovered from the co-nesting portion of BGI. In brief, we assumed

$$r_{y,d,AWPE} \sim \text{binomial}\left(n_{y,d}, \rho_{y,d,AWPE} * \theta_{y,d,AWPE} * \phi_{y,AWPE} * \psi_{y,d,AWPE}\right)$$

$$r_{y,d,LAXX} \sim \text{binomial}\left(n_{y,d}, \rho_{y,d,LAXX} * \theta_{y,d,LAXX} * \phi_{y,LAXX} * \psi_{y,d,LAXX}\right)$$

$$r_{y,d,MIX} \sim \text{binomial}\left(n_{y,d}, \left(\begin{array}{c}(1 - \rho_{y,d,AWPE}) * \theta_{y,d,AWPE} * \phi_{y,AWPE} + \\ (1 - \rho_{y,d,LAXX}) * \theta_{y,d,LAXX} * \phi_{y,LAXX}\end{array}\right) * \psi_{y,d,MIX}\right)$$

where $r_{y,d,AWPE}$, $r_{y,d,LAXX}$, and $r_{y,d,MIX}$ represent the number of tags recovered from each portion of BGI of $n_{y,d}$ tags released on day d of year y; $\theta_{y,d,AWPE}$ and $\theta_{y,d,LAXX}$ represent the probability a fish released on day d of year y was depredation rate by each genera; $\rho_{y,d,AWPE}$ and $\rho_{y,d,LAXX}$ represent the proportion of total depredated tags that were taken by birds nesting in the AWPE-only and LAXX-only areas of BGI respectively; $\phi_{y,AWPE}$ and $\phi_{y,LAXX}$ represent the probabilities that a tag consumed by each genera of bird was then deposited on the colony; and $\psi_{y,d,AWPE}$, $\psi_{y,d,LAXX}$, and $\psi_{y,d,MIX}$ represent the probabilities of recovering a deposited tag from each portion of the island. Full details on how $\rho_{y,d,AWPE}$ and $\rho_{y,d,LAXX}$ were informed are detailed in Appendix B. The influence of covariates could then be used to model AWPE predation rates as

$$\log\left(\frac{\theta_{AWPE,d}}{\theta_{OTHER,d}}\right) = \mathbf{X}_{j,c}^{T}\vec{\beta}_c + \sum_{i<d}\eta_i,$$

And, similarly, for LAXX, where $\eta_w \sim \text{normal}(0, \sigma_\eta)$ represents the optional inclusion of an autoregressive random error term.

Model comparisons were performed using Pareto smoothed importance-sampling leave-one-out cross-validation (PSIS-LOO; see also Vehtari et al. 2017). PSIS-LOO estimates pointwise out-of-sample prediction accuracy fitted Bayesian models using log-likelihood evaluations of simulated draws of parameter values from each joint posterior distribution. Log-likelihood values were determined only by the fit of recovered tags from the AWPE and MIX regions of BGI, whereas all LAXX recoveries were assumed to have been the result of nuisance parameters ancillary to the relevant predictive power of the models considered. The PSIS-LOO comparison framework is more robust than other common model comparison measures such as WAIC and is fully Bayesian in that it is not based solely on a point estimates like other measures such as DIC (Vehtari et al. 2017).

All models were implemented using the software STAN accessed through R version 4.1.0 (R Core Team 2021) using the rstan package (version 2.21.1; Stan Development Team 2020). To simulate random draws from the joint posterior distribution we ran four Hamiltonian Monte Carlo (HMC) Markov Chain processes. Each chain contained 2,000 adaptation iterations, followed by 2,000 posterior iterations. Posterior iterations were then thinned by a factor of 2. Chain convergence was verified using the Gelman-Rubin statistic (Gelman et al. 2013) and all accepted chains reported zero divergent transitions.

Results

Mark-recapture-recovery – In total, 464,189 URB Chinook smolts were PIT-tagged and released during 2008 – 2019 (Table 1). Of these, 354,792 were hatchery fish from the Priest Rapid Hatchery (PRH) that were released approximately 3 Rkm downstream of Priest Rapids Dam and 109,437 were wild fish captured and released into the Hanford Reach (HR) of the Columbia River approximately 55 Rkm downstream of Priest Rapids Dam (HR; Figure 1). Release numbers varied considerably by year (range = 7,807 – 52,882 per year) and rear-type (range = 2,956 – 42,955 per year, per rear-type). Numbers of tagged Chinook detected alive at downstream recapture sites also varied by detection site and year, as did the number of tags recovered dead on bird colonies (Table 1). In total, 9,172 tags (range = 435 – 1,325 per year) from URB Chinook smolts were recovered on bird colonies (Table 1). Only a small number and proportion of smolts released at PRH and HR returned to BON as adults, with adult returns ranging from 38 – 940 fish, per release year (Table 1). Numbers of tags recovered by predator species (CATE,

DCCO, LAXX, AWPE) are provided in Table 1, while the number recovered on each individual colony are provided in Appendix A, Table A2. Recapture and recovery probabilities are provided in Appendix A, Table A1.

Table 1. Numbers of PIT-tagged URB Chinook released in the middle Columbia River that were subsequently detected alive at downstream PIT tag arrays during out-migration or returning as an adult or recovered dead on bird colonies. PIT tag arrays were located at McNary Dam (MCN), John Day Dam (JDA), Bonneville Dam (BON), and a net detector (ND) in the estuary. Avian predator species included Caspian Terns (CATE), Double-crested Cormorants (DCCO), California Gulls and Ring-billed Gulls (LAXX), American White Pelicans (AWPE), and mixed colonies of AWPE and LAXX (Mix). See Figure 1 for a map of release, recapture, and recovery locations.

		Recaptured Alive				Recovered Dead				
Year	Released	MCN	JDA	BON	ND	Adult	CATE	DCCO	LAXX	AWPE	Mix
2008	19,645	1,202	698	465	47	165	65	279	22	69	0
2009	16,722	1,366	543	396	44	55	112	183	5	136	0
2010	7,807	662	276	273	29	68	30	75	5	105	0
2011	13,331	861	628	363	3	253	84	106	0	174	0
2012	47,735	3,213	4,317	1,707	74	820	327	319	26	290	0
2013	47,089	5,161	2,740	974	115	940	224	274	91	0	0
2014	52,843	7,311	3,162	2,509	226	187	286	191	117	315	0
2015	47,586	2,797	2,105	687	14	38	406	113	197	114	111
2016	52,881	4,458	2,078	1,587	71	127 [1]	271	49	186	85	245
2017	52,829	3,377	2,412	3,374	50	267 [1]	259	2	152	0 [2]	623
2018	52,882	2,659	2,139	1,817	39	169 [1]	199	39	137	47	902
2019	52,839	985	1,508	1,414	0	39 [1]	119	14	129	22	841

[1] Incomplete adult returns

[2] There was no area on Badger Island in 2017 were AWPE nested in isolation.

PIT tag Deposition Probabilities – Trial-specific deposition probabilities for AWPE nesting on Badger Island and Clear Lake Island ranged from 0.30 (95% credible interval = 0.10 – 0.54) to 0.66 (0.47 – 0.90; Figure 3). There was no evidence that deposition probabilities varied significantly by trial or by colony. Small sample sizes of consumed fish during some trials, however, resulted in imprecise estimates of deposition. Average annual deposition probabilities were estimated to be 0.43 (0.31 – 0.59) and 0.50 (0.36 – 0.69) at the Clear Lake Island and Badger Island colonies, respectively. Average annual deposition probabilities from all trials (n = 6) and colonies (Badger Island, Clear Lake Island) combined were estimated to be 0.47 (0.36 – 60), indicated that for every 100 tagged fish consumed by AWPE, on average, 47 tags (or 47%) were deposited on breeding colonies.
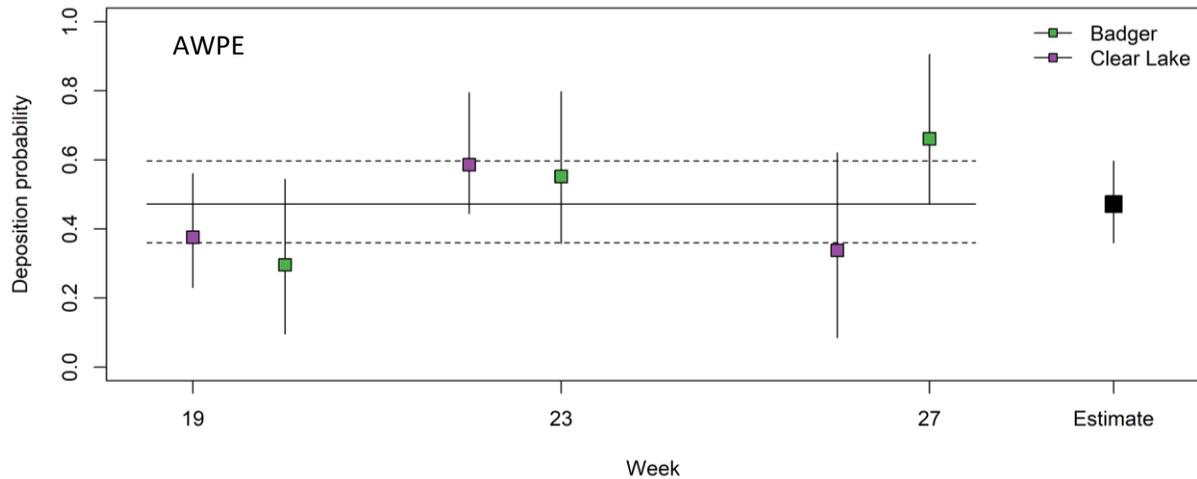
Figure 3. Trial-specific deposition probabilities (95% credible intervals) for American White Pelicans (AWPE) nesting on Badger Island and on Clear Lake Island during 2020. Weeks are those of the Julian calendar. Solid line and black shaded symbol denote the average annual deposition probability estimated (Estimate) across all colonies. Dashed line is the associated 95% credible interval for all colonies. See *Table 1* for sample sizes of consumed PIT-tagged fish by trial and pelican colony.

Predation Probabilities – Cumulative predation probabilities, measured as the impact of all 13 bird colonies on URB Chinook mortality from Release to the Pacific Ocean, ranged from 0.066 (95% CRI = 0.049 – 0.089) to 0.283 (0.21 – 0.419), depending on the year and the fish's rear-type (hatchery, wild; Figure 4). Of the bird species evaluated (CATE, DCCO, LAXX, AWPE), aggregated (species-specific) predation probabilities were often, but not always, the highest by AWPE and DCCO colonies (Figure 4). Aggregate effects of AWPE, which were limited to lone colony on Badger Island, were as high as 0.214 (0.146 – 0.347) on wild smolts, while aggregate effects of DCCO, which included two colonies, were as high as 0.079 (0.051 – 0.140) on wild smolts. The aggregate effects of predation by all LAXX colonies were appreciable in some, but not all years, with predation probabilities as high as 0.042 (0.033 – 0.054) observed on wild smolts. In general, the aggregate effects of predation by all CATE colonies were the lowest of four predator species evaluated, with the highest estimates being 0.027 (0.019 – 0.039) on hatchery smolts in 2009 (Figure 4).
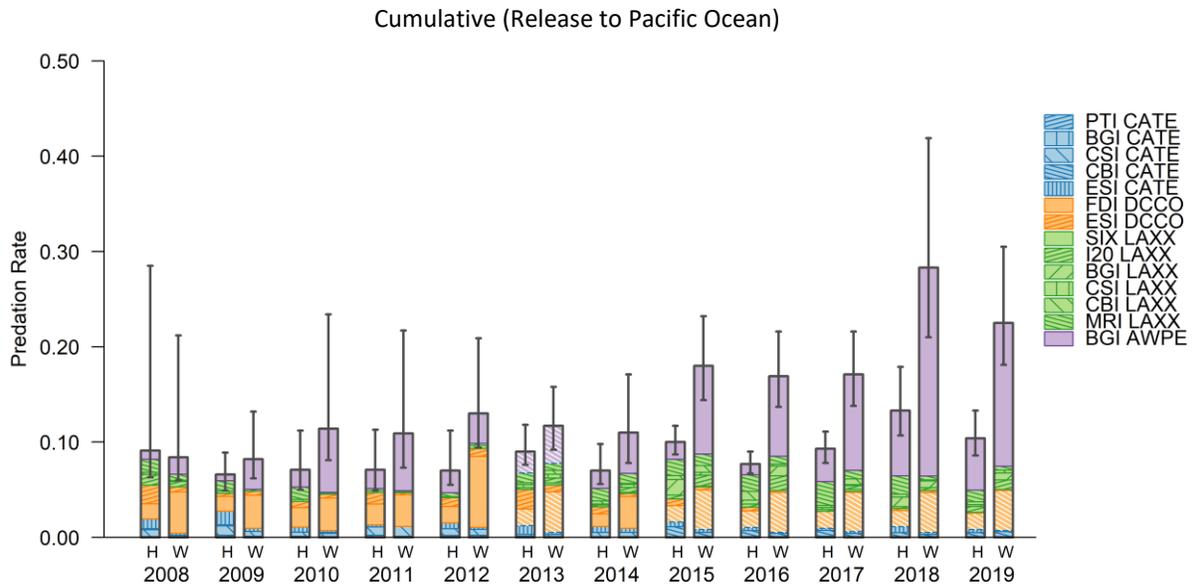
Figure 4. Estimated cumulative mortality due to avian predation (proportion of available fish consumed) of PIT-tagged hatchery (H) and wild (W) juvenile Upriver Bright fall Chinook during 2008 - 2019. Predator species include Caspian Terns (CATE), Double-crested Cormorants (DCCO), California and Ring-billed gulls (LAXX), and American White Pelicans (AWPE; see Figure 1 for colony names). Error bars represent 95% credible intervals. White cross hatching represents best-guess estimates based on cases where empirical data for that colony, in that year, were lacking and where the average rate from years past was used (see Methods).

Of the colonies capable of foraging in Reach 1 (Release to McNary Dam), the highest predation probabilities were those of the AWPE colony on Badger Island (BGI), with annual predation probabilities ranging from 0.006 (0.002 – 0.018) to 0.214 (0.146 – 0.347), and the DCCO colony on Foundation Island (FDI), with annual predation probabilities ranging from 0.013 (0.007 – 0.025) to 0.071 (0.043 – 0.132), depending on the colony, year, and smolt rear-type (Figure 5). Predation probabilities by all other colonies foraging in Reach 1 were generally less than 0.010 per colony, per year. Cumulative estimates of predation (predation by all colonies foraging in Reach 1 combined) ranged from a low 0.033 (0.028 – 0.040) on hatchery smolts in 2016 to a high 0.213 (0.153 – 0.317) on wild smolts in 2018 (Figure 5). In Reach 2 (McNary Dam to John Day Dam), predation probabilities were generally low (< 0.010) in most years, with the exception of predation by the AWPE colony on BGI where predation probabilities as high as 0.176 (0.094 – 0.332) and to a lesser degree LAXX colonies on Miller Rocks (MRI) where predation probabilities were as high as 0.016 (0.002 – 0.030; Figure 5). Similarly, predation probabilities in Reach 3 (John Day Dam to Bonneville Dam) were again low for most colonies in most years prior to 2014, but increased starting in 2015, with predation as high 0.158 (0.076 – 0.295) and 0.061 (0.021 – 0.146) on wild smolts by the AWPE colony on BGI and Miller Rocks Island (MRI) gull colonies, respectively (Figure 5). Predation probabilities in Reach 3 were especially high on wild smolts in 2015 and 2016, with cumulative estimates of 0.125 (0.11 – 0.157) and 0.22 (0.188 – 0.252), respectively. Results indicate that despite the location of the BGI colony in McNary Reservoir, birds were regularly commuting to forage on smolts downstream of John Day Dam, over 150 Rkm from their nesting site. Cumulative estimates of avian predation on wild smolts in 2018 were the highest reach-specific estimates observed during the 12-year study period. Estimates in Reach 3, however, were based on small sample sizes of wild fish (those surviving passage to below John Day and Bonneville dams) and relatively sparse recaptures, which resulted in imprecise estimates of predation in Reach 3. Of the colonies foraging in Reach 4 (Bonneville

Dam to the Pacific Ocean), predation probabilities were generally the highest by DCCO nesting on East Sand Island (ESI), with probabilities ranging annually from <0.001 to 0.04 (0.012 – 0.134) depending on the year and fish's rear-type (Figure 5). Cumulative estimates of predation by both DCCO and CATE in Reach 4 ranged annually from 0.014 (0.011 – 0.019) to 0.059 (0.040 – 0.090) on hatchery smolts and from 0.012 (0.006 – 0.027) to 0.077 (0.030 – 0.239) on wild smolts (Figure 1). Analogous to results in Reach 2 and 3, small sample sizes of surviving fish to below Bonneville Dam resulted in imprecise estimates of predation in Reach 4, particularly estimates on wild fish.

Comparisons of predation between hatchery and wild URB Chinook smolts indicated that wild fish were often, but not always, more likely to be predated than hatchery fish, with significant differences in predation probabilities observed in multiple river-reaches and years (Figure 4 and Figure 5). There was also evidence that predation, particularly predation on wild smolts, increased during the study period, with cumulative, average annual predation estimates increasing from 0.111 (0.091 – 0.136) during 2008 – 2014 to 0.208 (0.181 – 0.239) during 2015 – 2018 for wild-reared fish. Increases in predation during the latter part of the study period were largely associated with the AWPE colony on BGI. Increases in predation at the BGI colony site were also coincident with increase in the size of these colonies. For instance, the AWPE colony on BGI increased over the course of the study period, with the number of breeding birds observed in 2018 (ca. 3,330 birds) more than twice the number observed in 2008 (ca. 1,349 birds; Appendix A, Figure A.1). The LAXX colony on BGI formed in 2015 when large numbers (several thousand adults) of birds were documented breeding on the island for the first time since monitoring began in 2000 (Cramer et al. 2021). A more detailed analysis of factors that influence the susceptibility of URB Chinook smolts to predation by AWPE nesting on Badger Island is provided *below*.
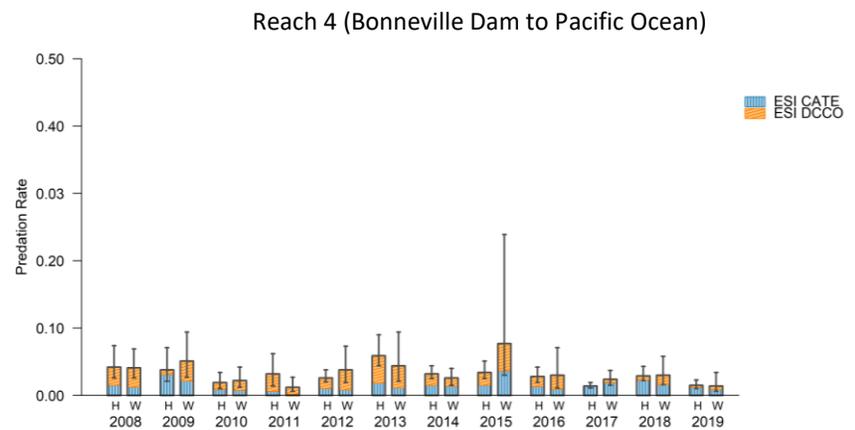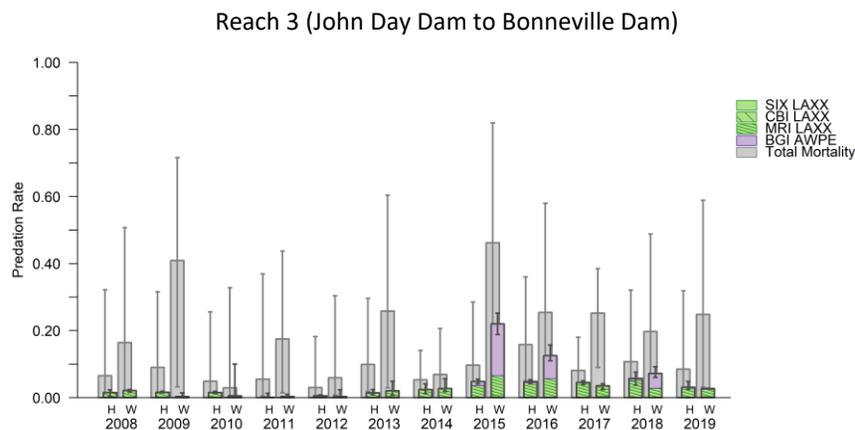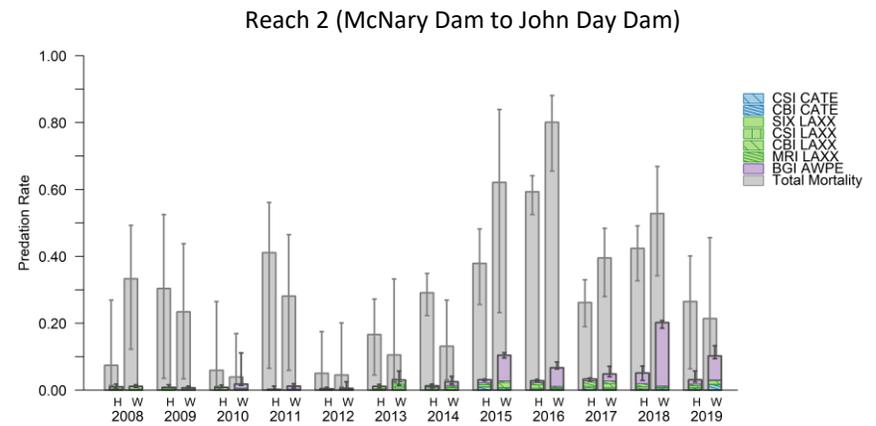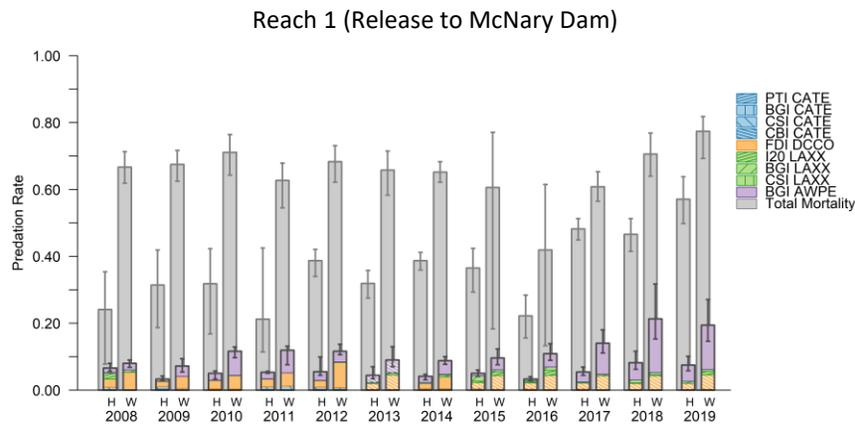
Figure 5. Estimated reach-specific total mortality (grey bars) and mortality due to avian predation (colored bars) of PIT-tagged hatchery (H) and wild (W) Upriver Bright fall Chinook smolts during 2008 − 2019. Predator species include Caspian Terns (CATE), Double-crested Cormorants (DCCO), California and Ring-billed gulls (LAXX), and American White Pelicans (AWPE; see Figure 1 for colony names and locations). Error bars represent 95% credible intervals. White cross hatching in Reach 1 represents best-guess estimates based on cases where empirical data for that colony, in that year, were lacking and where the average rate from years past was used instead (see *Methods*).

Total Mortality – Estimated total mortality (1 - survival) of URB Chinook smolts was highly variable depending on the river reach, year, and smolt rear-type (Figure 5). Total mortality was consistently the highest in Reach 1 (Release to McNary Dam), ranging annually from 0.212 (0.110 – 0.410) to 0.571 (0.50 – 0.639) in hatchery smolts and 0.419 (0.149 – 0.626) to 0.774 (0.705 – 0.826) in wild smolts. Results indicated more than 50% of all wild smolts died prior to reaching McNary Dam in 11 of the 12 study years evaluated. Total mortality was often, but not always, lower in Reach 2 and 3, with the majority of hatchery and wild smolts surviving passage in most years. Cumulative total mortality estimates indicated that the majority of Chinook smolts died prior to reaching Bonneville Dam, with estimates ranging from 0.369 (0.19 – 0.524) to 0.728 (0.690 – 0.782) in hatchery smolts and 0.723 (0.681 – 0.768) to 0.926 (0.855 – 0.978) in wild smolts. Coincident with increases in predation, there was some evidence that total mortality of URB Chinook, particularly wild smolts, increased during the study period, with estimates from 2015 - 2018 significantly higher than those during 2008 – 2014 in Reach 2 and 3 (Figure 5). An estimate of smolt mortality through Reach 4 could not be calculated because there were no PIT tag detection sites downstream of the bird colonies in the lower Columbia River estuary (Figure 1). Estimated total mortality to adulthood, based on the proportion of smolts released that die prior to returned to Bonneville Dam as adult, ranged annually from 0.962 (0.958 – 0.969) to 0.996 (0.996 – 0.997) in hatchery fish and 0.986 (0.984 – 0.988) to 0.997 (0.996 – 0.998) in wild fish during 2008 - 2015 (the last year with complete adult returns data available; Table 1). These translate into smolt-to-adult survival percentages of just 0.3% to 3.6%, depending on the out-migration year and the fish's rear-type.

Coincident with trends in predation, wild smolt were significantly more likely to die than hatchery smolts during out-migration in most, but not all, river reaches and years (Figure 5). For instance, in Reach 1, wild fish were significantly more likely to die than hatchery fish in 11 of the 12 study years evaluated. Similar levels of total mortality between hatchery and wild fish, however, were observed in Reaches 2 and 3 during 2008 - 2014, but during 2015 - 2018 wild fish were again more likely to die relative to their hatchery counterparts. Collectively (all reaches and years), results indicated that hatchery URB smolts were more likely to survive out-migration to Bonneville Dam and probabilities for returning as adults were generally higher compared to wild URB Chinook smolts.

Annual comparisons of total URB Chinook smolt mortality (1 - survival) and mortality due to bird predation indicated that avian predation accounted for 7.3% (4.3 – 11.9) to 16.2% (12.0 – 21.3) of hatchery fish mortality and 8.0% (5.5 – 12.4) to 29.1% (19.7 – 40.2) of wild fish mortality during smolt out-migration from the release to Bonneville Dam. The relative effects of avian predation were often the greatest on wild smolts in Reach 1, with bird predation accounting for 9.1% (5.9 – 25.0) to 28.6% (19.8-40.3) of total mortality per year. In Reach 2 and 3, avian predation accounted for less than 20% of total mortality in most years, with the exception of 2015 and 2016 where increases in predation probabilities coincided with increase in total mortality (Figure 5). Results indicate that although the cumulative effects of bird predation were a substantial source of URB Chinook mortality in some river reaches and years, it was not the dominate source of mortality, with most fish dying from non-avian causes during out-migration to Bonneville Dam.

Covariate Analysis – The best fitting covariate models of AWPE predation on URB Chinook, as measured by the estimated expected log pointwise predictive density (ELPD), included the model employing length and rear-type and the model employing length, rear-type, and estimated water transit time from Priest Rapids to McNary Dam (Table 1), the reach with highest levels of AWPE predation during 2015 – 2019

(Figure 5). The ELPDs for these two models were numerically close to identical and statistically indistinguishable (Table 2). The ELPDs next two best fitting models were also relatively similar, as their respective differences from the best models were within a standard deviation (Table 2). These models were like the top two with the covariate for rear-type left out, indicating relatively less evidence that rear-type significantly increases the predictive strength of the model. This analysis provides evidence that length has the strongest correlation with varying levels of predation by AWPE relative to the other covariates evaluated. The logistic regression parameter estimates for the length covariate was consistently negative and of similar magnitude across all the best fitting models, providing evidence that smaller-sized Chinook were more likely to be consumed by AWPE. The logistic regression parameter estimates for the rearing covariate consistently provided evidence that wild-reared juveniles were more likely to be consumed than their hatchery-reared cohorts, even after accounting for the differences in length. The logistic regression parameter estimates for water transit time provides evidence that slower moving water was significantly correlated to increases in the probabilities of predation by AWPE.

The best fitting models all also contained a random effect for day, indicating that significant extraneous variation in predation rates exists beyond what can be explained by the evaluated covariates alone (Table 2). Not all evaluated covariates, however, were found to be useful predictors of variation in predation rates. Of the abiotic factors considered, only water transit time appeared in any of the best fitting models. This provides evidence that biotic factors and variations in water transit time are more closely correlated with variations in predation rates than Julian release date, water temperature, or spill percentage at McNary Dam. It should be noted, however, that because all wild fish were generally released during a single week in early June, there was little contrast in release date amongst wild fish.

Table 2. Best fitting models explaining predation by AWPE on Badger Island as measured by the expected log pointwise predictive density (ELPD), along with the estimates of ELPD, standard error (SE) of ELPD estimates, estimated differences of ELPD from the "best fitting" model, and SE of those differences. Best fitting models included covariates for fish length, rearing type, and water transit times (WTT). Models including "(day)" indicate the inclusion of an additional (autocorrelated) random effect variable representing day of release. Parameter estimates for each covariate are provided along with 95% credible intervals.

Model	ELPD	SE (ELPD)	Diff	SE (Diff)	Length	Rearing	WTT
~ year + length + rearing + (day)	-15644.01	239.91	0	0	-0.73 (-0.94-0.51)	-0.46 (-0.54-0.38)	NA
~ year + length + rearing + WTT + (day)	-15644.02	239.9	0.01	2.05	-0.74 (-0.94-0.54)	-0.46 (-0.54-0.37)	-0.09 (-5.8-5.66)
~ year + length + WTT + (day)	-15656.12	240.11	12.11	14.78	-0.53 (-0.62-0.44)	NA	-0.08 (-5.77-5.96)
~ year + length + (day)	-15656.52	240.12	12.51	14.76	-0.53 (-0.62-0.44)	NA	NA
~ year + length + rearing	-15668.65	240.41	24.64	12.17	-1.25 (-1.44-1.1)	-0.55 (-0.63-0.46)	NA
~ year + length + rearing + WTT	-15668.69	240.4	24.68	12.18	-1.25 (-1.42-1.08)	-0.54 (-0.63-0.45)	-0.04 (-6.14-5.67)
...							
~ year	-15808.00	244.64	164.99	24.49	NA	NA	NA

Discussion

Results of this study provide the first estimates of PIT tag deposition probabilities from breeding colonies of AWPE. Pelican deposition probabilities, coupled with previously published DCCO, CATE, and LAXX deposition probabilities and colony-specific detection probabilities, provided the necessary input data to generate unbiased estimates of predation probabilities on URB Chinook smolts. Factors related to a fish's susceptibility to colonial waterbird predation were also investigated to broaden our understanding of predator-prey interactions and to elucidate potential management actions to reduce the effects of predation. Collectively, results provide a comprehensive, system-wide assessment of piscivorous colonial waterbird predation on URB Chinook smolts over the course of a 12-year study period.

Pelican Deposition Probabilities –
Results indicated that for every 100 PIT tags consumed by AWPE, on average, 47 were deposited on-colony where researchers could potentially recover them following the nesting season. Treusher et al. (2015) also investigated AWPE predation on PIT-tagged fish of conservation concern and fed PIT-tagged fish with known tag codes to breeding pelicans. However, independent estimates of detection probabilities were not developed as part of that study, so it was unknown what proportion of consumed tags were lost due to off-colony deposition of tags versus the imperfect detection of tags on bird colonies by researchers following the breeding season. Results of this and other studies indicate that detection probabilities vary by colony, year, and week, necessitating a direct measure of detection efficiency at each colony in each year (Evans et al. 2012, Osterback et al. 2013, Hostetter et al. 2015, Evans et al. 2016, Payton et al. 2019). Similar to the results of the DCCO, CATE, and LAXX deposition study conducted by Hostetter et al. (2015), AWPE deposition probabilities did not vary significantly by trial or period within the breeding season or by colony location. Small sample sizes of consumed tagged fish during some trials, however, resulted in imprecise weekly estimates of AWPE deposition probabilities and results were limited to a single year (2020). Despite these caveats, due to the lack of intra-annual variation in estimates of deposition and very similar estimates of deposition from two different AWPE colonies, results suggest that the AWPE deposition estimate derived from this study may be applicable or appropriate for use in other predation studies utilizing PIT-tagged fish.

Predation Impacts –
Numerous factors have been linked to URB fall Chinook mortality in the Columbia River basin, including harvest (Hyun et al. 2012), ocean conditions (Hyun et al. 2007), predation by piscivorous fish (Harnish et al. 2014), and passage restrictions and mortality associated with hydroelectric dams (Harnish et al. 2013). Results from this study indicate that predation from piscivorous colonial waterbirds, a previously unquantified source of mortality in URB Chinook, were substantial in some river-reaches and years. Predation probabilities were highly variable, however, with cumulative estimates ranging from 0.066 to upwards of 0.283, indicating birds consumed as few as 6.6% to as many as 28.3% of available smolts each year. Comparisons of total mortality (1 - survival) to mortality due to colonial waterbird predation indicated that avian predation accounted for 7.3% to 29.1% of all sources of URB Chinook smolt mortality annually during out-migration to Bonneville Dam. Even after passage through the hydrosystem, predation impacts by colonial waterbirds in estuary were high in some years, with upwards of 0.077 of available smolts consumed by birds in the estuary. Collectively, results indicated that the cumulative effects of avian predation were an important factor regulating the survival of URB fall Chinook smolts in some, but not all, river reaches and years.

A system-wide evaluation of colonial waterbird predation across multiple river reaches provided data to identify which bird species (CATE, DCCO, LAXX, AWPE) and individual colonies posed the greatest risk to URB Chinook smolts. Comparisons of Chinook smolt losses by predator species indicated that the AWPE colony on Badger Island and DCCO colony on Foundation Island and East Sand Island often consumed the largest proportion of available smolts compared with the other predator species and colonies evaluated. Predation probabilities at several other individual colonies, however, were often less than 0.03 per colony, per year. Predation by tern and gull colonies included in the study were generally the lowest of the predator species evaluated, with the exception of gull colony on Miller Rocks Island, a colony that was in close proximity to hydroelectric dams. Unlike pelicans, terns, and cormorants, gulls are omnivorous, and previous research indicated that juvenile salmonids comprised less than 10% of the diet (by mass) of gull colonies in the Columbia River basin (Collis et al. 2002). Despite this, predation probabilities on URB Chinook smolts by the Miller Rocks Island were similar to those of nearby pelican, tern, and cormorant colonies in some years. Hostetter et al. (2015) attributed high levels of gull predation on juvenile salmonids to the large size (tens of thousands of breeding adults) of gull colonies, coupled with behavior flexibility to exploit temporarily available food sources (Winkler 1996). Evans et al. (2016) observed that gulls nesting on Miller Rocks Island disproportionately consumed juvenile salmonids near John Day Dam, located just 18 Rkm upstream of the colony site. Studies have hypothesized that smolts may be more vulnerable to gull predation near dams due to delays in travel times associated with forebay passage, mortality and injury associated with turbine passage, or smolts temporarily being stunned or disoriented by hydraulic conditions in the tailrace of dams (Ruggurone 1996, Evans et al. 2016). Lower probabilities of predation by LAXX and CATE colonies compared with DCCO and AWPE colonies may also be related to predator-specific foraging behavior, whereby LAXX and CATE are plunge-diving predators that disproportionately consumed larger-sized smolts, like Steelhead Trout (*O. mykiss*; Hostetter et al. 2016, Evans et al. 2016, Hostetter et al. 2021), while DCCO and AWPE are pursuit divers and communal foragers, species that are capable of consuming multiple, smaller-sized fish during foraging bouts (Anderson 1991, Dorr and Weseloh 2014, Hostetter et al. 2021).

Estimates of avian predation presented herein represent minimum estimates of predation by all piscivorous colonial waterbird species and colonies because not all active colonies within foraging distance of URB Chinook smolts were scanned for PIT-tags in all years, nor were all avian predator species in the region included in the study. For instance, we did not investigate smolt predation probabilities for non-colonial or semi-colonial piscivorous waterbirds, such as Common Mergansers (*Mergus merganser)*, Forster's Terns (*Sterna forsteri)*, Great Blue Heron (*Ardea Herodias)*, Black-crowned Nightheron (*Nycticorax nycticorax)*, and grebes (*Aechmophorus spp*.). Although these piscivorous species are known to consume juvenile salmonids in the Columbia River, their predation impacts on smolts have been shown to be less than the impacts of colonial nesting piscivorous waterbirds (Wiese et al. 2008), primarily because the non-colonial and semi-colonial nesting species have smaller regional populations. It should be noted, however, that URB fall Chinook, which are smaller in size than most other salmonid smolts (Quinn 2005), are within the size range documented in the diet of mergansers and grebes and studies regarding predation impacts by these pursuit diving species on URB Chinook salmon are currently lacking. As a result, the impact of all piscivorous waterbirds on URB Chinook smolt mortality is unknown but is likely less than those CATE, DCCO, LAXX, and AWPE; the principal predator species of actively migrating salmonid smolts documented by this and other studies (Collis et al. 2002, Roby et al. 2003, Wiese et al. 2008, Evans et al. 2016, Cramer et al. 2021). It should also be noted that wild URB Chinook reside and otherwise rear in the Hanford Reach for several months prior to being PIT-tagged in June. The colonial

waterbird breeding season, however, generally starts in early-April (Adkins et al. 2012) so some unknown proportion of wild UBR Chinook smolts are susceptible to avian predation two months before they are PIT-tagged. Given our finding that smaller-sized URB Chinook were more susceptible to AWPE predation (see *below*) additional research to quantify the effects of colonial waterbird predation on wild URB chinook smolt during their resident, pre-smolt life-stage within the Hanford Reach are warranted.

Several other studies have documented that avian predation probabilities vary substantially based on the species of salmonid. For instance, Evans et al. (2012, 2016) documented significantly higher rates of predation on Steelhead Trout *O. mykiss* compared to Chinook Salmon in the Columbia River. Evans et al. (2019) reported alarmingly high rates of avian predation on Upper Columbia River steelhead, with more fish succumbing to predation by colonial waterbirds than from all other sources of mortality combined during out-migration from Rock Island Dam (Rkm 729) to Bonneville Dam. In the present study, avian predation on URB fall Chinook smolts was often, but not always, low and constituted a minor component of total mortality in some river-reaches and years. One possible component of unaccounted-for mortality in the present study is predation by piscivorous fishes (Harnish et al. 2014, McMichael 2018), such as the Northern Pikeminnow (*Ptychocheilus oregonensis*), Smallmouth Bass (*Micropterus dolomieu*), Walleye (*Sander vitreus*), and Channel Catfish (*Ictalurus punctatus*). Rieman et al. (1991) estimated that approximately 14% of juvenile salmonids passing through John Day Reservoir were consumed by Northern Pikeminnow, Smallmouth Bass, and Walleye combined and that mortality rates were highest for subyearling Chinook relative to other salmonid species and age-classes. Harnish et al. (2014) estimated there were large numbers of pikeminnow in the Hanford Reach of the Columbia River, with an estimated 37,392 predatory fish annually. In addition to piscivorous fish and birds, other sources of mortality on URB fall Chinook smolts occur, but data to quantify these impacts are generally lacking in published literature.

Covariate Analysis – The modelling of depredation's role in URB chinook smolt mortality demonstrated considerable differences in smolt susceptibility to avian predation depending on rearing type, with wild URB Chinook smolts considerably more impacted by avian predation than their hatchery counterparts. The differences in the relative susceptibility between hatchery and wild Chinook were especially pronounced at the AWPE Badger Island breeding colony, with predation probabilities on wild fish often 2 – 5 times greater than those on hatchery fish in the same year. Our covariate modelling allowed us to begin to identify and measure the strength of relationships between various biotic and abiotic factors and probabilities of predation by avian predators in general and AWPE specifically, providing important insight into the suite of factors that influence smolt susceptible to avian predation. Hatchery URB chinook are, on average, considerably larger than their wild counterparts and smolt length has been shown to be a factor in predation susceptibility in many other groups of fish (Hostetter et al. 2012, Osterback et al. 2014, Evans et al. 2019). The covariate analyses performed here similarly provided evidence that fish size was an important factor, whereby smaller-sized smolts were, on average, more susceptible to AWPE predation than their larger counterparts and hatchery fish were, on average, larger than wild smolts. However, further evidence demonstrated that this relationship was apparent even after accounting for rear-type, whereby smaller-sized fish were still more likely to be depredated than larger-sized smolts, suggesting rear-type alone was not the only factor associated with variation in predation. In fact, evidence that rear-type was a significant factor in varying levels of predation after the consideration of length was less than conclusive. In addition to differences in fish size, higher predation on wild smolts by birds nesting on Badger Island could also be due to the close proximity of the breeding site to the

Hanford Reach (where wild fish were captured, tagged, and released) compared with the tailrace of Priest Rapid Dam further upstream. Additionally, wild URB Chinook smolts were captured and released in shallow water habitats in the Hanford Reach, areas where fish are more susceptible to predation by pelicans, cooperative foragers that corral fish in shallow water (Knopf and Evans 2004). Evidence that wild URB fall Chinook smolts were more susceptible to avian predation than their hatchery counterparts also has important implications from a population enhancement perspective. For instance, unlike many other Chinook stocks in the Columbia River basin, natural spawning URB fall Chinook outnumber hatchery returning adults, with approximately 60 – 70% of adult returns from wild origin fish (Stuart Ellis, CRITFC, personal communication). Given higher avian predation rates on wild URB fall Chinook, efforts to reduce avian predation would have a greater benefit to the wild population, benefits that could result in substantially more adult returns in the future.

Results of this study provide less evidence as to which abiotic conditions experienced by smolts during out-migration contribute to smolt susceptibility to avian predation after accounting for biotic factors (i.e., a fish's rear-type and size). Of all abiotic factors considered, only water transit time was included in the best fitting models. This resembles previous research finding statistically significant correlation between fluctuations in WTT and temporal variation in avian predation. For instance, previously Hostetter et al. (2012) also observed that increased river flows were related to a decrease in Caspian tern predation probabilities on smolts originating from the Snake River. Also, Payton et al. (2017) observed that faster water transit times were associated with lower predation by CATE on smolts passing through the Wanapum and Priest Rapids reservoirs in the Columbia River. Water transit time was implemented in this analysis as a proximate measure of travel time. Differences in the behavior of wild and hatchery smolts also likely explain differences in the relative susceptibility of smolts to avian predation. For instance, longer residence times of wild fish compared with hatchery fish make wild fish more susceptible to predation and there was some evidence that slower water transit times were associated with high probabilities of predation, presumably due to increase exposure time to predators (Hostetter et al. 2021). However, differences in the observed travel times of hatchery and wild reared fish from release to McNary Dam were inconsistent among years and difficult to contextualize. In general, the influence of WTT on the travel times is tenuous since the measure of travel time is inherently dependent on the fish's survival to McNary Dam, which is itself related to a fish's rear type and length, which is highly correlated with rates of predations. Additionally, pelicans are capable of commuting long distances from their breeding sites to forage (over 300 km; Scoppettone et al. 2006), so pelicans nesting on Badger Island were able to consume smolts in multiple river-reaches, including downstream of John Day Dam in The Dalles Reservoir, over 150 Rkm downstream of Badger Island. The JMS model can broadly estimate the location of impacts but, over such a broad area, determining what factors in which reaches should be assessed are difficult to identify from week to week and year to year. In aggregate, such issues make it difficult to disentangle these abiotic factors from the biotic factors that have been shown to be of primary consideration. Collectively, results indicate that predator-prey interactions were complex and dynamic with multiple individual and population-level factors associated with URB Chinook smolt susceptibility to predation.

Concluding Remarks – Results of this study indicate that predation by colonial waterbirds was an important mortality factor for URB Chinook during the smolt life stage, although impacts were highly variable based on the predator-species, colony location, river-reach, and year. Results suggest that wild fish were more likely to be consumed relative to their hatchery counterparts and that factors such as fish

length, migration-timing, fish behavior, and predator characteristics (e.g., colony location and size and foraging strategies) may better explain differences in smolt susceptibility to avian predation relative to inherent differences between hatchery and wild smolts. A lack of consistently over-lapping run-timing and the differences in sizes of hatchery and wild URB Chinook made it difficult, but not impossible, to disentangle competing hypotheses describing the influences of inherent behavioral tendencies and size-selectivity on survival and predation of hatchery- vs wild-reared smolts. Finally, studies of avian predation often describe the interaction between a single predator and prey species and how individual prey characteristics may result in increased predation risk (Hostetter et al. 2012, Osterback et al. 2014, Evans et al. 2019). However, predators and prey do not occur in isolation, but are nested inside complex multi-predator, multi-prey systems that include a variety of ecological processes and factors (Hostetter et al. 2021). Holistic studies focused on these factors will have tremendous application to both basic and applied ecology and towards the potential management of predators to increase prey survival.

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Table A1. Average annual recovery probabilities (95% credible intervals) of smolt PIT tags on colonial waterbird breeding sites. Recovery probabilities are from Caspian Tern (CATE), Double-crested Cormorant (DCCO), California and Ring-billed Gull (LAXX), and American White Pelican (AWPE) colonies (see Figure 1 for map of colony locations and names). Recovery probability is shown as the deposition probability multiplied by the detection probability. Data are those previously reported by Evans et al. (2019), with the exception of BGI AWPE colony, where estimates were derived as part of this study (see *Methods*). Blanks cells indicate the colony sites was either inactive or was not scanned for PIT tags (see *Table A1*).

Recovery	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
PTI CATE	0.46 (0.29-0.62)	0.33 (0.19-0.46)	0.42 (0.28-0.59)	0.45 (0.27-0.59)	0.41 (0.25-0.58)	0.48 (0.32-0.65)	0.50 (0.24-0.72)		0.54 (0.23-0.77)			
I20 LAXX	0.12 (0.05-0.18)					0.13 (0.08-0.17)	0.13 (0.08-0.17)	0.13 (0.09-0.18)	0.12 (0.08-0.17)	0.13 (0.09-0.17)	0.15 (0.11-0.2)	0.14 (0.1-0.19)
FDI DCCO [2]	0.37 (0.23-0.51)	0.36 (0.22-0.49)	0.32 (0.19-0.45)	0.25 (0.13-0.39)	0.19 (0.08-0.31)		0.10 (0.03-0.2)					
BGI AWPE	0.31 (0.12-0.49)	0.4 (0.19-0.63)	0.34 (0.16-0.56)	0.35 (0.16-0.59)	0.33 (0.14-0.55)		0.33 (0.14-0.55)	0.31 (0.13-0.49)	0.29 (0.13-0.48)	0.29 (0.12-0.48)	0.26 (0.1-0.45)	0.23 (0.09-0.41)
BGI LAXX								0.12 (0.07-0.17)[1]	0.09 (0.03-0.14)[1]	0.12 (0.07-0.16)	0.05 (0.02-0.09)	0.06 (0.02-0.1)
BGI CATE										0.68 (0.50-0.85)[1]		
CSI LAXX	0.13 (0.09-0.18)	0.11 (0.08-0.16)	0.12 (0.08-0.16)	0.11 (0.07-0.16)	0.13 (0.08-0.18)	0.12 (0.07-0.17)	0.14 (0.09-0.19)					
CSI CATE	0.48 (0.34-0.64)	0.58 (0.41-0.74)	0.60 (0.43-0.76)	0.60 (0.41-0.76)	0.55 (0.36-0.73)	0.61 (0.42-0.78)	0.62 (0.42-0.78)					
CBI LAXX						0.12 (0.09-0.15)	0.15 (0.11-0.18)	0.14 (0.11-0.18)	0.14 (0.1-0.18)	0.14 (0.11-0.18)[1]	0.14 (0.11-0.17)[1]	0.15 (0.12-0.18)[1]
CBI CATE	0.69 (0.55-0.81)	0.67 (0.52-0.79)	0.55 (0.31-0.78)[1]	0.56 (0.29-0.75)		0.56 (0.31-0.78)[1]	0.55 (0.27-0.76)[1]	0.57 (0.43-0.69)	0.55 (0.43-0.67)	0.38 (0.29-0.49)	0.28 (0.19-0.38)	0.23 (0.15-0.34)
MRI LAXX	0.13 (0.09-0.18)	0.12 (0.08-0.17)	0.12 (0.08-0.16)	0.12 (0.08-0.17)	0.13 (0.08-0.17)	0.13 (0.09-0.18)	0.13 (0.08-0.18)	0.14 (0.09-0.19)	0.13 (0.08-0.17)	0.11 (0.07-0.16)	0.13 (0.09-0.18)	0.13 (0.09-0.17)
ESI CATE	0.66 (0.48-0.83)	0.65 (0.47-0.81)	0.59 (0.42-0.75)	0.55 (0.38-0.7)	0.54 (0.34-0.74)	0.42 (0.26-0.6)	0.48 (0.29-0.65)	0.61 (0.4-0.77)	0.56 (0.38-0.73)	0.50 (0.34-0.66)	0.54 (0.36-0.71)	0.45 (0.28-0.61)
ESI DCCO	0.34 (0.2-0.46)	0.33 (0.22-0.47)	0.38 (0.24-0.51)	0.36 (0.23-0.51)	0.36 (0.2-0.51)	0.34 (0.21-0.49)	0.39 (0.25-0.55)	0.40 (0.25-0.55)	0.30 (0.18-0.45)	0.36 (0.22-0.5)	0.46 (0.29-0.63)	0.43 (0.27-0.57)

[1] Variation in detection probability partially inferred from other years (see also Evans et al. 2019)

[2] Colony was not scanned in 2013 and 2015-2019 but average annual estimates of recovery probabilities from other years were used to impute estimates of predation in those years (see Methods)

Table A2. Numbers of PIT-tagged URB fall Chinook smolts recovered dead on bird colonies in the Columbia River basin. Bird colonies include Caspian Terns (CATE), American White Pelicans (AWPE), Double-crested Cormorants (DCCO), and California and Ring-billed Gulls (LAXX; see Figure 1 for map of colony locations). NC denotes there was no colony at the site and year. Green dashed-lined denote that the colony was active but was not scanned and predation rate estimates were imputed based on data from other years at that colony site. Red dashed-line denotes that colony was active but was not scanned and that average annual estimates of predation were used in those years (see *Methods*)

Colony	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
Potholes Reservoir, CATE	1	5	1	4	32	11	0	NC	0	NC	NC	NC
Badger Island, CATE	NC	NC	NC	-	-	NC	NC	NC	NC	18	NC	NC
Crescent Island, CATE	23	54	16	75	166	53	152	NC	NC	NC	NC	NC
Central Blalock Islands, CATE	1	1	1	0	-	0	0	270	190	109	56	52
East Sand Island, CATE	40	52	12	5	129	160	134	136	81	54	143	67
BGI AWPE	69	136	105	174	290	-	315	114	85	-	47	22
BGI Mix (AWPE/LAXX)	NC	NC	NC	NC	NC	NC	NC	111	245	623	902	841
Island 20, LAXX	-	-	-	-	-	12	15	29	32	13	14	46
Crescent Island, LAXX	1	0	0	0	5	14	7	NC	NC	NC	NC	NC
Central Blalock Islands, LAXX	-	-	-	-	-	8	14	28	46	17	15	19
Miller Rock Island, LAXX	16	5	5	0	21	57	81	101	97	118	104	64
Foundation Island, DCCO	236	163	62	90	181	-	72	-	-	-	-	-
East Sand Island, DCCO	43	20	13	16	138	274	119	113	49 [2]	2 [2]	39	14

[1] The area made up exclusively of nesting AWPE on BGI was not scanned, however predation was inferred from other information
[2] DCCO temporarily abandoned the nesting site at times during the breeding season; this atypical behavior likely resulted in fewer tags being deposited.
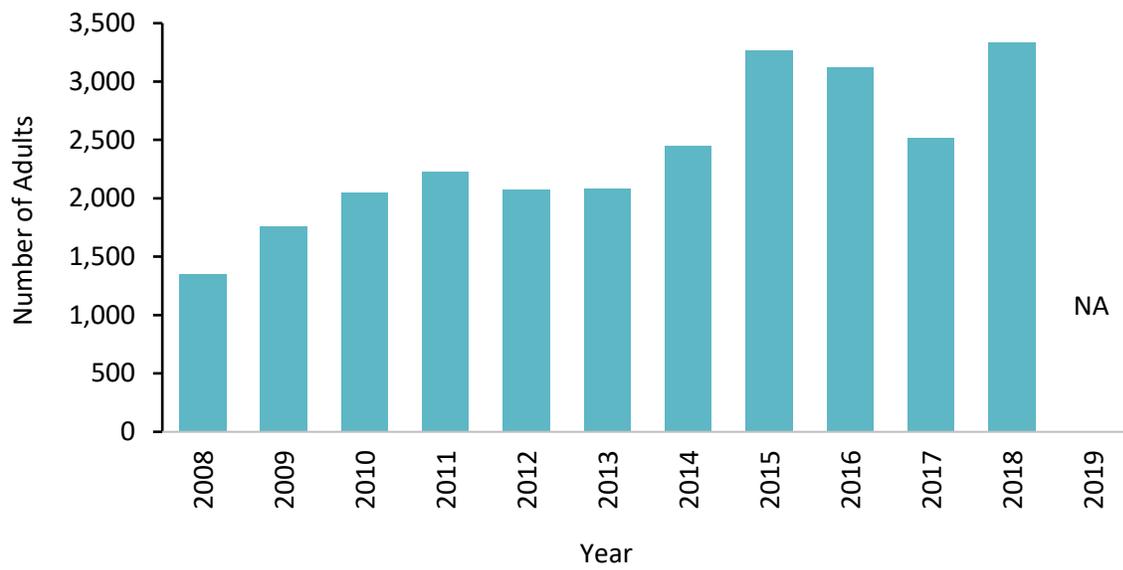
Figure A.1. Numbers of American White Pelicans counted on Badger Island during the peak nesting period of June. Comparable counts were not available (NA) in 2019 but a colony existed in that year. Counts are those of Cramer et al. (2021).

Two species of colonial waterbirds, American White Pelicans (*Pelecanus erythrorhynchos,* hereafter "AWPE") and Gulls (*Larus californicus and L. delawarensis,* collectively hereafter "LAXX"), established colonies on Badger Island (BGI) during 2015 through 2019. A portion of each of these colonies overlapped spatially creating a "mixed" or co-nesting colony. To estimate AWPE predation probabilities, and to evaluate what biotic and abiotic factors best explain temporal variation in those impacts, necessitated the simultaneous modelling of LAXX predation from BGI as well.

Modelling predation involves the consideration of the recovery of tags from the two portions of BGI, labelled "AWPE" for the portion only inhabited by pelicans and "LAXX" for the portion only inhabited by gulls (each referred to hereafter as "only" portions) and the portion of BGI in which the colonies intermixed labelled "MIX" (referred to hereafter as the "mixed" area). We let

$$r_{y,d,AWPE} \sim \text{binomial}\left(n_{y,d}, \rho_{y,d,AWPE} * \theta_{y,d,AWPE} * \phi_{y,AWPE} * \psi_{y,d,AWPE}\right)$$

$$r_{y,d,LAXX} \sim \text{binomial}\left(n_{y,d}, \rho_{y,d,LAXX} * \theta_{y,d,LAXX} * \phi_{y,LAXX} * \psi_{y,d,LAXX}\right)$$

$$r_{y,d,MIX} \sim \text{binomial}\left(n_{y,d}, \left(\begin{array}{c} (1 - \rho_{y,d,AWPE}) * \theta_{y,d,AWPE} * \phi_{y,AWPE} + \\ (1 - \rho_{y,d,LAXX}) * \theta_{y,d,LAXX} * \phi_{y,LAXX} \end{array}\right) * \psi_{y,d,MIX}\right)$$

where $r_{y,d,AWPE}$, $r_{y,d,LAXX}$, and $r_{y,d,MIX}$ represent the number of tags recovered from each portion of BGI of $n_{y,d}$ tags released on day *d* of year *y*; $\theta_{y,d,AWPE}$ and $\theta_{y,d,LAXX}$ represent the probability a fish released on day *d* of year *y* was depredation rate by each genera; $\rho_{y,d,AWPE}$ and $\rho_{y,d,LAXX}$ represent the proportion of total depredated tags that were taken by birds nesting in the AWPE-only and LAXX-only areas of BGI respectively; $\phi_{y,AWPE}$ and $\phi_{y,LAXX}$ represent the probabilities that a tag consumed by each genera of bird was then deposited on the colony; and $\psi_{y,d,AWPE}$, $\psi_{y,d,LAXX}$, and $\psi_{y,d,MIX}$ represent the probabilities of recovering a deposited tag from each portion of the island.

To inform our estimates of $\rho_{y,d,AWPE}$ and $\rho_{y,d,LAXX}$, we assume that the odds of a tag consumed by a given species being deposited in the "only" portions versus in the "mixed" delineation to be similar to the odds of a bird of that genera nesting in the "mixed" delineation. The proportion of tags recovered from each delineation varies considerably within each year which strongly suggests these odds vary over the year. We only have one observed count of birds for each genera each year which we must assume to be a random observation of the proportion of birds nesting within each, represented by $\rho'_{y,AWPE}$ and $\rho'_{y,LAXX}$. That is, we assume

$$\bar{\rho}_{y,species} \approx \rho'_{y,species}$$

$$b_{y,species} \sim \text{binomial}\left(B_{y,species}, \rho'_{y,species}\right)$$

$$\bar{\rho}_{y,species} = \sum_d w_d\, \rho_{y,d,species}$$

where $w_d = \frac{n_{y,d}}{\Sigma_d\, n_{y,d}}$ represent weights for constructing a geometric average based on daily sample sizes.

We are interested in estimating

$$\vec{\theta}_d = [\theta_{AWPE,d}, \theta_{LAXX,d}, \theta_{OTHER,d}].$$

This is how we must parameterized our model, however, it may be more elucidating to express $\theta_{AWPE,d}$ as $\theta_{AWPE,0}^{both} = \theta_{AWPE,0}^{only} + \theta_{AWPE,0}^{mixed}$, and similarly for LAXX.

We assume the respective probabilities among days closer in time to be more similar than of those further apart. We therefore model the variation in probabilities across time as an autoregressive process using a logistic framework with the probability of a fish being depredated by neither AWPEs nor LAXXs ($\theta_{OTHER,d}$) to be the reference level. For example, we assume

$$\log\left(\frac{\theta_{AWPE,d}^{only}}{\theta_{OTHER,d}}\right) = \log\left(\frac{\theta_{AWPE,1}^{only}}{\theta_{OTHER,1}}\right) + \sum_{i<d} \epsilon_i$$

where $\epsilon_i \sim \text{normal}(0, \sigma_\epsilon)$ is the random effect of day and let

$$\theta_{AWPE,d}^{only} = \frac{\exp\left(log\left(\frac{\theta_{AWPE,d}^{only}}{\theta_{OTHER,d}}\right)\right)}{\sum_i \exp\left(\log\left(\frac{\theta_{i,d}}{\theta_{OTHER,d}}\right)\right)}.$$

Similarly, for the mixed portion of the colony, we let $\delta_i \sim \text{normal}(0, \sigma_\epsilon)$ represent the random effect of day. Assuming a prior of $\vec{\theta}_d \sim \text{dirichlet}(\vec{\mathbf{1}})$ allows for a fully identifiable parameter space.

We can then derive $\theta_{AWPE,d}^{only}$ (and similarly $\theta_{LAXX,d}^{only}$) by equating the odds of a bird nesting on the "only" versus "mixed" portions of a colony with the weighted average of the odds of predation on the "only" versus "mixed" portions of a colony can be expressed

$$\sum_d w_d \frac{\dfrac{\exp\left(log\left(\frac{\theta_{AWPE,d}^{only}}{\theta_{OTHER,d}}\right)\right)}{\sum_i \exp\left(\log\left(\frac{\theta_{i,d}}{\theta_{OTHER,d}}\right)\right)}}{\dfrac{\exp\left(log\left(\frac{\theta_{AWPE,d}^{mixed}}{\theta_{OTHER,d}}\right)\right)}{\sum_i \exp\left(\log\left(\frac{\theta_{i,d}}{\theta_{OTHER,d}}\right)\right)}} = \frac{\rho'_{y,AWPE}}{1 - \rho'_{y,AWPE}}$$

$$\to \sum_d w_d \left(\frac{\exp\left(log\left(\frac{\theta_{AWPE,1}^{only}}{\theta_{OTHER,d}}\right) + \sum_{i<d}\epsilon_i\right)}{\exp\left(log\left(\frac{\theta_{AWPE,1}^{mixed}}{\theta_{OTHER,d}}\right) + \sum_{j<d}\delta_j\right)}\right) = \frac{\rho'_{y,AWPE}}{1 - \rho'_{y,AWPE}}$$

$$\rightarrow \sum_d w_d \left(\frac{\frac{\theta_{AWPE,1}^{only}}{\theta_{OTHER,1}} \prod_{i<d} e^{\epsilon_i}}{\frac{\theta_{AWPE,1}^{mixeed}}{\theta_{OTHER,1}} \prod_{j<d} e^{\delta_j}} \right) = \frac{\rho'_{y,AWPE}}{1 - \rho'_{y,AWPE}}$$

$$\rightarrow \frac{\theta_{AWPE,1}^{only}}{\theta_{AWPE,1}^{mixed}} \sum_d w_d \left(\frac{\prod_{i<d} e^{\epsilon_i}}{\prod_{j<d} e^{\delta_i}} \right) = \frac{\rho'_{y,AWPE}}{1 - \rho'_{y,AWPE}}$$

Let $\overline{\Delta} = \sum_d w_d \left(\frac{\prod_{i<d} e^{\epsilon_i}}{\prod_{j<d} e^{\delta_j}} \right)$.

$$\rightarrow \frac{\theta_{AWPE,1}^{only}}{\theta_{AWPE,1}^{both} - \theta_{AWPE,1}^{only}} \overline{\Delta} = \left(\frac{\rho'_{y,AWPE}}{1 - \rho'_{y,AWPE}} \right)$$

$$\rightarrow \theta_{AWPE,1}^{only} = \left(\frac{\rho'_{y,AWPE}}{\overline{\Delta}\left(1 - \rho'_{y,AWPE}\right)} \right) \left(\theta_{AWPE,0}^{both} - \theta_{AWPE,1}^{only} \right)$$

$$\rightarrow \theta_{AWPE,1}^{only} \left(1 + \left(\frac{\rho'_{y,AWPE}}{\overline{\Delta}\left(1 - \rho'_{y,AWPE}\right)} \right) \right) = \left(\frac{\rho'_{y,AWPE}}{\overline{\Delta}\left(1 - \rho'_{y,AWPE}\right)} \right) \theta_{AWPE,1}^{both}$$

$$\rightarrow \theta_{AWPE,1}^{only} \left(\frac{\overline{\Delta}\left(1 - \rho'_{y,AWPE}\right) + \rho'_{y,AWPE}}{\overline{\Delta}\left(1 - \rho'_{y,AWPE}\right)} \right) = \left(\frac{\rho'_{y,AWPE}}{\overline{\Delta}\left(1 - \rho'_{y,AWPE}\right)} \right) \theta_{AWPE,1}^{both}$$

$$\rightarrow \theta_{AWPE,1}^{only} = \left(\frac{\rho'_{y,AWPE}}{\overline{\Delta}\left(1 - \rho'_{y,AWPE}\right) + \rho'_{y,AWPE}} \right) \theta_{AWPE,1}^{both}$$