

ARTICLE

Quantifying Avian Predation on Fish Populations: Integrating Predator-Specific Deposition Probabilities in Tag Recovery Studies

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Abstract

Accurate assessment of specific mortality factors is vital to prioritize recovery actions for threatened and endangered species. For decades, tag recovery methods have been used to estimate fish mortality due to avian predation. Predation probabilities derived from fish tag recoveries on piscivorous waterbird colonies typically reflect minimum estimates of predation due to an unknown and unaccounted-for fraction of tags that are consumed but not deposited on-colony (i.e., deposition probability). We applied an integrated tag recovery modeling approach in a Bayesian context to estimate predation probabilities that accounted for predator-specific tag detection and deposition probabilities in a multiple-predator system. Studies of PIT tag deposition were conducted across three bird species nesting at seven different colonies in the Columbia River basin, USA. Tag deposition probabilities differed significantly among predator species (Caspian terns *Hydroprogne caspia*: deposition probability = 0.71, 95% credible interval [CRI] = 0.51–0.89; double-crested cormorants *Phalacrocorax auritus*: 0.51, 95% CRI = 0.34–0.70; California gulls *Larus californicus*: 0.15, 95% CRI = 0.11–0.21) but showed little variation across trials within a species or across years. Data from a 6-year study (2008–2013) of PIT-tagged juvenile Snake River steelhead *Oncorhynchus mykiss* (listed as threatened under the Endangered Species Act) indicated that colony-specific predation probabilities ranged from less than 0.01 to 0.17 and varied by predator species, colony location, and year. Integrating the predator-specific deposition probabilities increased the predation probabilities by a factor of approximately 1.4 for Caspian terns, 2.0 for double-crested cormorants, and 6.7 for California gulls compared with traditional minimum predation rate methods, which do not account for deposition probabilities. Results supported previous findings on the high predation impacts from strictly piscivorous waterbirds nesting in the Columbia River estuary (i.e., terns and cormorants), but our findings also revealed greater impacts of a generalist predator species (i.e., California gulls) than were previously documented. Approaches used in this study allow for direct comparisons among multiple fish mortality factors and considerably improve the reliability of tag recovery models for estimating predation probabilities in multiple-predator systems.

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Predation is an important source of mortality in many fish populations (Sih 1987). Multiple predator species can individually and collectively shape fish communities and exert top-down controls on population dynamics (Botsford et al. 1997; Steinmetz et al. 2003). Quantifying the contribution of each predator species is a critical issue in community and applied ecology (Sih et al. 1998). Factor-specific mortality estimates provide vital information for prioritizing management actions but are often among the greatest limitations in the development and assessment of recovery plans (Yoccoz et al. 2001).

Avian predation on fish populations is a frequent concern among fisheries managers (Draulans 1988; Steinmetz et al. 2003; NOAA 2008). Capture–mark–recovery methods are commonly used to estimate fish mortality due to avian predation (e.g., Boström et al. 2009; Jepsen et al. 2010; Evans et al. 2011, 2012; Halfyard et al. 2012). In general, such studies have applied a similar study design. First, samples of fish are captured and tagged to identify individuals or groups and then are returned to mix with the remainder of the population of interest. After some period of time, nearby bird colonies are searched to detect tags that were deposited by birds after consuming the tagged fish. Recoveries of tags on bird colonies do not directly reflect predation probabilities, as some proportion of consumed tags may be deposited off-colony, damaged prior to deposition, or deposited on-colony but missed during the recovery process (Evans et al. 2012; Osterback et al. 2013; Figure 1). Statistical models have been applied to address the challenge of imperfect recovery of tags deposited on avian colonies, and those models provide estimates of minimum predation rates (Evans et al. 2012; Frechette et al. 2012). The predation rates remain minimum estimates because the proportion of tags that are deposited on-colony is still unknown and assumed to be 1.0 (i.e., all consumed tags are deposited

on-colony). Osterback et al. (2013) developed a Bayesian hierarchical model to integrate on-colony deposition probabilities if such probabilities are available. To date, however, deposition probabilities for PIT tags are only available for a single bird species (western gull *Larus occidentalis*) in a single year (Osterback et al. 2013). Studies using other tag types and avian species indicate that deposition probabilities are low and variable among different bird species and in different years, but this has yet to be verified by using the same tag type across multiple bird species or multiple years (Boström et al. 2009; Osterback et al. 2013; Scoppettone et al. 2014).

Avian predation on juvenile salmonids *Oncorhynchus* spp. in the Columbia River basin is considered a limiting factor in the recovery of multiple salmonid populations that are listed as threatened or endangered under the U.S. Endangered Species Act (ESA; NOAA 2008). Capture–mark–recovery studies using PIT tags in the Columbia River basin have documented minimum predation rates for numerous piscivorous bird colonies over the past decade (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Evans et al. 2012; Sebring et al. 2013). However, no previous published study has integrated deposition probabilities or investigated the possibility that deposition probabilities may vary among avian predator species. Measurement and integration of predator-specific deposition probabilities are required to produce unbiased estimates of avian predation probabilities and to allow balanced comparisons among multiple sources of fish mortality.

The objectives of this study were twofold: (1) to evaluate predator-specific PIT tag deposition probabilities for three important avian predators on juvenile salmonids in the Columbia River basin: Caspian terns *Hydroprogne caspia* (hereafter, terns), double-crested cormorants *Phalacrocorax auritus* (hereafter, cormorants), and California gulls *L. californicus*

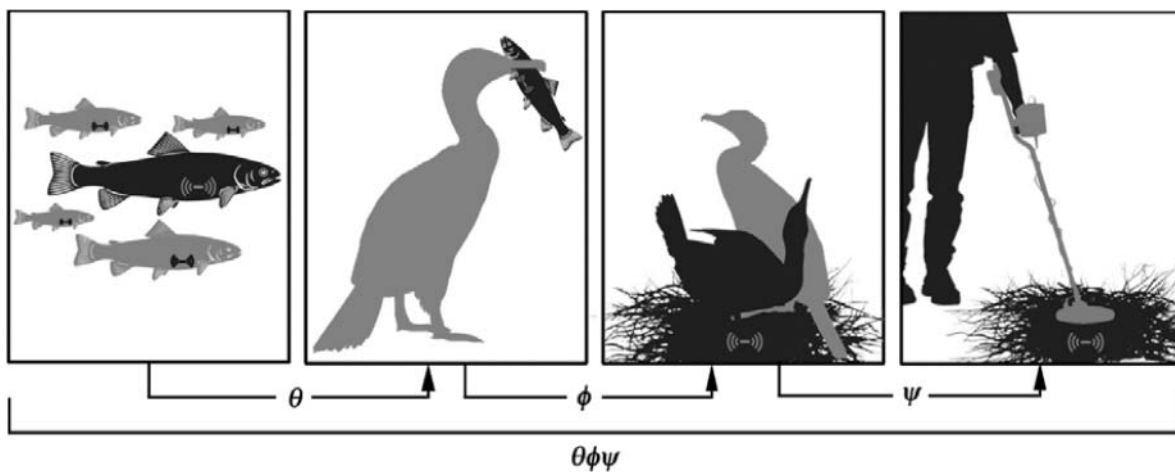


FIGURE 1. Conceptual model of the tag recovery process in capture–mark–recovery studies of avian predation on fish populations (following Osterback et al. 2013). The probability of recovering a fish tag on a bird colony is the product of three probabilities: the probability that a tagged fish is consumed (predation probability θ), the probability that the tag is deposited on the nesting colony (deposition probability ϕ), and the probability that the tag is detected by researchers (detection probability ψ).

(hereafter, gulls); and (2) to estimate annual predation probabilities for ESA-listed (threatened) Snake River steelhead *O. mykiss* (anadromous Rainbow Trout) that integrate multiple levels of uncertainty in the tag recovery process, including imperfect detection of tags on bird colonies, on-colony tag deposition probabilities that may vary among bird species, variable fish tagging effort, and temporal changes in fish availability to predators. We investigated a 6-year data set (2008–2013) that encompassed the current period of survival standards for ESA-listed Snake River steelhead in the Federal Columbia River Power System (NOAA 2008). Results of this work build upon previous tag recovery studies and yield several important contributions, including (1) estimates of PIT tag deposition probabilities for terns, cormorants, and gulls; (2) avian predation probability estimates for ESA-listed Snake River steelhead that account for predator-specific deposition probabilities; and (3) a flexible framework for estimating avian predation probabilities based on tag recoveries from multiple colonies of avian predators.

STUDY AREA

Juvenile steelhead were PIT-tagged and released in the Snake River basin, a major tributary of the Columbia River. Breeding colonies of piscivorous waterbirds were located from the Columbia River mouth to islands approximately 545 river kilometers (rkm) upstream in Washington and Oregon (Figure 2). In total, seven individual bird colonies were surveyed for this study based on previous publications on avian predation in the Columbia River basin (Evans et al. 2012; Adkins et al. 2014a). Colonies were located in one of three reaches of the Snake and Columbia rivers (Figure 2): (1) downstream of Bonneville Dam in the lower Columbia River (estuary); (2) between McNary Dam and Bonneville Dam

(MCN–BON) on the mid-Columbia River; or (3) between Lower Monumental Dam on the lower Snake River and McNary Dam (LMN–MCN). Specific breeding colonies that were evaluated included tern colonies on East Sand Island (rkm 8; estuary) and Crescent Island (rkm 510; LMN–MCN); a cormorant colony on East Sand Island; and gull colonies on Miller Rocks (rkm 333; MCN–BON), Blalock Islands (rkm 445; MCN–BON), Crescent Island, and Island 20 (rkm 545; LMN–MCN).

METHODS

Capture–mark–recovery data for Snake River steelhead were collected during 2008–2013 as part of a larger study assessing the impacts of avian predation on ESA-listed Pacific salmonids throughout the Columbia River basin (Collis et al. 2001, 2002; Roby et al. 2003; Evans et al. 2012). Multiple independent data sets were combined to estimate three processes: (1) the probability that tagged steelhead smolts were consumed (predation probability), (2) the probability that ingested tags were deposited on the nesting colony (deposition probability), and (3) the probability that deposited tags were detected by researchers during tag recovery efforts (detection probability; Figure 1). In general, predation probability is of the greatest ecological interest. However, accurate estimation of detection and deposition probabilities are required to properly estimate predation probabilities from tag recoveries on bird colonies (Osterback et al. 2013; Figure 1).

Smolt Availability

Definitions of Snake River steelhead availability to predators followed those of Evans et al. (2012) and are only briefly described here. Each year, thousands of Snake River steelhead

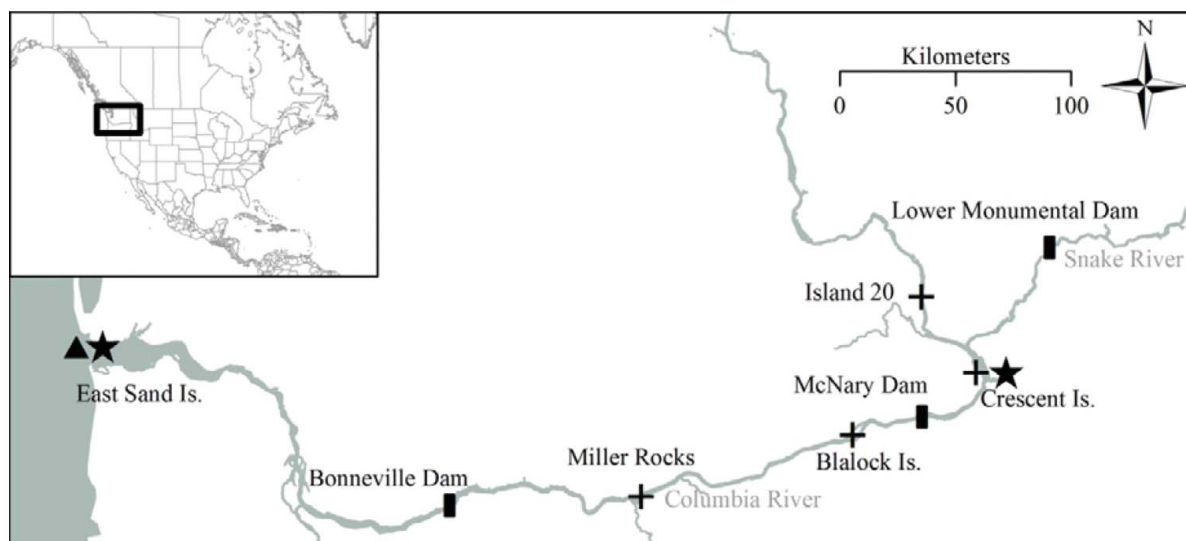


FIGURE 2. Locations of the avian breeding colonies that were included in this study (stars = Caspian tern colonies; plus symbols = California gull colonies; triangle = double-crested cormorant colony). Hydroelectric dams mentioned in the paper are denoted by rectangles.

smolts are PIT-tagged and released in the Snake River basin. A portion of these PIT-tagged smolts is subsequently detected at downstream main-stem hydroelectric dams on the Snake and Columbia rivers during the smolt out-migration to the Pacific Ocean (Figure 2). In accordance with the definitions provided by Evans et al. (2012), we considered a PIT-tagged steelhead to be available to avian predators nesting at a particular colony if that steelhead was detected at the nearest upstream hydroelectric dam with adequate smolt interrogation capabilities (Figure 2). Smolt availability to predators was limited to April–July for birds nesting at inland colonies (weeks 13–31) and March–August for birds nesting at estuary colonies (weeks 9–35; Evans et al. 2012); these periods correspond with both active steelhead smolt out-migration and avian nesting (Evans et al. 2012; Adkins et al. 2014a). Detection data were retrieved from the PIT Tag Information System (PTAGIS), a regional salmonid tag database maintained by the Pacific States Marine Fisheries Commission (www.ptagis.org).

Detection Study

Recovery of PIT tags on bird colonies followed the methods of Ryan et al. (2001) and Evans et al. (2012). In brief, scanning for PIT tags was conducted after birds dispersed from their breeding colonies following the nesting season (August–November). Colony areas were scanned using flat-plate and pole-mounted PIT tag antennas. The area scanned by researchers was determined based on colony- and year-specific aerial photography and colony visits during the nesting season (Adkins et al. 2014a).

The probability that a PIT tag was detected by researchers given that the tag was deposited on-colony (i.e., detection probability) required surveys of tags that were known to have been deposited on-colony (see Evans et al. 2012). Bird colonies could not be scanned during the breeding season, which is the period of interest for estimation of smolt mortality. Therefore, PIT tags that were identical to those used in other components of this study were sown across each bird colony (i.e., thrown by a researcher walking through the colony area) during two to four discrete occasions (weeks) throughout the nesting season (hereafter, “test tags”). Detections (i.e., recoveries) of the test tags during scanning efforts conducted after the birds had dispersed from the colony were used to model the probability of detecting a tag given that it was deposited on-colony during the nesting season. This process was repeated during each year and at each colony of interest.

Deposition Study

Once a fish and its tag are consumed by a bird, two additional processes must occur for the tag to be recovered: deposition of the tag on the breeding colony; and detection of the tag by researchers (Figure 1). Deposition probability (i.e., the probability that a tag consumed by a nesting bird will be

deposited on its breeding colony) can be estimated by feeding tagged fish to the birds of interest and subsequently recovering those tags from the breeding colony (Osterback et al. 2013; Scopettone et al. 2014). In this study, deposition probabilities were estimated by feeding PIT-tagged hatchery Rainbow Trout (length = 80–225 mm) with known tag codes to nesting birds of the three study species and then subsequently recovering the tags from those bird colonies. Deposition studies were repeated within season and across multiple seasons for each bird species, with each discrete study considered a separate trial. Specific methods for individual bird species are described below; additional details of trial-specific sample sizes are available in Supplementary Table S.1 in the online version of this article.

Caspian terns.—Studies to measure deposition probabilities for terns were conducted during 2004–2006. In the first study (2005–2006), nesting adult terns were captured at Crescent and East Sand islands using monofilament noose mats that were placed around active nests. Once captured, each adult tern was fed a single PIT-tagged Rainbow Trout and was then released ($n = 31$ –59 trout consumed per trial; Table 1).

In the second study (2004–2006), Rainbow Trout were PIT-tagged and placed into one of three net-pen enclosures anchored in Columbia or Snake River backwater areas that were less than 23 km from the Crescent Island tern colony. Net-pens were monitored daily (8–15 h/d) from a nearby blind to record the number of fish that were successfully removed by terns. When not monitored, the net-pens were covered with fine-mesh netting to prevent access to and undocumented removal of PIT-tagged Rainbow Trout. Net-pens were monitored from April 28 to June 3 (weeks 17–23) in 2004; from April 21 to July 1 (weeks 16–26) in 2005; and from April 28 to June 28 (weeks 17–26) in 2006. Only Rainbow Trout that were verified as having been consumed by a tern were included in this study ($n = 80$ –94 trout consumed per trial). In total, feeding and net-pen studies resulted in seven separate deposition trials for terns (4 feeding trials; 3 net-pen trials), with a total of 456 PIT-tagged Rainbow Trout being consumed by terns during the studies (Table 1).

Double-crested cormorants.—During 2012 and 2013, PIT-tagged Rainbow Trout were thrown to cormorants that were nesting adjacent to observation blinds on East Sand Island during multiple weeks in 2012 and in 2013 (weeks 18–25; Table 1). Only Rainbow Trout that were verified as having been consumed by an adult cormorant were included in the study. In total, six separate deposition trials were conducted ($n = 37$ –101 trout consumed per trial), and a total of 428 PIT-tagged trout were consumed by cormorants (Table 1).

California gulls.—Deposition trial methods for California gulls were the same as those for cormorants but were conducted at different locations. In 2012, trials were conducted on gull colonies at Miller Rocks and Crescent Island. In 2013, the study was expanded to include gull colonies at the Blalock Islands and Island 20 in addition to the Miller Rocks and

TABLE 1. Sample sizes for studies of on-colony PIT tag deposition by Caspian terns, double-crested cormorants, and California gulls. The number of trials, number of PIT-tagged Rainbow Trout that were consumed, and number of tags that were recovered on-colony (unadjusted for detection probability) are shown. See Table S.1 for trial-specific sample sizes.

Bird species	Trials	Years	Trout consumed	Tags recovered
Caspian tern	7	2004–2006	456	198
Double-crested cormorant	6	2012–2013	428	142
California gull	18	2012–2013	1,812	232

Crescent Island colonies (Figure 2). In total, 18 deposition trials were conducted with gulls ($n = 98$ – 105 trout consumed per trial), and 1,812 PIT-tagged trout were consumed by gulls (Table 1).

Net-pen studies were conducted for terns but not for gulls or cormorants due to differences in foraging ecology and behavior among the bird species. For instance, gulls and cormorants readily consumed fish that were thrown onto the colony from nearby blinds. This noninvasive “feeding” technique, however, did not work for terns; therefore, physical capture and handling were required to facilitate the use of terns in the feeding studies. Alternatively, the noninvasive net-pen studies of terns were successful due to the terns’ plunge-dive foraging strategy and aerial consumption of prey. The former attribute allowed successful use of relatively small net-pens, while the latter attribute allowed verification of fish consumption.

Modeling of Predator-Specific Deposition Probabilities

We applied an integrated tag recovery model based on detection/nondetection records to simultaneously estimate detection probability and deposition probability in a Bayesian context. Multiple deposition trials for a given avian species (tern, cormorant, or gull) were simultaneously analyzed to estimate trial-specific deposition probabilities and an overall predator-specific (i.e., bird species-specific) deposition probability.

Following the methods of Evans et al. (2012), we used logistic regression to model detection probability as a function of week:

$$c_{wjs} \sim \text{Binomial}(h_{wjs}, \psi_{wjs}),$$

$$\text{logit}(\psi_{wjs}) = \alpha_{js} + \beta_{js} \cdot wk_{wjs},$$

where c_{wjs} is the number of test tags recovered out of the number sown (h_{wjs}); ψ_{wjs} is the detection probability for colony s , year j , and week w ; α_{js} is the logit-scale regression intercept; wk_{wjs} is the covariate value (i.e., week number) for test tags sown on colony s in year j and week w ; and β_{js} the logit-scale estimate of change in detection for each unit change in wk at colony s in year j .

The probability of recovering a Rainbow Trout tag consumed during a deposition trial was then the product of two

probabilities: the probability that the tag was deposited (ϕ); and the probability that the tag was detected (ψ ; Figure 1).

$$l_{wjs} \sim \text{Binomial}(m_{wjs}, \phi_{wjs} \cdot \psi_{wjs}),$$

where l_{wjs} is the number of trout tags recovered out of the number consumed (m_{wjs}) during the deposition trial; and ϕ_{wjs} is the colony-, year-, and week-specific deposition probability. Trial-specific deposition probabilities were ascribed a hyperdistribution to estimate predator-specific deposition probabilities as part of the model:

$$\text{logit}(\phi_{wjs}) \sim \text{Normal}(\mu_{\phi}, \sigma_{\phi}^2),$$

where the hyperparameters μ_{ϕ} and σ_{ϕ}^2 describe the predator-specific deposition probability (μ_{ϕ}) and variance (σ_{ϕ}^2) on the logit scale. We back-transformed μ_{ϕ} , and hereafter we present the results on the probability scale. This process was repeated independently for terns (2004–2006), cormorants (2012–2013), and gulls (2012–2013).

Modeling of Predation Probabilities

Predation probabilities were modeled independently for each year j and colony s due to dispersed colony locations and high variability in colony size and steelhead availability (BRNW 2013; Adkins et al. 2014a). For simplicity, each parameter described below is only indexed by week (w), but the process was repeated independently across colonies (s) and years (j).

The probability of recovering an available in-river PIT-tagged steelhead is the product of all three probabilities—that the tagged steelhead was consumed (θ), that the tag was deposited on-colony (μ_{ϕ}), and that the tag was detected (ψ ; Figure 1):

$$k_w \sim \text{Binomial}(n_w, \theta_w \cdot \mu_{\phi} \cdot \psi_w),$$

where k_w is the number of PIT tags recovered from the number of PIT-tagged smolts available (n_w) in week w ; and θ_w is the predation probability in week w . Detection probability (ψ_w) data were available from test tags, and ψ_w was modeled as a logistic function of week as previously described. Predator-specific deposition probabilities μ_{ϕ} were available

from the previously described deposition studies. Specifically, an informative prior for μ_ϕ was applied across all years because μ_ϕ values were relatively consistent (see Results) and because empirical deposition data were unavailable for some years. Deposition probability priors were described by a beta prior distribution for terns (16.20, 6.55), cormorants (15.98, 15.29), and gulls (33.71, 183.61); these priors are methods-of-moments estimators for the μ_ϕ values described in the Results. Weekly predation probabilities for a given year and colony (θ_w) were considered random effects; this allowed each week to have a unique predation probability while sharing information among weeks to improve the precision of predation probability:

$$\text{logit}(\theta_w) \sim \text{Normal}(\mu_\theta, \sigma_\theta^2).$$

Estimating the annual proportion of tagged fish that are consumed by birds nesting at a specific colony has been the principal objective of many tag recovery studies focused on avian predation (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Evans et al. 2012; Sebring et al. 2013). We derived a comparable annual predation probability that was updated as part of the model. Specifically, the annual predation probability was determined as the sum of the estimated number of PIT-tagged steelhead consumed each week divided by the total number of tagged individuals available in that year:

$$\text{Annual predation probability} = \frac{\sum_{\text{all } w} (\theta_w \cdot n_w)}{\sum_{\text{all } w} (n_w)}.$$

Implementation

We implemented all models in a Bayesian framework by using the software JAGS (Plummer 2003) accessed through R version 3.0.1 (Su and Yajima 2013; R Development Core Team 2014). We ran three parallel chains for 50,000 iterations each, with a burn-in of 5,000 iterations. To reduce autocorrelation of successive Markov-chain Monte Carlo samples, the chains were thinned by 20, resulting in 6,750 saved iterations. Chain convergence was tested using the Gelman–Rubin statistic (\hat{R} ; Gelman et al. 2004), which is a measure of among-chain versus between-chain variance. Values of \hat{R} less than 1.1 indicate convergence; in our study, \hat{R} -values for all monitored parameters were less than 1.05. As previously described, informative priors were used for predator-specific deposition probabilities when estimating predation probabilities (see *Modeling of Predation Probabilities*). Noninformative priors were used for all other parameters. Specifically, we used independent Uniform(0, 1) priors for $\text{logit}^{-1}(\mu_\theta)$ and $\text{logit}^{-1}(\mu_\phi)$ (when originally estimating predator-specific deposition probabilities); Normal(0, 1,000) priors for logistic regression coefficients (α and β); and Uniform(0, 20) priors for the parameters

σ_ϕ and σ_θ . Several other diffuse priors were explored and found to have no effect on results. We report results as posterior medians as well as 2.5th and 97.5th percentiles for 95% credible intervals (CRIs), which represent the Bayesian equivalent of 95% confidence intervals.

Between-species differences in μ_ϕ were calculated during each Markov-chain Monte Carlo iteration (e.g., $\mu_{\phi, \text{tern}} - \mu_{\phi, \text{gull}}$). Differences were considered significant if the resulting 95% CRI of the difference did not overlap zero. Finally, minimum predation rates (sensu Evans et al. 2012) were also calculated by setting predator-specific deposition probabilities to 1.0. Therefore, we were able to perform a direct comparison of methods that integrate versus ignore predator-specific deposition probabilities.

RESULTS

Detection Probability

Annual colony-specific detection probability varied among colonies and among years (Table 2). At all colonies and in all years, median weekly detection probability increased with successive weeks, indicating that tags deposited later in the season were more likely to be recovered during postseason scanning efforts than tags deposited earlier in the season. Temporal trends in detection probability were significant for 28 of the 32 analyses (Table 2). In general, detection probability was most variable at colonies consisting of exposed bare sand substrates (Crescent Island tern and gull colonies). Nonsignificant temporal trends (4 of 32 comparisons; Table 2) were only observed at colonies with an increased complexity of nesting substrate (rocks and sand at the Miller Rocks gull colony; stick nests and sand at the East Sand Island cormorant colony).

Deposition Probability

The PIT tag deposition probabilities were highest for terns (0.71; 95% CRI = 0.51–0.89), followed by cormorants (0.51; 95% CRI = 0.34–0.70) and then gulls (0.15; 95% CRI = 0.11–0.21; Figure 3). The deposition probability for gulls was significantly lower than that for terns (difference = 0.56; 95% CRI = 0.35–0.74) or cormorants (difference = 0.35; 95% CRI = 0.17–0.55; Figure 3). Mean deposition probabilities were generally higher for terns than for cormorants, but there was noticeable overlap (difference = 0.21; 95% CRI = –0.06 to 0.44; Figure 3). Overall, the differences in deposition probability among bird species (Figure 3) were much larger than the differences among trials for a given species (Figure 4).

Caspian terns.—Trial-specific deposition probabilities for terns ($n = 7$ trials) ranged from 0.54 (95% CRI = 0.33–0.75) to 0.84 (95% CRI = 0.65–0.99; Figure 4a). Differences among trials were often small, and the trial-specific 95% CRIs consistently overlapped. There was no evidence of seasonal or annual trends in deposition probability. In general, deposition

TABLE 2. Range of median weekly detection probabilities (first week to last week) for PIT tags that were sown at avian colonies in the Columbia River basin. The total number of test tags sown (n) and the number of tag releases (r) per year are also shown. Significant temporal trends (i.e., 95% credible interval of the slope parameter did not overlap zero) are denoted by asterisks.

Colony location	Bird species	Year					
		2008	2009	2010	2011	2012	2013
Island 20	California gull						0.64–0.91* ($n = 150, r = 3$)
Crescent Island	Caspian tern	0.28–0.89* ($n = 800, r = 4$)	0.27–0.98* ($n = 400, r = 4$)	0.33–0.97* ($n = 400, r = 4$)	0.55–0.96* ($n = 200, r = 4$)	0.31–0.93* ($n = 200, r = 4$)	0.50–0.96* ($n = 200, r = 4$)
	California gull	0.54–0.95* ($n = 200, r = 2$)	0.59–0.85* ($n = 200, r = 2$)	0.68–0.89* ($n = 200, r = 2$)	0.53–0.84* ($n = 100, r = 2$)	0.43–0.96* ($n = 100, r = 2$)	0.52–0.89* ($n = 150, r = 3$)
Blalock Islands	California gull						0.72–0.90* ($n = 150, r = 3$)
Miller Rocks	California gull	0.82–0.84 ($n = 200, r = 2$)	0.68–0.88* ($n = 200, r = 2$)	0.60–0.92* ($n = 200, r = 2$)	0.71–0.87 ($n = 100, r = 2$)	0.67–0.92* ($n = 100, r = 2$)	0.73–0.91* ($n = 150, r = 3$)
	Caspian tern	0.84–0.97* ($n = 600, r = 4$)	0.84–0.95* ($n = 600, r = 4$)	0.60–0.93* ($n = 400, r = 4$)	0.66–0.85* ($n = 300, r = 3$)	0.44–0.92* ($n = 200, r = 2$)	0.39–0.72* ($n = 300, r = 3$)
East Sand Island	Double-crested cormorant	0.47–0.81* ($n = 400, r = 2$)	0.61–0.69 ($n = 600, r = 2$)	0.61–0.84* ($n = 400, r = 2$)	0.71–0.72 ($n = 400, r = 2$)	0.56–0.81* ($n = 200, r = 2$)	0.62–0.72* ($n = 400, r = 2$)

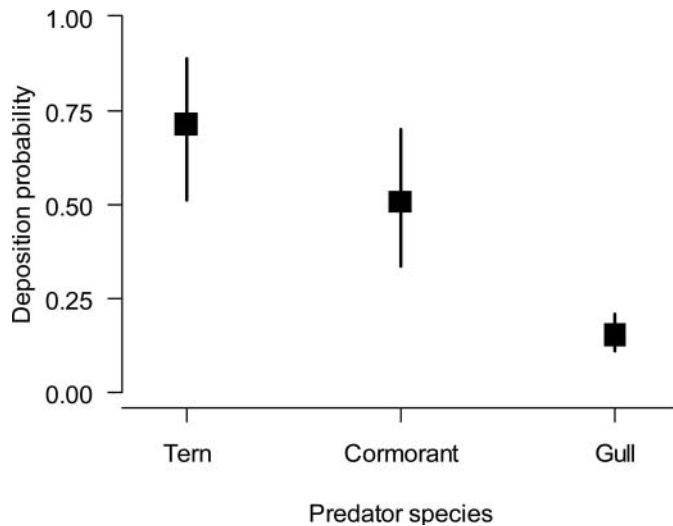


FIGURE 3. Median ($\pm 95\%$ credible interval) predator-specific tag deposition probabilities for Caspian terns (tern), double-crested cormorants (cormorant), and California gulls (gull).

probabilities were higher for the feeding studies than for the net-pen studies, but 95% CRIs were widely overlapping (Figure 4a). The mean PIT tag deposition probability for terns (0.71; 95% CRI = 0.51–0.89) indicated that about 71 of 100 consumed PIT tags were subsequently deposited on-colony.

Double-crested cormorants.—Trial-specific deposition probabilities for cormorants ($n = 6$ trials) ranged from 0.53 (95% CRI = 0.31–0.77) to 0.65 (95% CRI = 0.46–0.87; Figure 4b). As with terns, differences among trials were often small, and the trial-specific 95% CRIs consistently overlapped (Figure 4b). The mean PIT tag deposition probability for cormorants (0.51; 95% CRI = 0.34–0.70) indicated that about 51 of 100 consumed PIT tags were subsequently deposited on-colony.

California gulls.—Trial-specific deposition probabilities for gulls ($n = 18$) were consistently the lowest among the three bird species investigated (Figure 4c). Trial-specific deposition probabilities ranged from 0.08 (95% CRI = 0.03–0.14) to 0.35 (95% CRI = 0.25–0.46). Interannual differences were small, and trends were inconsistent across colonies. Late-season deposition probabilities at Miller Rocks were sometimes higher, but the 95% CRIs overlapped with multiple estimates from earlier in the season (Figure 4c). The mean PIT tag deposition probability (0.15; 95% CRI = 0.11–0.21) indicated that only about 15 of 100 PIT tags consumed by gulls were subsequently deposited on-colony.

Predation Probability

Predation probabilities varied by year, bird species, and colony location (Figure 5). The eight highest predation probabilities were all associated with cormorants and terns nesting at East Sand Island (Figure 5). In 2009, predation probabilities

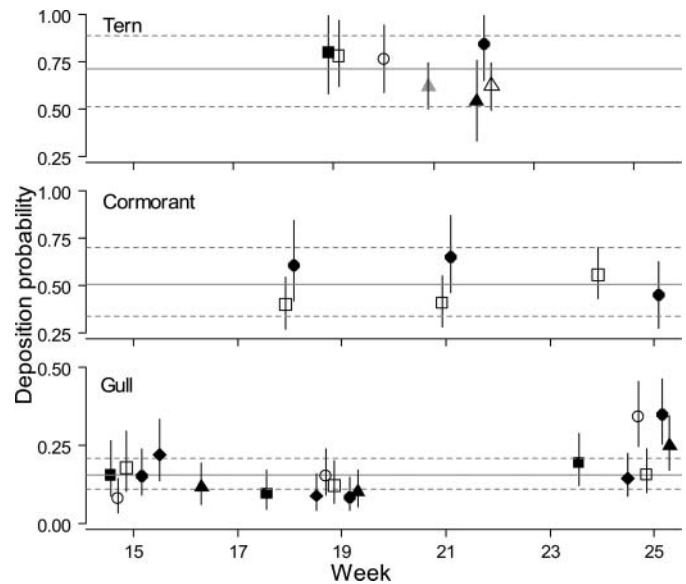


FIGURE 4. Trial-specific median ($\pm 95\%$ credible interval [CRI]) probabilities of PIT tag deposition on the nesting colony for three avian predator species: (top) Caspian terns in feeding trials at Crescent Island (squares) or East Sand Island (circles) and in net-pen trials at Crescent Island (triangles; gray shaded symbols = 2004; open symbols = 2005; black shaded symbols = 2006); (middle) double-crested cormorants in feeding trials at East Sand Island in 2012 (open squares) or 2013 (black shaded circles); and (bottom) California gulls in feeding trials at Crescent Island (squares), Miller Rocks (circles), Blalock Islands (triangles), or Island 20 (diamonds; open symbols = 2012; black shaded symbols = 2013). Horizontal lines denote the predator-specific deposition probability (solid line) and associated 95% CRI (dashed lines). Note the different y-axis scale for the bottom panel. See Table S.1 for trial-specific sample sizes.

for cormorants and terns nesting at East Sand Island were 0.17 (95% CRI = 0.12–0.26) and 0.15 (95% CRI = 0.12–0.22), respectively. Substantial interannual variation in predation probability was evident at these colonies. For instance, in 2013, the predation probability for cormorants nesting at East Sand Island was only 0.03 (95% CRI = 0.02–0.04), down from the high of 0.17 in 2009. Colony location was also associated with differences in predation probability, even if colonies were located in the same river reach. For instance, predation probability estimates associated with gulls nesting at Miller Rocks were often greater than 0.05, whereas gulls nesting at the Blalock Islands (in the same river reach) had one of the lowest predation probability estimates recorded in this study (0.01; 95% CRI = 0.01–0.02).

Integrating the predator-specific deposition probabilities increased the predation probabilities by a factor of approximately 1.4 for terns, 2.0 for cormorants, and 6.7 for gulls in comparison with minimum predation rates (Figure 5). As expected, minimum predation rates consistently underestimated actual predation. Predation probabilities were often significantly higher than minimum predation rates, with little to no overlap of 95% CRIs in many cases. Effects of integrating predator-specific deposition probabilities were most dramatic

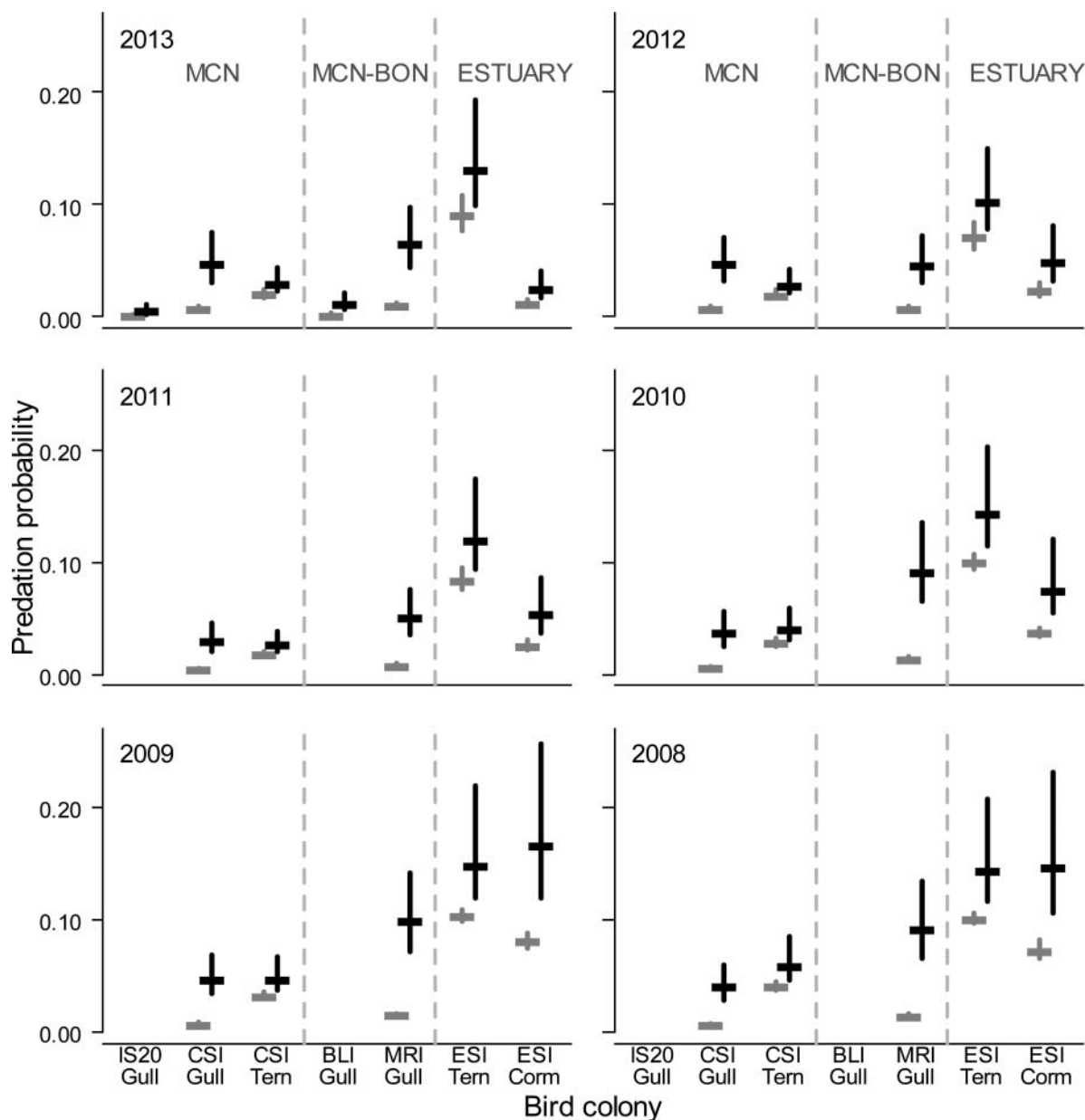


FIGURE 5. Predator-specific predation probabilities for Snake River steelhead that out-migrated in the Columbia River basin during 2008–2013. Predation probabilities were estimated by either integrating (black) or ignoring (gray) predator-specific tag deposition probabilities for Caspian terns, double-crested cormorants, and California gulls (avian colony locations: IS20 = Island 20; CSI = Crescent Island; BLI = Blalock Islands; MRI = Miller Rocks; ESI = East Sand Island). Vertical lines separate avian colonies located in different river reaches (upstream of McNary Dam [MCN]; McNary Dam to Bonneville Dam [MCN–BON]; or downstream of Bonneville Dam [ESTUARY]; see Figure 2). Tags were not recovered from the IS20 or BLI gull colonies prior to 2013.

for gulls due to their low deposition probability (median = 0.15; Figures 3, 5). For instance, the median probability of predation on Snake River steelhead by the Miller Rocks gull colony in 2009 increased from 0.01 to 0.10 after accounting for the gulls' tag deposition probability (Figure 5). Predation probabilities that were very close to zero, however, often remained negligible regardless of the low deposition probability. For example, in 2013, the minimum predation probabilities for Snake River steelhead by gulls nesting at either the

Blalock Islands or Island 20 were less than 0.01 but only increased to 0.01 after accounting for the deposition probability.

Once the predator-specific deposition probabilities were integrated, predation probabilities associated with some gull colonies were similar to or higher than the predation probabilities for tern and cormorant colonies (Figure 5). At Crescent Island, predation probabilities for gulls were similar to those for terns even though minimum predation rates by gulls were

much lower. Similarly, predation probabilities associated with gulls nesting at Miller Rocks were often greater than 0.05—substantially higher than values estimated based on minimum predation rates.

In this study, the precision (coefficient of variation [CV] = SD/mean) in predation probability was most affected by uncertainty in deposition probabilities. The CVs for minimum predation rate (i.e., with only detection probability being integrated) were consistently smaller than the CVs for predation probability (i.e., with both detection probability and deposition probability being integrated). In general, the predation probability CVs for terns and cormorants increased to a greater extent than those for gulls due to the greater uncertainty in deposition probabilities for terns and cormorants (Figures 3, 5). For instance, the predation probability CV for terns nesting at East Sand Island in 2008 was 6.4 times larger after deposition probability was integrated, whereas the predation probability CV for gulls nesting at Miller Rocks in the same year only increased by a factor of 2.3 after integration of deposition probability (Figure 5). Conversely, increasing the number of test tags used to estimate detection probability had a negligible effect on the predation probability CV. For instance, predation probability CVs for terns nesting at Crescent Island in 2008 and 2009 were similar at 0.16 and 0.17 even though 800 and 200 test tags, respectively, were used to estimate detection probability (Table 2; Figure 5). Similarly, the number of available PIT-tagged steelhead had negligible effects on the predation probability CV, as sample sizes in this study were often very large (range = 4,768–59,948; Table 3). Predation probability CVs for terns nesting at East Sand Island were 0.16 in 2010 and 0.18 in 2012 even though 40,024 and 4,768 tagged steelhead, respectively, were available (Table 3; Figure 5).

DISCUSSION

Approaches developed in this study considerably increase the applicability of tag recovery models to the estimation of avian predation probabilities in multiple-predator systems. An understanding of all three processes associated with fish tag

recovery on bird colonies (i.e., consumption, deposition, and detection) improves our ability to interpret tag recovery data and allows for direct comparisons of avian and non-avian mortality factors. Factor-specific mortality estimates representing the actual impacts of avian predation (rather than minimum predation estimates) provide important information for the development and assessment of recovery plans for fish species of conservation concern.

Tag recovery methods are commonly used to estimate avian predation on fish populations (Boström et al. 2009; Jepsen et al. 2010; Evans et al. 2011, 2012; Halfyard et al. 2012). Tag recovery studies, however, often only produce minimum estimates of avian predation. Predator-specific deposition probabilities provide vital information that is required to estimate actual predation impacts and to understand important predator–prey dynamics (Osterback et al. 2013; Scopettone et al. 2014). Our results build upon previous deposition studies focused on a single colony of western gulls (PIT tags; Osterback et al. 2013) and a single colony of American white pelicans *Pelecanus erythrorhynchos* (T-bar anchor tags; Scopettone et al. 2014) by quantifying deposition probabilities from four California gull colonies, two Caspian tern colonies (including the East Sand Island colony, which is the largest Caspian tern colony in the world; Suryan et al. 2004), and a double-crested cormorant colony (North America's largest such colony; BRNW 2013; Adkins et al. 2014b). Deposition probabilities were surprisingly consistent across multiple years and among colonies for a given bird species. The PIT tag deposition probabilities associated with California gulls (~0.15) were also similar to PIT tag deposition probabilities previously documented for western gulls in central California (~0.17; Osterback et al. 2013) but were consistently and substantially lower than the deposition probabilities for terns (~0.71) and cormorants (~0.51). Variation in deposition probabilities among avian species could be due to several factors, including the differential deposition of tags at off-colony locations or the differential destruction of tags during ingestion or egestion. Future studies that investigate predator-specific deposition probabilities for additional bird species, locations, or tag types (PIT tags, coded wire tags, acoustic tags, floy tags, etc.) will lead to an increased understanding of the mechanisms underlying differential deposition probabilities and will assist in improving the application of tag recovery models to estimate avian predation probabilities.

Incorporation of colony- and year-specific detection probability was important for the accurate estimation of deposition and predation probabilities. Similar to the study by Evans et al. (2012), our results indicated that the probability of recovering a PIT tag on a bird colony was often negatively associated with the amount of time (weeks) for which the tag was present on the colony. The strength of detection probability trends appeared to be associated with nesting substrate, as more variable detection probabilities were observed at colonies with exposed bare sand substrates (e.g., the Crescent

TABLE 3. Numbers of PIT-tagged Snake River steelhead smolts detected as passing dams upstream of avian colonies on the Snake and Columbia rivers (LMN = Lower Monumental Dam, lower Snake River; MCN = McNary Dam, mid-Columbia River; BON = Bonneville Dam, lower Columbia River).

Year	LMN	MCN	BON
2008	28,653	15,449	19,572
2009	52,220	29,877	23,311
2010	10,951	17,806	40,024
2011	59,948	16,759	7,028
2012	27,767	8,840	4,768
2013	11,958	9,391	8,516

Island tern and gull colonies) than at colonies with substrate complexity (e.g., the Miller Rocks gull colony and East Sand Island cormorant colony). The occasional lack of temporal trends at structurally complex colonies may be due to either increased retention of tags that are deposited earlier in the season (e.g., tags are not washed or blown off the colony) or decreased detection of tags that are deposited later in the season (e.g., increased tag interference; Evans et al. 2012). Whenever possible, researchers should verify assumptions about perfect or constant detection probability (Collis et al. 2001; Ryan et al. 2003; Maranto et al. 2010; Sebring et al. 2013) when the rate of tag loss as a function of date within the nesting season is unknown (Frechette et al. 2012; Osterback et al. 2013).

High predation impacts from strictly piscivorous avian predators (e.g., terns and cormorants) and from generalist avian predators (e.g., gulls) have been documented in multiple aquatic ecosystems (Mather 1998; Steinmetz et al. 2003; Koed et al. 2006; Evans et al. 2012; Osterback et al. 2013). Predation probabilities associated with some of the gull colonies in our study were much greater than previously published minimum predation rates for this species (Collis et al. 2001; Evans et al. 2012) and were similar to or greater than those of some tern and cormorant colonies where substantial predation has been documented (Collis et al. 2001; Roby et al. 2003; Evans et al. 2012; Sebring et al. 2013). Predation impacts associated with certain gull colonies were probably enhanced by their large colony size (Adkins et al. 2014a) and behavioral flexibility to exploit temporally available prey populations (Osterback et al. 2013). Predation impacts from gull colonies were highly variable, however, and often included some of the lowest colony-specific predation probabilities (≤ 0.01). Variation in colony size alone does not explain the differential predation probabilities associated with gull colonies. For instance, predation probabilities for gulls were often highest at the Miller Rocks colony, which has fewer breeding pairs than the gull colonies at Island 20 and Crescent Island (Adkins et al. 2014a). Overall, our results challenge long-standing generalizations regarding the impacts of generalist predators (e.g., gulls) on salmonid smolt survival in the Columbia River basin (Collis et al. 2001; Evans et al. 2012) and support the need to investigate both generalist and specialist predators when assessing food web dynamics (Sih 1998; Osterback et al. 2013).

Avian predation appears to be one of the primary sources of smolt mortality for multiple ESA-listed salmonid species in the Columbia River basin (Evans et al. 2012; Sebring et al. 2013; present study). Smolt mortality rates associated with particular avian colonies in this study were comparable to or higher than (1) mortality rates reported from local-scale predation by Northern Pikeminnow *Ptychocheilus oregonensis* (<0.01 to 0.11 per reservoir; Rieman et al. 1991; Ward et al. 1995) and (2) mortality rates associated with smolt passage at individual dams on the Columbia River and lower Snake River (<0.01 to 0.07 per dam; Muir et al. 2001; Ferguson et al.

2006; Skalski et al. 2009). The ability to directly compare avian and non-avian sources of smolt mortality has important management implications and would not have been possible without a comprehensive effort to document predator-specific deposition probabilities.

Quantification of mortality factors is a major challenge in conservation biology (Williams et al. 2002). Data collection methods and modeling approaches applied herein provide an important framework for studies investigating avian predation on fish stocks. Avian predation was a major source of mortality in a 6-year study of ESA-listed Snake River steelhead. Our results support previous findings of relatively high predation rates by birds nesting at colonies in the Columbia River estuary, but our findings also revealed predation rates by an omnivorous avian predator (California gull) that were higher than previously documented (Collis et al. 2001; Ryan et al. 2003; Evans et al. 2012). Efforts to evaluate predation probabilities for other ESA-listed fish species and to validate deposition probabilities across multiple bird colonies, years, and tag types will provide important information for management and research efforts. We strongly recommend that future studies incorporate both tag deposition and tag detection processes when estimating avian predation probabilities by using tag recovery methods. Excluding either of these observational processes will likely lead to a survey program with unreliable estimates of avian predation impacts on fish populations.

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