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Comparison of Research Findings on Avian Predation Impacts on Salmon Survival

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Comparison of Research Findings on Avian Predation Impacts on Salmon Survival

Executive Summary

This ISAB report evaluates similarities and differences in data, analytical approaches, conclusions, and management implications of two studies of avian predation on juvenile steelhead in the Columbia River Basin. Both studies focused on determining whether the effects of avian predation on overall survival were additive (meaning that the predation reduces overall survival) or compensatory (meaning that other aspects of mortality offset or compensate for predation). Haeseker et al. (2020) focused on bird predation in the Columbia River estuary of migrating smolts from the Snake River Basin and its effect on survivorship (return probability) of adults returning to Bonneville Dam. Haeseker et al. concluded that mortality from avian predation was consistent with full compensation. In contrast, Payton et al. (2020) estimated the effects of bird predation both in the river and in the estuary on Upper Columbia Basin smolts at two life stages: from release at Rock Island Dam to Bonneville Dam as smolts and from release to adult return to Bonneville Dam. Payton et al. concluded that predation mortality was super-additive for smolts between Rock Island and Bonneville, and partially additive from release to adult return to Bonneville Dam. Super-additive means causing more smolts to die than the number of smolts estimated to be consumed by bird predators. Sources for additional undetected mortality include deposition of PIT tags at locations other than the colony, smolts being stolen by gulls, wounding or injury that results in mortality but not capture by the predator, or consumption by birds that occupy areas other than the colonies monitored for PIT tags.

Both studies relied on data from PIT-tagged smolts, detections of survivors at distinct points in the hydrosystem, and mark-recapture models to estimate survival to a given life stage. Bird predation was estimated from PIT-tags recovered from nesting colonies of Caspian terns and double-crested cormorants at East Sand Island (in both studies) and bird colonies, including gull species, located upstream of Bonneville Dam (in Payton et al. 2020). While the studies were conducted in different basins and employed only partially overlapping time series, we compared data and analyses from migration to adult return life stage to illuminate the nature of conclusions and interpretations.

There are important differences in definitions and underlying models used to distinguish additivity and compensation that could partly account for differences in conclusions between the studies. Haeseker et al. (2020) used a correlation-based criterion to define and model additivity and compensation, with full additivity or full compensation as strict theoretical limits

of the analysis and partial additivity between these two limits. Payton et al. (2020) used a regression-based definition and a model that also defines full additivity, full compensation, and partial additivity, but also allowed for over-compensation and super-additivity as theoretical possibilities that exceed the limits used by Haeseker et al. The analysis by Haeseker et al. de-emphasized the distinction between partial and full additivity, instead interpreting a significant negative correlation between survival and bird predation as indicating additivity (partial or full) and an observed lack of correlation as consistent with full compensation.

The ISAB review responded to the following questions:

1. Were the Haeseker et al. 2020 and Payton et al. 2020 analyses scientifically sound, and were the data used appropriate for addressing the question?

Compared with all other species and populations of salmonids in the Columbia Basin, steelhead smolts are most vulnerable to avian predation (Roby et al. 2021). Accordingly, both studies focused on steelhead. Both studies used reasonable approaches to assess mortality imposed on steelhead from bird predation. Each analysis has a lengthy list of assumptions (some explicit, others implicit, and discussed or not). Both studies attempted to test complicated hypotheses with analysis of a complex dataset from tagging studies that were not designed specifically for this purpose. Differences in annual mortality and tag recovery were identified across tagging and release locations, but the ISAB found no evidence of significant bias in the context of analysis across steelhead cohorts within years. Nonetheless, both studies demonstrate that tagging data can be adapted for the important purpose of assessing effects of predators at multiple sites in the Columbia Basin.

2. Were the conclusions drawn by Haeseker et al. 2020 and Payton et al. 2020 analyses supported by their results?

In general, the conclusions of both studies are reasonably supported within the context of their different model frameworks and definitions. Analytical differences between studies were substantive, but these were not a result of variation in data quality or analysis. Differences in conclusions, namely full compensation (Haeseker et al.) vs. partial additivity (Payton et al.) in smolt-to-adult survival, could result from differences in statistical power between approaches, differences in the definitions of additivity and compensation, differences in stocks studied, or differences in the portion of the life cycle included within each analysis.

3. How do the modeling approaches of Haeseker et al. 2020 and Payton et al. 2020 differ, and do these analytical differences or other reasons account for the contrasts in their conclusions?

The ISAB report highlights the following key differences between studies that could affect differences in conclusions:

- Differences between models: Definitions, underlying models, and the theoretical bounds imposed on additivity and compensation differed substantively between studies as outlined above. In addition, models differed in how estimates of survival and predation were accounted for in statistical models. Haeseker et al. estimated the correlation of survival and predation across cohorts in all years combined, but Payton et al. estimated an additivity parameter across cohorts within each year and included random year effects in their model. Haeseker et al. included environmental covariates in their model and Payton et al. did not.
- Populations considered: Haeseker et al. analyzed Snake River steelhead, whereas Payton et al. analyzed Upper Columbia River steelhead. Population and predation levels could vary across watersheds, and this may affect estimates of correlations or regression slopes. However, Payton et al. 2021 analyzed Snake River steelhead for both basins.
- Time period of observations: The time series only partially overlap. Haeseker et al. examined smolt-to-adult returns (SAR) for smolts from 2000 to 2015; Payton et al. examined in-river survival for smolts from 2008 to 2018, and SAR from 2008 to 2016. Population and predation levels vary from year to year, and this may affect estimates of correlations or regression slopes.
- Life-cycle domain: Payton et al. evaluated avian predation relative to both in-river smolt survival (Rock Island Dam [RIS] to Bonneville Dam [BON]) and SAR (RIS smolts to BON adult returns), whereas Haeseker et al. only evaluated predation effects on SAR (BON smolts to BON adults).

4. Does the ISAB have recommendations to improve the analysis?

The ISAB recommends the following approaches to improve analyses of avian predation effects on steelhead and salmon:

- Conduct a side-by-side analysis employing both modeling approaches on the same dataset(s) with the goal of understanding differences in statistical power, potential for bias, and robustness to violations of model assumptions.
- Include possible effects of ecological interactions among bird predators. Competition, interference, or synergisms among predators could play a role in determining total mortality and might modify the conclusions regarding additivity or compensation on local scales.
- Evaluate assumptions underlying estimation of baseline survival (i.e., survival in the absence of avian predation) and explore use of environmental covariates in the Payton et al. model.
- Evaluate effects of possible bias associated with tagging and release localities, especially across cohorts within years.

- Incorporate avian predation results into models that account for harvest and other factors associated with salmon survival over the entire life cycle. Suppression of avian predators is one of a number of management actions that can be used to increase in-river survival and SARs. Inclusion of observed predation risks into life-cycle models could help identify what combination of management actions make the most impact on steelhead survival.
- Encourage the use of comparable metrics with clear management implications as analysis endpoints, including equivalence-factor metrics and a change in population growth rate metric (ISAB 2016-1).

5. What are the management implications of the results?

There appears to be strong additivity of predation during smolt migration (Payton et al.), but mortality during the estuarine/marine phase is either largely (Payton et al.) or fully (Haeseker et al.) compensatory. Results of both studies are consistent with the possibility of low-level partial additivity of predation effects on SAR, although the Haeseker et al. results are also consistent with full compensation over this part of the life cycle. For populations at risk, avian predation that is partially additive could affect population sustainability. If no further analyses were possible, the most prudent conclusion from a management perspective would be that avian predation is partially additive. Additional studies are needed to fully evaluate the relative importance of avian predation in a population conservation context, perhaps best employed in a life-cycle model that accounts for environmental variation at different life stages. Avian predators exert a greater negative impact on steelhead survival than on other Columbia Basin salmonids (Payton et al. 2021), but inclusion of avian predation risk might improve life-cycle modeling efforts for other salmonid species as well.

A major question for management is whether an increase in SARs is worth the cost of suppressing avian predators or is critical to the support of ESA-listed salmonid species. Answering these questions requires estimates of the magnitude of avian predation effects rather than estimates of the degree of additivity or compensation and also requires consideration of social concerns, cost effectiveness, and ecosystem consequences of avian control actions (ISAB 2019-1). Reconciling results from these studies in a side-by-side analysis, evaluating additional methods for obtaining predation effect size from tagging data, and incorporating these into life cycle models for different species and populations of salmonids are the next steps toward understanding how avian predation fits into broader management strategies and goals for Columbia Basin salmonids. Until these steps can be implemented, the ISAB recommends that the finding of partial additivity/partial compensation over the entire life cycle of steelhead is the most prudent conclusion from a management perspective.

Background

Columbia Basin fish and wildlife managers, policy makers, and researchers have expressed concern about differences in the conclusions and management implications of the following two publications on Columbia River Basin Steelhead Trout (*Oncorhynchus mykiss*): *Avian predation on steelhead is consistent with compensatory mortality* (Haeseker et al. 2020) and *Measuring the additive effects of predation on prey survival across spatial scales* (Payton et. al 2020).

Significant questions remain about the extent to which avian predation is additive or compensatory. At their extremes, (completely) *additive* means that changes in predation are reflected one-to-one in changes in the overall survival, whereas (completely) *compensatory* means that other life cycle factors operate to negate or counteract the effects of predation so that long-term survival is unaffected by the predation in question. More often in nature, mixtures of additivity and compensation are observed rather than the extremes of complete additivity or compensation (Haeseker et al. 2020; Payton et. al 2020). Results of analyses examining compensatory versus additivity in survival, such as the Haeseker et al. and Payton et al. papers, can strongly affect decisions about future regional management actions designed to reduce avian fish predators (i.e., hazing, re-locating, culling, etc.). For example, Haeseker et al. (2020) concluded that avian predation is fully compensatory and that "[m]anagement efforts to reduce the abundance of the bird colonies are unlikely to improve the survival or conservation status of steelhead…" The contrasting conclusion of Payton et al. (2020) that Caspian tern predation is either a completely or partially additive source of mortality would provide evidence that active avian predator management could increase survival of steelhead and salmon.

The Columbia River Inter-Tribal Fish Commission asked the ISAB to review and compare the Haeseker et al. (2020) and Payton et al. (2020) analyses, results, and interpretations in the context of the *Avian Predation Synthesis Report* that was compiled by Real Time Research for the U.S. Army Corps of Engineers. The synthesis report summarizes available information on avian predation on salmonids in the Columbia River Basin.

Summary of Haeseker et al (2020) and Payton et al. (2020)

To avoid repetition of general information across the five questions assigned to the ISAB, we first summarize the two approaches, data sets, and methods, noting their similarities and differences.

The purpose of these two studies was to estimate avian predation probabilities on juvenile steelhead in the Columbia Basin and to evaluate whether that predation has had an additive effect on overall survival or if other ecological processes compensate for it. If predation mortality has a direct inverse relationship with overall survival (i.e., the reduction in survival is equal to the increase in predation mortality) its effect is said to be additive; if there is no relationship between the two, the effect is said to be compensatory. Additivity and compensation occur along a continuum in which the relative importance of one decreases as the importance of the other increases. Payton et al. (2020) use a definition in which the terms (degree of compensation versus additivity) are subdivided into five categories defined by an additivity parameter a defined as the proportionate reduction in prey survival associated with increases in predation (Table 1).

Similar categories can be defined based on the sign of the correlation between survival and predation (Haeseker et al. 2020), where a zero correlation ($\rho = 0$) means full compensation while a negative correlation ($\rho < 0$) indicates some degree of additivity. Haeseker et al. 2020 consider positive correlations ($\rho > 0$) to be "biologically implausible" (Table 1). Note that the two parameters (a and ρ) are defined with opposite signs — this can lead to confusion in interpretation. The two models of additivity are not interconvertible except at the zero value, as the correlation does not include the magnitude of the slope, only its sign, so that a negative correlation does not distinguish among partial, full, and super-additivity. That the two studies use different definitions of these fundamental terms can lead to confusion in interpreting the results. The underlying biological models leading to these definitions are explained and compared in Appendix A.

Both Haeseker et al (2020) and Payton et al. (2020) used PIT-tag mark-recapture-recovery time series, which is arguably the best type of data for this type of analysis. They also used similar methods to estimate probabilities of detection of PIT-tags from consumed fish deposited in nesting colonies of avian predators, converted those to estimates of avian predation by bird species and colony (Hostetter et al. 2015), and used similar models to estimate survival between various points in the steelhead life cycle. However, they differed in many other aspects including the study domain and modeling approaches. Table 1 summarizes the main differences between the two studies.

In addition to these two studies, we also considered analyses in Chapter 8 (Payton et al. 2021) of the Avian Predation Synthesis Report prepared for the US Army Corps of Engineers, Bonneville Power Administration, and other agencies, which applied the approach described in Payton et al. (2020) to other populations and species. Results of analyses are reported for upper Columbia River steelhead, Snake River yearling and sub-yearling Chinook salmon, upper Columbia River yearling Chinook salmon, and Snake River Sockeye salmon; however, the chapter does not describe the analyses in detail.

Table 1. Summary of the approach and methods of Haeseker et al (2020) and Payton et al. (2020).

	Haeseker et al. (2020)	**Payton et al. (2020)**
Definitions of Compensatory and Additive Mortality in terms of Model Parameters	Correlation (ρ), where $\rho = 0$: compensatory mortality; $\rho < 0$: additive mortality; $\rho > 0$: "biologically implausible"	Slope (a), where $a < 0$: over-compensatory; $a = 0$: compensatory mortality; $0 < a < 1$: partial additivity; $a = 1$: additive mortality; $a > 1$: super additivity
Study Domain		
Steelhead Population	Snake River	Upper Columbia River
Time Span	2000-2015 (16 years)	2008-2018 (11 years)
Time Subdivisions	6 biweekly cohorts per year	9 to 11 weekly cohorts per year
Life Cycle Domain	1) Estuary/Ocean: 2) Smolts at BON to Adults at BON	1) In-River: Smolts at RIS to Smolts at BON 2) In-River/Estuary/Ocean: Smolts at RIS to adults at BON
Predators	Caspian terns; Double-crested cormorants	Caspian terns; Other (gulls, cormorants)
Predator Colonies	East Sand Island (ESI)	8 colonies for terns; 7 for other species
Statistical Model	Process correlation model; Aggregating data across cohorts and years; Included environmental covariates	Estimated a and the difference between survival with and without predation (Φ^{Δ}) for each cohort within a year
Model of Survival Components	Independent binomial probabilities for predation and total survival	Multinomial "life-path" probabilities; constrains components to sum to one
Tag Detection Probabilities on Colonies	Methods of Hostetter et al. (2015)	Methods of Hostetter et al. (2015)
Environmental Correlates to Survival	Water transit time, Arrival date at Bonneville, PDO, Winter ichthyoplankton biomass	None

Study Domain and Data

The two studies differ in the spatial and temporal scope of evaluation of avian predation and survival and in the data sets used. Haeseker et al. examined data for Snake River steelhead spanning 16 years of smolt outmigration (2000 - 2015). Within each year, they subdivided outmigrants into 6 two-week cohorts based on their date of migration through Bonneville Dam (BON) and used these to estimate cohort-specific estimates of predation and survival. Their data set included all Snake River PIT-tagged steelhead that were detected at BON, which included hatchery wild steelhead tagged as either parr or smolts. Predation was estimated separately for two predators (Caspian terns and double-crested cormorants) at breeding colonies on East Sand Island in the Columbia River estuary. Estimates of survival spanned the estuary and ocean life-history stages and were based on adults returning to BON (with some adjustment for incomplete sampling at Bonneville based on returns to Lower Granite Dam) divided by smolts at BON. Effects of avian predation on juveniles upstream of Bonneville dam were not analyzed. In this calculation of survival, they assumed all survival variation occurred during the first year in the ocean and there is a constant mortality for the second year in the ocean.

Payton et al. (2020) examined data for upper Columbia River steelhead spanning 11 smolt years (2008-2018). Within each year, they subdivided outmigrants into 9 to 11 weekly cohorts based on their date of passage at Rock Island Dam (RIS). They used steelhead smolts randomly selected from the total number passing RIS that were tagged there. Their estimates of predation and survival considered two overlapping life-history domains: in-river, spanning smolt outmigration from RIS to BON (with additional detections from estuarine pair-trawl sampling), and smolt-to-adult, spanning from RIS smolts to returning adults at BON. For each of these domains, they estimated survival and predation separately for each of two sets of predators: Caspian terns and other birds (including double-crested cormorants and two gull species). They based predation estimates on tags recovered at several breeding colonies (8 colonies for Caspian terns, 7 colonies for other birds), using only data for colonies above BON for the in-river domain, and adding lower river and estuary colonies for the smolt-to-adult domain. Sources for undetected predation-related mortality include deposition of PIT tags at locations other than the colony, smolts being stolen by gulls, wounding or injury that results in mortality but not capture by the predator, or consumption by birds that occupy areas other than the colonies monitored for PIT tags. The smolt-to-adult analysis used 8 years of data, as complete adult returns were not yet available for smolt years beyond 2015.

Modeling Approaches

Both studies use similar underlying models to describe the relationship between overall survival and predation (see Appendix A). Both studies employ Bayesian random-effects estimation models based on PIT tag capture-recapture-return data and include component submodels for predation, survival, and the relationship between the two. Both fit component models simultaneously using Markov Chain Monte Carlo (MCMC) methods that iteratively approximate the Bayesian posterior distributions of model parameters based on component submodels and assumed prior information about the parameters. Both also use similar sampling models to describe the relationship between predation and tag detections on bird colonies based on three processes: predation, deposition, and detection (Hostetter et al. 2015). Beyond these similarities, the details of their statistical models differ.

Haeseker et al. (2020) used independent submodels to estimate predation and overall survival. They estimated predation using the observed number of tags detected on the East Sand Island colonies, adjusted for detection and deposition probabilities. The estimated predation probability for a cohort is a simple ratio of adjusted recoveries on the colonies and number of smolts in the release group. Predation by the two bird species (terns and cormorants) were evaluated separately, and estimates were assumed to be independent for each cohort in each year, though this assumption of independence was not investigated. They estimated survival as the number of tagged adults returning to BON over two years as a fraction of the tagged smolts leaving BON (less than 0.5% returned after three years and were not included in the analysis). Their estimate of survival does not partition mortality into various components; all sources of mortality are aggregated. Estimates of survival and predation were combined to estimate their correlation via a Bayesian random effects model. To compensate for non-predation sources of variation in survival, this model also incorporated four environmental variables (date of smolt passage at BON, cohort-averaged flow at BON, mean summer Pacific Decadal Oscillation [PDO], and an index of winter marine ichthyoplankton biomass) in a regression of logit-transformed survival. Date and flow variables were cohort-specific, while PDO and ichthyoplankton indices were annual.

Payton et al. (2020) estimated survival, predation, and baseline survival simultaneously using a multinomial model (Payton et al. 2019) that ensures that all constraints on model parameters are met. The joint likelihood for survival and the components of mortality contains terms estimated using detections that are similar to a classic Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992). Unlike Haeseker et al., estimates of avian predation were constrained in a multinomial model with other mortality components. Weekly estimates of survival and mortality were “smoothed” by assuming a random walk across weekly period within a year, unlike Haeseker et al., where values for biweekly cohorts were assumed to be independent.

Most importantly, definitions of categories used to assess additivity and compensation differed between the two studies. As noted above, Haeseker et al. (2020) used a correlation-based definition of additivity/compensation that considers full compensation and full additivity to be the most extreme possible states, while Payton et al. used a regression-based definition that describes five levels including super-additivity and over-compensation.

Haeseker et al. (2020) focused on estimating the correlation between predation and survival. To do this, they used temporal subdivisions that produce 16 years x 5-6 biweekly periods/year or around 80-90 estimates of survival and predation (see their Figures 4 and 5). They used a multi-variate normal distribution model for the joint distribution of the logit-transformed survival and predation probabilities to estimate overall (across all years and cohorts within years) means, variances, and correlation of the transformed survival and predation probabilities. They analyzed each predator species separately and thus have independent analyses for terns and cormorants.

Payton et al. (2020) focused on estimating the slope of a regression relationship between survival and predation. Their model produces about 90 pairs of estimates of survival and predation by birds. Rather than using a simple straight-line relationship between the two values, they use a piecewise model that reflects constraints of the relationship (see their Equation 3 and Figure 1). They perform two independent analyses of overlapping life-history domains (smolts at RIS to either smolts at BON or to adults returning to BON).

Detailed Responses to the Assigned Questions

1. Were the Haeseker et al. 2020 and Payton et al. 2020 analyses scientifically sound, and were the data used appropriate for addressing the question?

Both studies used similar data and statistical methods, as described above. The fundamental approach used by both studies should be scientifically sound for estimating predation mortality and for evaluating whether that mortality is additive or compensatory. When viewed separately, the two analyses can each be considered as reasonable approaches to assessing the type of mortality imposed on steelhead from bird predation. Each analysis has a long list of assumptions (explicit, implicit, and discussed or not). Both analyses attempted to test a complicated hypothesis with analysis of a complex dataset from tagging studies that were not designed specifically for this purpose. The idea of quantitatively combining PIT-tag survival with bird predation is important and, if done appropriately, the two alternative analyses can be used to infer conclusions likely stronger than either single analysis. With some coordination, this could be viewed as a multi-model analysis that is commonly used in other fields (e.g., climate change).

Haeseker et al. (2020) examined the effects of predation by Caspian Terns and Double-crested Cormorants in the estuary on Snake River steelhead SARs (defined as survival from smolts at Bonneville Dam [BON] to adult returns at BON). As noted above, they used a correlation-based definition of additivity and compensation, which limits the analysis to distinguishing only full compensation versus the presence of some degree of additivity. They provided only a general description of the model used and do not provide details of the likelihood equations and implementation of the model, which makes it difficult to fully assess the reliability of the analysis. While they cite Otis and White (2004) as the basis for their methods, it is not clear how closely they followed those methods.

Because estimates of survival and estimates of predation are in independent submodels, it is possible for sampling artefacts to occur. These could arise as inconsistencies between components of mortality (e.g., adding to more than 1) for a bi-weekly cohort because information is not shared across models. However, this is unlikely to occur given the low total survivals (SARs) observed in this study.

There is also a potential problem in the Haeseker et al. analysis that used multiple cohorts in a year. In the final analysis, all cohorts within a year and across years are combined into a single estimate of the correlation coefficient, which could introduce issues with non-independence of observations across the time series. The real question is if the measurements within a year are correlated after adjusting for other factors. Correlation induced by year effects can be addressed by including a random year effect or by including other variables that fully account for year effects.

Both studies depended on adequate contrast in predation probabilities and survival probabilities. In Haeseker et al., there was little contrast in cormorant predation or steelhead survival across multiple years (see Fig. 4 in Haeseker et al., reproduced as Fig. 1 here). Rather, most of the contrast was within years, with substantial contrast in survival for 9 of the 16 years of record (based on visual inspection). The generally low survival probabilities and low contrasts in predation across years make it difficult to detect correlations, which could lead to the potential of a false conclusion of no effect (false negative) that would be interpreted as total compensation.

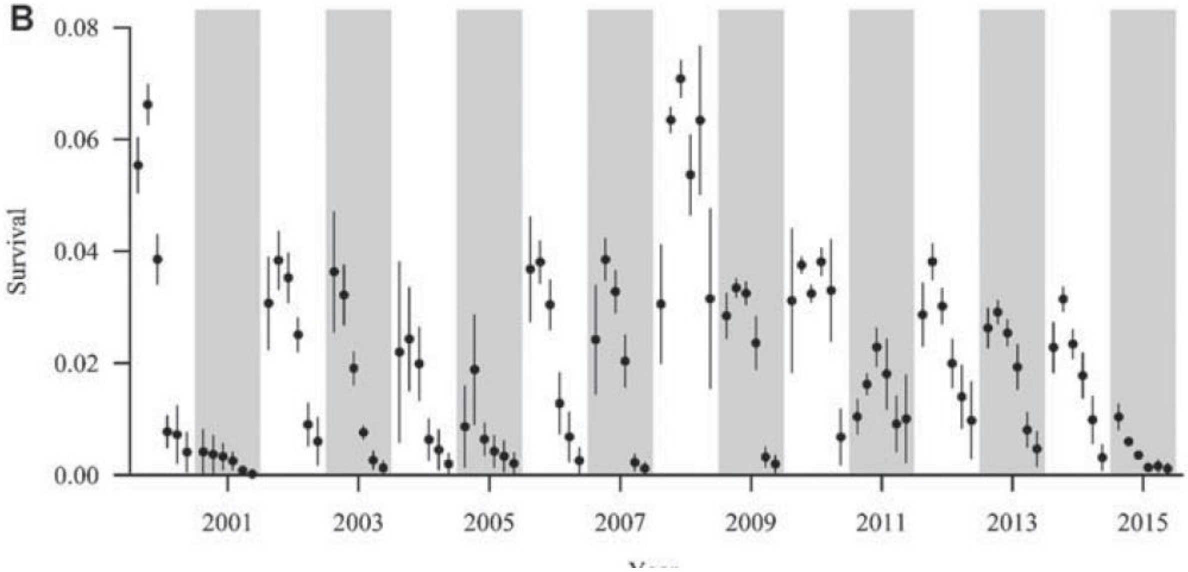


Figure 1. Estimated survival rates (±SE) for steelhead cohorts from the Snake River Basin, USA, 2000–2015 (Figure 4B in Haeseker et al. [2020]).

Conversely, smolt-to-adult return probabilities across cohorts within years decrease as a function of tern predation probability in many years (Fig. 2; illustration from Fig. 8.S3 in Payton et al. 2021). These relationships are not apparent when data are combined across years (last panel in Fig. 2). The combined data are consistent with full compensation, whereas data partitioned by year are indicative of partial additivity for some years. These observations raise concerns about whether there is sufficient statistical power to detect additivity when data are combined across years. It should be noted that weak contrasts are present in datasets used in both Haeseker et al. (2020) and Payton et al. (2020). The difference is that low-value contrasts are subsumed in total variance in the Haeseker et al. model, whereas low contrasts in individual years are observed in the Payton et al. analysis. The intensity of avian predation varies by year, population, and river.

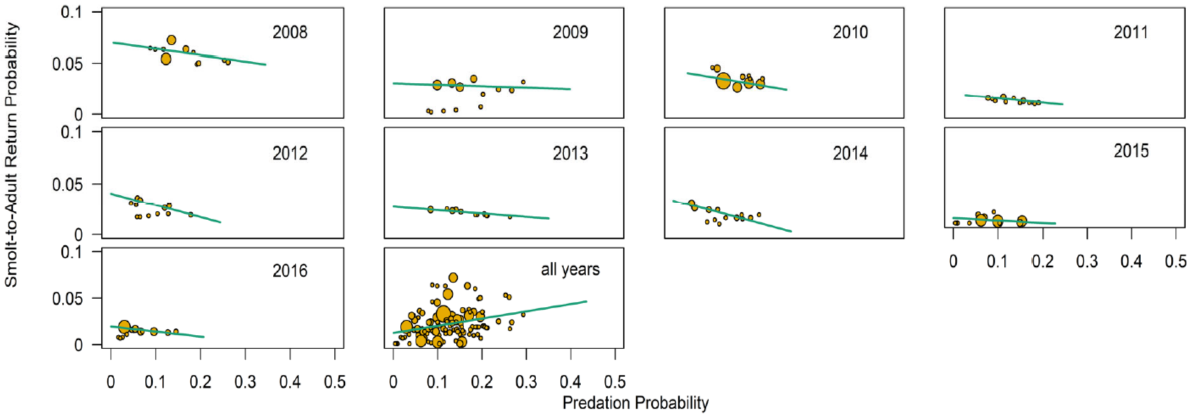


Figure 2. Weekly smolt-to-adult survival probabilities to Bonneville Dam for Snake River steelhead as a function of Caspian tern predation probabilities in the Columbia River estuary in each year from 2008 to 2016 and all years combined (Figure 8.S3 in Payton et al. 2021). The size of the circles depicts the relative number of PIT-tagged steelhead smolts available passing Bonneville Dam. Blue lines represent simple weighted least-squares regression lines among the estimates.

In their estimation model, Haeseker et al. included a set of environmental covariates to explain part of the variation in ocean mortality. By including these covariates, they reduced the proportion of unexplained variation in survival in their model, which should make any correlations with predation mortality easier to detect. However, this leads to a philosophical quandary about causality and statistics. If these covariates are in reality causally linked to marine survival, then accounting for them in the analysis produces a legitimate reduction in the residual variation and produces a more precise analysis of the correlations. On the other hand, if they are not causally linked, then the reduction in variation is essentially spurious, and the estimated correlations will appear to be more precise than they are in reality. Thus, the analysis can only be properly interpreted conditionally on the acceptance of a model with selected covariates. The "best" model selected includes date of smolt detection at BON, river flow, and winter marine ichthyoplankton biomass as covariates. Of these, date and flow are the most likely to have causal links, while the biological justification for causality for ichthyoplankton is suspect as this is an index of coastal conditions, whereas steelhead spend very little of their marine life history in coastal waters (Daly et al. 2014). In any event, model selection with multiple environmental covariates can overfit the models and lead to selecting covariates with ephemeral relationships. In other words, variables selected depend strongly on the time period of the analysis, with relationships that may appear to shift over time (Walters 1987; Litzow et al. 2019; Wainwright 2021).

Payton et al. (2020) examined the effects of predation by Caspian Terns and "other" birds both above and below Bonneville Dam on Columbia River steelhead over two life-stage scales: in-river (survival of smolts from Rock Island Dam [RIS] to BON), and SARs (survival from RIS to adult returns at BON). They used the slope-based definition of additivity and compensation, which allows them to estimate degrees of additivity and compensation, not just presence or absence. Because of this, they can estimate the full range of possible relationships from over-compensation to super-additivity. Overall, the data, the model structure, and its implementation are well described, but the model is complicated, and it is difficult to assess all the assumptions that may affect results.

Analysis of avian predation requires sufficient sample sizes to detect additivity or compensation. Low returns are a problem with both studies, but it is especially acute in Payton et al. (2020), especially later in the time series, because they analyze within-year patterns of survival. Sample size is a major limitation for analysis of adult returns, which are very low (including zero) in several years. This can lead to wide confidence intervals in results, but also may lead to problems in interpretation of slopes in those years. The hierarchical model “shares” data across years, which means years with higher returns could influence the slope estimates in poor data years.

Payton et al. appears to show a consistent correlation between tern predation probability and annual survival probability over the RIS-BON outmigration segment, perhaps because of correlations induced by estimating both variables within the same multinomial model (Fig. 3). For example, results from 2017 may be an artefact of the hierarchical structure imposed on the *a* term so that a few years with a strong correlation “impose” it on the rest of the years (albeit with a wider CI). The single high point in 2016 is also an outlier, and it would be worthwhile to explore the reasons for that point. Figure 4 appears to show some relationship between tern predation probability and SAR, although it is weaker than the relationship in the in-river analysis. Some cohorts within a year are very flat (e.g., 2015) because virtually no adults returned. Again, the hierarchical structure shares information across years, making it difficult to evaluate individual year effects. The ISAB recommends that Payton et al. evaluate assumptions and modeling of baseline survival.

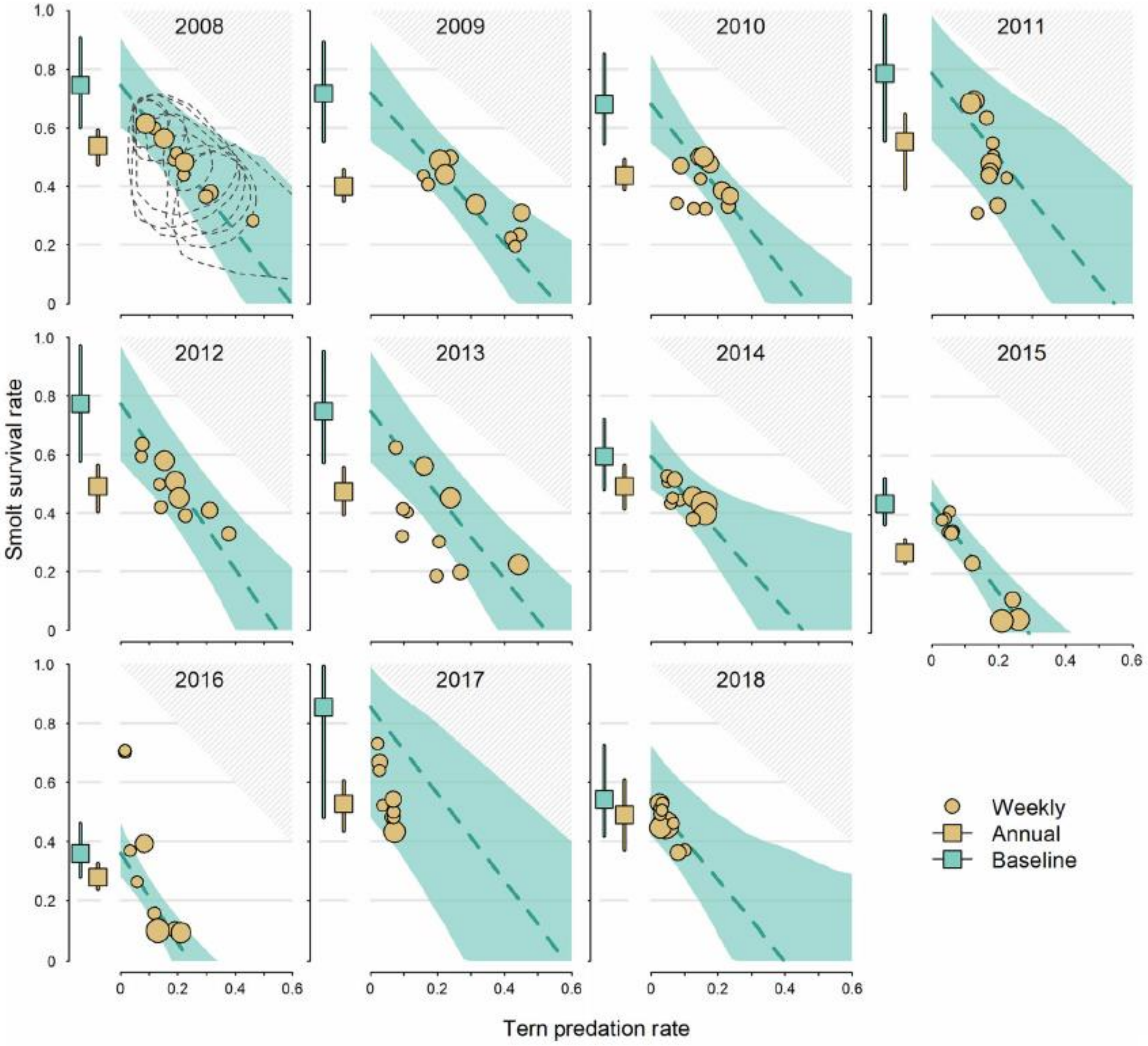


Figure 3. Weekly probability estimates of steelhead smolt survival and Caspian Tern predation along with the estimated annual relationships between survival and predation during out-migration from Rock Island Dam to Bonneville Dam (Figure 3 in Payton et al. [2020]). The size of light brown circles depicts relative numbers of steelhead smolts tagged and released each week at Rock Island Dam. Approximate 95% credible regions are depicted for joint survival and predation estimates in 2008 to demonstrate uncertainty, and error bars denote 95% CRI.

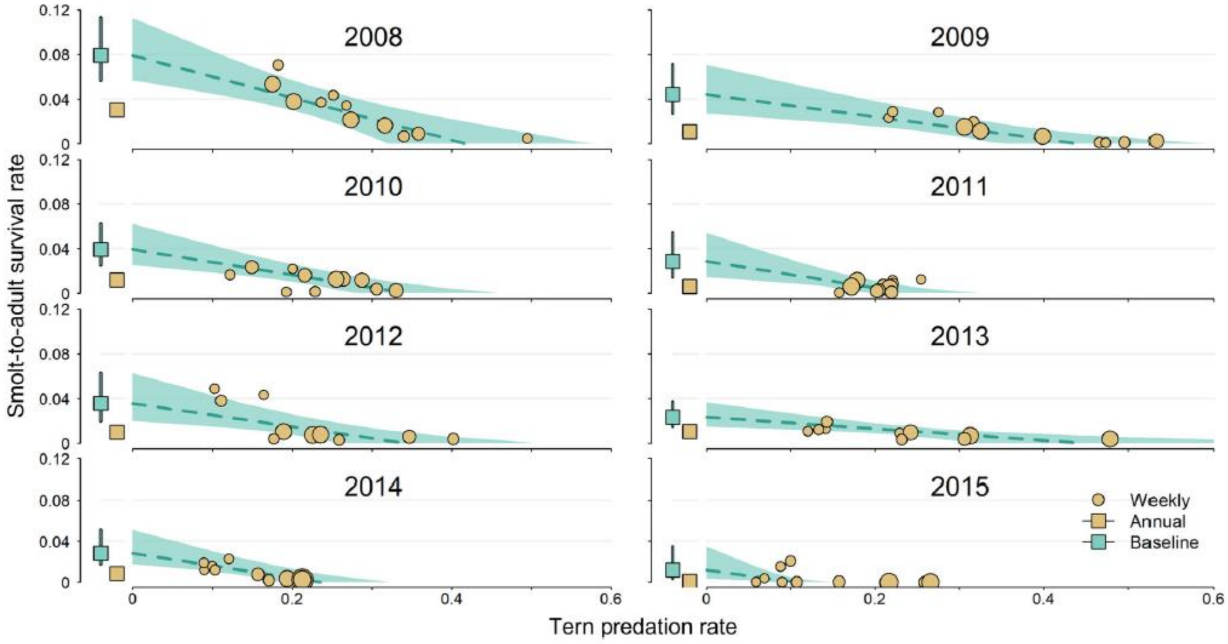


Figure. 4. Estimated annual relationships between PIT-tagged steelhead smolt-to-adult survival probabilities and Caspian Tern predation probabilities during smolt out-migration from Rock Island Dam to the Pacific Ocean (Figure 4 in Payton et al. [2020]). The size of the light brown circles depicts the relative numbers of steelhead smolts tagged and released each week at Rock Island Dam. Dashed lines represent the estimate of the best linear fit to the data and shading denotes 95% credible intervals (CRI) around the best fit. Annual estimates of survival with Tern predation (light brown box) and baseline survival in the absence of Tern predation (dark blue box) are also provided (error bars denote 95% CRI).

Payton et al. found stronger evidence of additive mortality during in-river smolt migration than either they or Haeseker et al. found for SAR. This may be due in part to the much larger contrast in tern predation and in-river survival seen across cohorts in some years (Figure 3).

An additional issue arose late in the review process regarding potential biases in the tagging groups used by Payton et al. (2020). This involved potential survival biases in steelhead tagged at Rock Island Dam vs those tagged above Rocky Reach Dam. We examined the evidence regarding the issue (Appendix B) and concluded that that there does not appear to be strong evidence that tagging location bias affected estimation of the additivity coefficient or other parameters in Payton et al. (2020) in a way that would invalidate conclusions and interpretation, especially at the smolt to adult return (SAR) life stage. Nonetheless, the ISAB recommends that possibilities for survival bias associated with tagging and release localities, especially across cohorts within year be thoroughly evaluated.

In summary, while both studies have potential issues in modeling and treatment of data (e.g., untested assumptions), both are scientifically sound analyses that use reasonable treatment, processing, and modeling of their respective datasets.

2. Were the conclusions drawn by Haeseker et al. 2020 and Payton et al. 2020 analyses supported by their results?

Payton et al. (2020) estimated the parameter a, which measures the degree of additivity of mortality due to avian predation for cohort and averaged across cohorts each year. Values of $a \leq 0$ were interpreted as over- and fully compensatory response of steelhead survival to avian predation. Positive values of a were interpreted as partial additivity ($0 < a < 1$) and super additivity ($a > 1$). They also estimated mortality from avian predation in excess of baseline mortality. They concluded that avian predation was super-additive in-river (smolts RIS to BON), and partially additive for SARs (smolts at RIS to adults at BON). Both conclusions are well supported by their results.

Haeseker et al. (2020) conclude that predation in the estuary is consistent with full compensation when considered at the SAR (BON smolts to BON adults) scale. This conclusion, as stated, is supported by their analysis. However, in their discussion they assume that their results, being consistent with full compensation, implies that they are inconsistent with additivity. In this, they fall into the common statistical fallacy that failure to reject the null hypothesis (that correlations are zero) implies that all alternative hypotheses are false. They clearly state this fallacy in their methods: "We interpreted estimates of ρ_c near zero with credible intervals that overlapped zero as indicating compensatory mortality, and we interpreted negative estimates of ρ_c with credible intervals that did not overlap zero as indicating additive mortality." This means that they depended on finding a significantly negative correlation of adult survival and avian predation to infer additivity. In other words, they require stronger evidence to accept additivity than to accept compensation. Under this standard, any data set for which there are sufficiently wide error intervals would lead inevitably to a conclusion of compensation whereas the reason would be variability in the data. Examination of the credible intervals for their correlation estimates (their Tables 2 and 3) for their best model include zero (thus being consistent with full compensation), but also include a range of negative values (thus being consistent with some degree of additivity). In fact, for terns, their mean estimate is slightly negative, providing more evidence for some degree of additivity than for full compensation. For the above reasons, the ISAB finds that results and conclusions of Haeseker et al. are consistent with full compensation but are not inconsistent with partial additivity. Given these alternative interpretations, we suggest that conclusions be used cautiously. A practical question is whether there is a material difference in outcomes that depend on a finding of full compensation versus partial additivity in terms of expected effects of avian predator management on adult returns. Resolving this question requires further analysis described in our response to Question 5.

3. How do the modeling approaches of Haeseker et al. 2020 and Payton et al. 2020 differ, and do these analytical differences or other reasons account for the contrasts in their conclusions?

The major differences in approach were discussed above. To summarize, the approaches differed in:

- **Definitions of additivity and compensation:** Haeseker et al. used a definition based on the simple correlation between predation and survival, while Payton et al. used a definition based on the initial slope of a piecewise relationship between predation and survival.
- **Populations considered:** Haeseker et al. analyzed Snake River steelhead, while Payton et al. analyzed Upper Columbia River steelhead. There may be different rates of predation between these two drainages, but Payton et al. (2021) reported similar values for steelhead survival and tern predation in both basins.
- **Time period of observations:** The time series only partially overlap – Haeseker et al. examined SAR for smolts from 2000 to 2015, Payton et al. examined in-river survival for smolts from 2008 to 2018, and SAR from 2008 to 2016. Population and predation levels vary from year to year, and this may affect estimates of correlations or regression slopes.
- **Life-cycle domain:** Payton et al. evaluated avian predation relative to both in-river smolt survival (RIS to BON) and SAR (RIS smolts to BON adult returns), whereas Haeseker et al. only evaluated predation effects on SAR (BON smolts to BON adults).
- **Details of the models:** The models differed in some details, notably pooling of estimates (Haeseker et al. estimated correlation across all years combined, Payton et al. estimated the additivity parameter (a) for each year), and inclusion of environmental covariates (Haeseker et al. included them; Payton et al. did not).

Any of these differences could lead to differences in conclusions, and it is not possible to evaluate which are most important without side-by-side comparison of the models for the same data sets, ideally including sensitivity analyses for main assumptions of each model. The fundamental definitions used may lead to different biases and thus different conclusions. The correlation-based definition used by Haeseker et al. may be problematic in ignoring the constraints on additivity of predation that are accounted for in the piecewise regression definition of Payton et al. (see Appendix A for details). Use of correlation also can confuse the issues of mean effect and variability about that mean because a low correlation cannot distinguish between a lack of an effect or high variability (either process variation or sampling error).

Different populations may have different inherent ecology surrounding predation, or there may simply be different levels of predation and survival and variability in the two that affects data contrasts and thus the ability (statistical power) to detect effects. The same problems could arise from differences in the time periods examined in the two studies.

Differences in life-cycle stages analyzed by the two studies can also explain the different conclusions. Haeseker et al. looked only at marine survival from BON smolts to BON adults, while Payton et al. looked at two overlapping life stages: first, in-river migration from RIS smolts to BON smolts, then total survival (SAR) from RIS smolts to BON adults. Haeseker et al. conclude that predation effects on marine survival are consistent with their compensation hypothesis but fail to note that they are also consistent with partial additivity (see discussion under Question 2) for this life stage. Payton et al. conclude that there is super-additivity in the effect of upstream predation on in-river survival and partial additivity for the effect when in-river and marine survival are combined. In fact, Payton et al. state that "[o]ver a scale as large as SARs, representing the vast majority of an anadromous salmonid’s potential lifespan, any source of mortality encountered early on will be mostly compensatory."

It is noteworthy that their conclusions are not inconsistent because of the differences in life-cycle domains of the two studies. Haeseker et al. did not look at in-river survival, and therefore did not produce results related to the conclusion of super-additivity during that life stage in Payton et al. Similarly, Payton et al. looked at SARs from RIS to BON, which includes in-river survival, and therefore did not produce results for the same spatial extent of the for BON-BON SARs in Haeseker et al. For BON-BON SARs, where they do overlap, both studies are consistent with either full compensation or a low degree of partial additivity in the marine environment. Moreover, the Payton et al. result of partial additivity for in-river + marine survival could result from super-additivity in the in-river stage being partially offset by full compensation or a low degree of partial additivity in the marine stage.

Details of the models and their implementation also raise a number of possible reasons for different results. However, the analyses were done separately and thus it is difficult to separate data differences from statistical method differences. Somewhere in the mix of data and methods, one can pinpoint WHY differences arose. This has not been done to date. Such inter-analysis comparisons were started to be investigated in the Chapter 8 of the Avian Predation Synthesis Report (Payton et al. 2021). However, this was mostly a verbal argument as to why there are differences in the results of the two analyses and was from one set of authors. What is needed is a more rigorous comparison where the two methods are applied to the same data, and each method is applied to the other study's dataset. One can then begin to disentangle how data and method differences contribute to the differences in results. These known differences can then be transparently judged, and the results used to inform better management actions.

Some major issues to investigate would be to compare how both analyses estimated the predation effect from bird data, the temporal and spatial scaling of matching the bird pressure with the steelhead survival, and use of covariates. Part of this is to compare the responses and explanatory variables and their interpretation.

One conclusion that is clear (and likely obvious) is that bird predation is a major factor for some years and for some stocks (see chapters for other stocks than steelhead in the Avian Predation Synthesis Report [Roby et al. 2021]). The next level of interpretation (compensatory, additive) depends on the shape of the relationship and is much less certain. This is expected because the analysis to determine the amount of predation relies on the general magnitude while analysis of the shape of the survival relationship requires additional confidence on how estimates of survival vary across a range of bird predation rate.

4. Does the ISAB have recommendations to improve the analysis?

The ISAB recommends that both approaches be employed in side-by-side analysis of the same datasets (possibly including simulated datasets where the "true" answer is known) to simultaneously evaluate robustness to assumptions, statistical power, interpretations of each modeling framework. Side-by-side analysis could discern whether differences in model design and analytical power, or differences in location and population studied are most important in explaining alternative interpretations and conclusions of these studies. This is the best way to resolve issues of definitions, methodology, and data differences that limit comparison of the results and conclusions of these two studies.

The ISAB recommends that future studies have better focus on management-related results rather than on estimating degrees of additivity and compensation. While theoretically important, the shape of the survival predation relationship is less important for management than estimates of the actual effect of in-river predation on adult returns. Payton et al. (2020) address the actual effect in their estimate of average annual SAR with or without predation (their ϕ^{Δ}), but this could be improved for example by incorporating "adult equivalents" to put super-additive mortality above BON into context with survival over entire life cycle, and by providing independent estimates of baseline survival. As part of this recommendation, we reiterate the recommendation from the ISAB Predation Metrics Report (ISAB 2016) to encourage the use of comparable metrics with clear management implications as analysis endpoints, including *equivalence-factor* metrics (for example, adult equivalents) and a *change in population growth rate* metric (aka *delta-lambda*, Δλ). Integration of avian predation findings with life cycle modeling efforts to understand how other environmental correlates potentially interact with susceptibility to avian predation could provide an important management tool

Both analyses also could be improved by examining several aspects of model formulation and implementation. First is the question of bias in the analyses. Haeseker et al. rely on an earlier study (Otis and White 2004) to indicate that their approach would have low bias, but Otis and White specifically excluded consideration of the logit-transform that Haeseker et al. used in their analysis. This transformation results in some degree of bias in parameter estimates or their credible intervals, but it is not known how large bias could be. Payton et al. did a simulation study of their model and found some degree of bias, but do not discuss any bias corrections in their results. Additional studies of bias and methods of correcting for it would enhance the reliability of both studies.

Although both studies model the effects of multiple predators in the same location and life-stage, their models do not include possible effects of ecological interactions among the predators. Competition, interference, or synergisms among predators could play a role in determining total mortality and might modify the conclusions regarding additivity or compensation on local scales. Including such interactions in future models might be useful.

Neither model takes harvest of steelhead into account in their estimates of SAR. This may not be a substantial source of mortality for these steelhead populations as compared to higher rates of commercial harvest for other species. Harvest possibly could be as important as avian predation on an adult-equivalent basis and may also be an additional source of year-to-year variation in SAR. Estimates of non-treaty harvest impacts for winter steelhead range between 0.2% and 9.4% since 2000, while estimates for summer A-run steelhead range from 1.5% to 8.6% for hatchery-origin fish and from 0.4% to 1.7% for natural-origin fish (Joint Columbia River Management Staff 2021, Tables 9 and 11a). Adjusting mortality estimates for losses to harvest of adults could be useful, perhaps included as another category of predator. However, the lack of PIT tag detections in the harvest could make this difficult.

Several further analyses should be conducted to help understand differences and similarities of those approaches. A comparison of the assumptions in a table format would help highlight similarities and differences between the two analyses. Our Table 1 above is a start; more details would further enable identification of similarities and differences and inform a comparative analysis of the two methods and datasets. Similarly, exchanging datasets and methods, as well as applying both methods to the same dataset, would begin to separate the issues that confound comparisons across results generated to date (independently) by the two analyses.

Ideally, these comparisons would be conducted collaboratively with representatives from the two sets of authors, perhaps with a few “outside” people.

The ISAB recommends additional steps to improve the utility of individual studies:

- Haeseker et al. chose the single best environmental correlate model based on the Deviance Information Criterion (DIC). While this is appropriate in a model-selection process (i.e., where one is trying to test for the most supported hypothesis), it is not the best method for drawing inferences about the modeled system, as it makes all results conditional on the selected model. Model averaging or other forms of multi-model inference would have been more appropriate here (Burnham and Anderson 2002).
- Both studies may suffer from problems with very low tag recoveries in some years, which may influence the estimates that are pooled across years. It would be helpful to redo the correlational analysis dropping cohorts with say < 10 PIT-tags recovered to see if this has an influence.
- Haeseker et al. analyzed each bird species individually, and Payton et al. analyzed mortality attributable to Caspian terns separately from “other” birds. While there is value in treating bird species separately in analysis, it would be simple to combine estimates of predation into one index and look at the combined effects.
- Payton et al. constrain survival and mortality estimates to sum to unity, which could introduce sampling correlations in the estimates. They should investigate the extent of such correlations and whether they influence parameter estimates.

5. What are the management implications of the results?

The Payton et al. (2020) study makes a convincing case for additive to super-additive effects of avian predation during downstream in-river migration, leading to the conclusion that avian predation is likely to significantly reduce the number of smolts leaving the river. For SARs, the case is not so clear. While Payton et al. (2020) found that in-river survival was additive, they found only low-level partial additivity when estuarine and ocean life stages were included as well as the in-river stage. This is not inconsistent with Haeseker et al. (2020), who found that estuarine and ocean survival was fully compensatory but did not include the in-river life-history segment. The two studies’ conclusions would be consistent with a model of additive in-river mortality and compensatory (or partially additive) marine (estuarine + ocean) mortality. However, there is so much variability in the marine environment that there may be little power to detect additive effects in SARs. From these two studies, we cannot conclude whether there are compensatory processes in the marine environment that might fully offset the effects of in-river predation on smolts or if partial additivity is hidden by the high variability in marine survival.

For populations at risk, even a small additive effect could affect population sustainability, so avian predation could be a life-cycle risk factor. If no further analyses were possible, this would be the most prudent conclusion from a management perspective. Additional studies are needed to fully evaluate the relative importance of avian predation in a population conservation context. In particular, life-cycle models that partition mortality into its measurable components (direct hydrosystem effects, predation by both birds and marine mammals, harvest, and climate-driven effects) and look at population-level responses would be beneficial.

A major question for management is whether any increase in SARs is worth the cost of suppressing avian predators or is critical to the support of ESA-listed salmonid species. Answering this question requires estimates of the size of the effect rather than estimates of the degree of additivity or compensation. Payton et al. address this to some degree with their estimates of annual survival with and without predation (their variable ϕ^{Δ}). These values are reported for other stocks and species in Payton et al (2021). SAR-based estimates for other salmon species in the Upper Columbia River and Snake River reported in Payton et al. (2021) were lower than those for Upper Columbia River steelhead in Payton et al (2020). This suggests that the effect of in-river and estuarine avian predation on SARs is small, but perhaps not negligible, for most species and basins. This management question should also be addressed in the context of an integrated ecosystem/socioeconomics approach, considering social concerns, cost effectiveness, and ecosystem consequences of avian control actions (ISAB 2019-1).

Within a broader ecosystem/socioeconomic approach, the results would indicate how socioeconomic benefits would be affected by changes in bird predation. Thus, the results would inform whether and by how much benefit would result from alternative management actions to lower bird abundances. Resolving the two analyses within this context could also provide important information on how such management actions could be implemented to ensure they are effective. Key questions for management include: how much suppression or control of bird predators is needed to ensure a certain socioeconomic benefit? Under what conditions and year-types should efforts for bird reduction be focused? What is the range of possible responses one can expect with different levels of bird suppression? Will control actions simply cause avian predators to move to other locations, a response that potentially occurred with double-crested cormorants in the lower Columbia River (Lawes et al. 2021)? Are control actions consistent with federal and state regulations for protection of double-crested cormorants and Caspian terns?

Appendix A: Comparison of the predation equations used by Payton et al. (2020) and Haeseker et al. (2020)

Although both Haeseker et al. (2020) and Payton et al. (2020) use similar underlying models for the relationship between predation and overall survival (based on that of Burnham and Anderson 1984), they apply different parameter constraints, use different variable names, terminology, and definitions of additivity. This appendix puts the underlying models into the same notation to facilitate direct comparison. Table A1 lists notations used by study authors and Burnham and Anderson (1984). In the analysis that follows, we use the Burnham and Anderson (1984) notation because it is older and more commonly used, but other notations are mathematically equivalent (Table A1).

Table A.1. Notation used in the survival-predation equations.

Definition	Burnham and Anderson (1984)	Haeseker et al. (2020)*	Payton et al. (2020)
Survival probability	S	S	ϕ
Survival probability in the absence of predation	S_0		ϕ^0
Predation probability	K	θ	θ
Absolute slope of survival vs. predation	$b_{S,K}$		$-a$
Normalized slope of survival vs. predation	$b = -b_{S,K}/S_0$		a/ϕ^0
Correlation between survival and predation		ρ	
Predation threshold	K_{sat}†		θ^{sat}
Basic equation when predation is below the threshold	$S = S_0(1 - bK)$		$\phi = \phi^0 - a\theta$

*Haeseker et al. (2020) do not include the model explicitly, so they do not have all the symbols in their notation.

†A symbol for the predation threshold is not included in Burnham and Anderson (1984) but is included here to be consistent with their other notation.

Both studies begin with the classic equation for the effects of hunting (or avian predation, in this case) on wildlife populations, as formulated by Burnham and Anderson (1984). Burnham and Anderson develop a model relating survival to predation:

$$S = S_0(1 - bK).$$

where *S* is survival probability, S_0 is survival probability in the absence of hunting/predation (*baseline survival*), *K* is the kill probability or predation probability, i.e., the probability that an individual is killed by hunters/predators, and *b* is the slope of the relationship between *S* and *K* "normalized such that $0 \leq b \leq 1$" (Burnham and Anderson 1984, p. 106).

Note that in practical application, the equation applies over some set of pre-defined time intervals, and the variables would have subscripts for time and other indices (subpopulation, predator colony, etc.); here, we ignore those subscripts for simplicity. In practice, the way these subscripts are derived has important implications for the statistical analyses, as discussed in the main report.

Burnham and Anderson (1984) recognized the constraints on the parameter *b* as defining two extreme hypotheses in the relationship: *fully compensatory* ($b = 0$), when "non-hunting mortality compensates for hunting mortality up to a threshold point" and *fully additive* ($b = 1$), when "hunting mortality is totally additive to other mortality forces" (Burnham and Anderson 1984, p. 105). Intermediate values of *b* are referred to variously as *partially additive*, *partially compensatory*, or simply *mixed*. The analysis in Haeseker et al. is derived from this underlying model.

Payton et al. re-parameterize the model, substituting $a = bS_0$, to obtain their model ($S = S_0 - aK$). While their formulation is algebraically equivalent to that of Burnham and Anderson. However, in statistical estimation, the substitution of $a = bS_0$ can result in differences in parameter estimates depending on the estimation method. In addition, Payton et al. (2020) follow Sandercock et al. (2011) in recognizing *over-compensation*, when *a* (or, equivalently, *b*) is negative, and *super-additivity*, when $a = bS_0 > 1$. While these possibilities have been rarely documented in nature, they are justified in ecological theory.

In their analysis of duck hunting, Burnham and Anderson noted the existence of a threshold point above which their equation breaks down but did not include it in their analysis, implicitly assuming that hunting rates fell below that threshold point. Other authors have followed suit, including Haeseker et al. (2020). This assumption is valid for many situations, but not when predation rates are very high relative to baseline survival rates.

Payton et al. (2020), however, followed other authors (Schaub and Lebreton 2004; Sandercock et al. 2011) in considering the effects of that threshold on parameter estimation. The threshold arises from two necessary constraints on the equation: 1) that the sum of survival and all sources of mortality must equal one, and 2) that survival cannot be below zero. The second constraint holds for all studies and is not considered further here. Payton et al. refer to the first constraint as the *saturation* threshold that represents the point where predation exceeds additive or compensatory capacity of the system. Algebraically, they derive expressions for this saturation level as (using the Burnham and Anderson notation; cf. Eq. 2 in Payton et al. 2020):

$$K_{sat} = \begin{cases} \dfrac{1 - S_0}{1 - bS_0} & \text{when} \quad b < 1 \\ \dfrac{1}{b} & \text{when} \quad b \geq 1 \end{cases}$$

The fully constrained equation is then (cf. Eq. 3 in Payton et al. 2020):

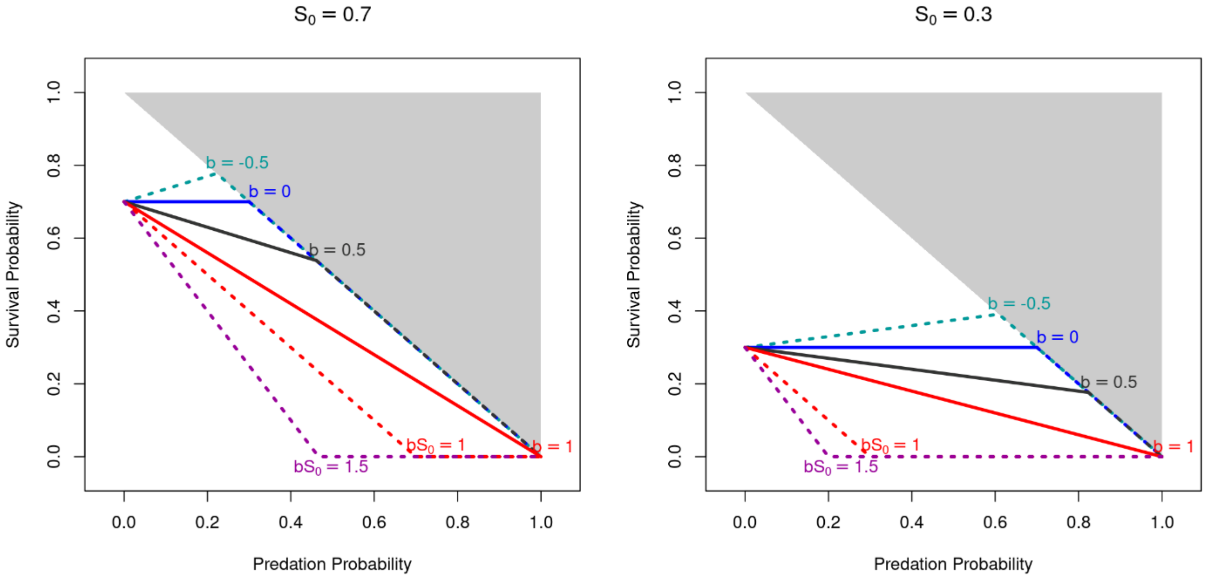
$$S = \begin{cases} S_0(1 - bK) & \text{when} \quad K \leq K_{sat} \\ 1 - K & \text{when} \quad K > K_{sat} \text{ and } b \leq 1 \\ 0 & \text{when} \quad K > K_{sat} \text{ and } b > 1 \end{cases}$$

While the two studies share the similar underlying models (algebraically equivalent when $0 \leq b \leq 1$ and predation is below the threshold), they differ in their definitions of additivity and compensation. Burnham and Anderson define these in terms of the normalized slope (*b*) with $b = 1$ meaning full additivity and $b = 0$ meaning full compensation. Haeseker et al. follow Otis and White (2004) in using the correlation (ρ) to define full compensation as $\rho = 0$ (corresponding to $b = 0$) and additivity (partial or full) as $\rho < 0$ (corresponding to $b > 0$). Payton et al. use a definition base on the absolute slope ($a = bS_0$) with full compensation at $a = 0$ and full additivity at $a = 1$. Thus, both definitions agree about full compensation but not about full additivity. Under the Payton et al. definition, full additivity means that a unit increase in predation results in exactly a unit decrease in survival, while under the Burnham and Anderson definition a unit increase in predation results in less than a unit decrease in survival. A final difference is that Payton et al. include the possibilities of over-compensation and super-additivity, which Haeseker et al. and Burnham and Anderson do not.

Thus, there are five different possible categorizations of the predation-survival relationships (Figure A1):

- Super-additive: $bS_0 > 1$ (used only by Payton et al.); magenta lines in Fig. A1
- Fully additive: $b = 1$ (Burnham and Anderson), $\rho < 0$ (Haeseker et al.) or $bS_0 = 1$ (Payton et al.); red lines
- Partially additive, partially compensatory: $0 < b < 1$ (Burnham and Anderson), $\rho < 0$ (Haeseker et al.) or $0 < bS_0 < 1$ (Payton et al.); grey lines
- Fully compensatory: $b = bS_0 = \rho = 0$ (all authors); blue lines
- Over-compensatory: $bS_0 < 0$ (used only by Payton et al.); cyan lines

Note that the base model (Burnham and Anderson 1984; solid lines in Figure A1) is a restricted case of the more general model (solid and dashed lines) used by Payton et al. (2020); when predation is below the threshold and $0 \leq b \leq 1$, the two formulations are identical. Note also that the saturation threshold is inversely related to baseline survival, so that when baseline survival is high (left panel in Figure A1), the threshold is relatively low, and when baseline survival is low (right panel), the threshold is high. In the case of the two steelhead studies, smolt-to-adult (SAR) survival is quite low (generally below 0.1) and avian predation probabilities are moderate, so the threshold is unlikely to be reached. This means that for the analysis of SARs, where slope estimates are below 1 and the saturation threshold is not reached, the two studies are using similar equations, and, to the extent that their statistical methods are comparable, the results are also comparable. The saturation threshold becomes important when Payton et al. (2020) analyze in-river survival, where annual baseline survival estimates range up to about 0.8 and predation probability estimates up to about 0.4. The effect of these constraints in this case is illustrated in their Figure 3, where in some years the credible intervals are distorted at the saturation threshold.


$S_0 = 0.7$

$S_0 = 0.3$

Figure A.1. The full set of equations relating total survival to predation probabilities, with solid lines representing cases included by both authors, and dashed lines representing cases included only by Payton et al. (2020). Left panel: high base survival (S0 = 0.7); right panel: low base survival (S0 = 0.3). Grey triangle represents the constrained zone where predation plus survival would exceed unity. Cyan – over-compensation; blue – full compensation; grey – partial additivity or partial compensation; red – full additivity under two different definitions (solid line, Burnham and Anderson 1984; dashed line, Payton et al. 2020); magenta – super-additivity.

Appendix B: Effects of mortality associated with tagging and handling at dams

Accurate characterization of effects of avian predation on salmon survival requires that tagging is random with respect to factors that influence survival that are explicitly modeled in the analysis. Factors that influence survival and response to bird predation include species, population, run timing, life stage, body size and condition, and rearing type (e.g., hatchery- vs. natural origin). Both the Payton et al. (2020) and Haeseker et al. (2020) analyses assume that survival is random and that tagged-fish samples they analyze are representative of the entire population of migrating steelhead within basins (Upper Columbia River or Snake River, respectively). The Payton et al. analysis represents the effect on survival due to differing predation levels across cohorts within years and compares summary metrics across years. The Haeseker et al. analysis assumes survival is random (or attributable to environmental factors included in their model) across years and represents predation effects on survival of cohorts within years.

In a memo dated 19 February 2021, the Fish Passage Center (FPC) documented differences in survival of steelhead released at Rocky Reach Dam (RRE) and Rock Island Dam (RIS) and claimed that fish tagged and released at RIS experienced lowered survival compared with those tagged and released upstream at RRE. In a second memo dated 17 March 2021, FPC presented data indicating that steelhead tagged at Lower Granite Dam (LGR) also experienced lowered survival compared with counterparts tagged upstream and suggested a general effect of tagging at dams that lowers survival of steelhead smolts. Furthermore, in both memos, mean recovery rates of tags deposited in avian colonies were higher for steelhead tagged at dams (versus those tagged upstream) suggesting increased risk of bird predation. These findings represent a potential source of non-random variation in steelhead survival not explicitly accounted for in the Payton et al. (2020) analysis, namely, tagging location. The Haeseker et al. (2020) study focused on steelhead tagged upstream of LGR that are presumably unbiased with respect to survivorship and predation susceptibility affected by tagging location.

In response to the 19 February FPC memo, Real Time Research (RTR) and CRITFC presented an analysis (in a memo dated 15 March 2021) that attributed differences in survival and deposited tag recovery to run timing and rearing type of RRE-tagged fish relative to RIS-tagged fish and not tagging site *per se*. They documented that RRE fish were composed of earlier runs that, based on previous research, were expected to experience higher survival and decreased likelihood of recovery of deposited tags regardless of tagging site. They also claimed that RRE-tagged fish were not fully representative of Upper Columbia River steelhead smolts, but rather composed of a greater proportion of hatchery-origin fish than the RIS-tagged samples. Finally, when analyzed by cohort (rather than annually as done in the FPC memo), they found few cohorts where the odds of predation by Caspian terns were significantly greater for RIS fish compared with RRE fish. In their 17 March memo, FPC concurred that run time of RRE-tagged fish averaged 2 to 10 days earlier but disputed its relevance for explaining differences in steelhead survival across release locations.

The Payton et al. (2020) analysis estimates the additivity coefficient (a) as the slope of a fitted relationship of cohort-specific survival and predation with intercept S_0 = baseline (annual) survival estimated from the same model. Thus, if the reduced-survival effect of tagging and handling at RIS is uniform or random across cohorts within a year, then their estimates of *a* and S_0 are still informative regarding the effects of avian predation on steelhead smolts. Conversely, if tagging and handling differentially affects some cohorts and not others within a year, then the Payton et al. analysis will be biased. In the RTR rebuttal, an analysis by cohort suggests that survival (Figure 3 in RTR rebuttal) and predation risk does not differ across RRE and RIS cohorts (Figure 5 in the RTR rebuttal). If true, then values of the additivity coefficient are not obviously biased, and conclusions about the nature of mortality from avian predation (whether additive or compensatory) are valid for RIS-tagged fish. However, these conclusions can be reasonably extended to the entire Upper Columbia River steelhead smolt population if results for RIS fish are strongly correlated to those observed for RRE fish (assuming RRE is representative).

Examination of data presented in Tables 4 and 5 of the 19 February FPC memo indicates that annual SARs and tag-recovery rates of RRE and RIS-tagged samples are strongly and positively correlated despite consistent differences in survival and raw recovery probability (i.e., not expanded for deposition or detection probabilities) at Potholes Reservoir bird colony between RRE and RIS samples (see Fig. B1 below).

Based on information presented in the FPC memos and the RTR response, the ISAB concludes that there does not appear to be strong evidence that tagging location bias affected estimation of the additivity coefficient or other parameters in Payton et al. (2020) in a way that would invalidate conclusions and interpretation, especially at the outmigrating smolt to adult return (SAR) life stage. However, the ISAB agrees with FPC statements that lowered survival and higher raw tag recovery associated with tagging at dams is an important factor and consideration for future monitoring and research. The nature, causes, and consequences of survival bias need to be thoroughly examined in the context of particular studies.

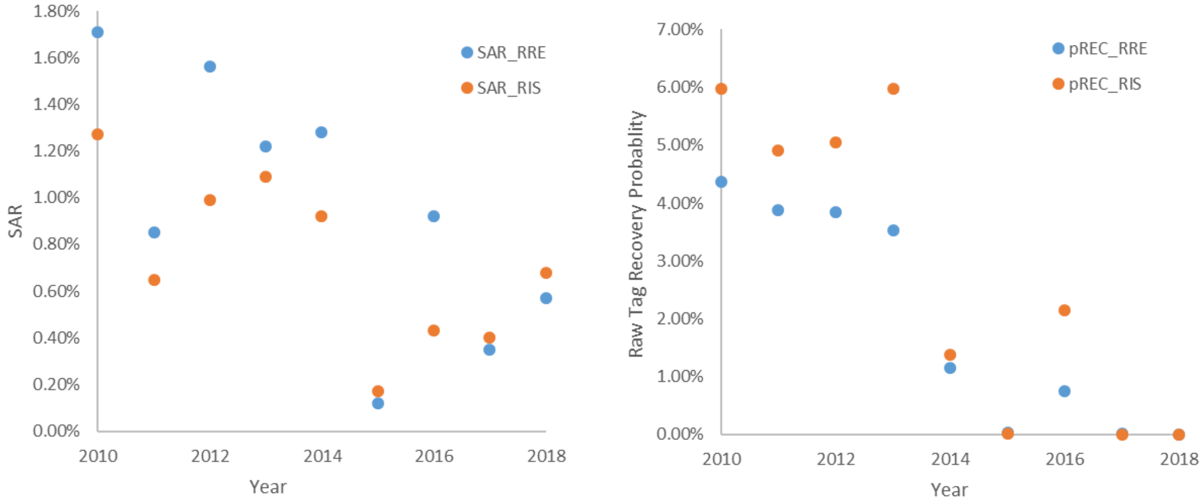


Figure B.1. SARs and raw tag recovery probability at Potholes Reservoir. The left panel shows annual SARs (y-axis) plotted by year from 2010 to 2018. The right panel shows raw recovery probabilities (not expanded for deposition or detection probabilities) at Potholes Reservoir (x-axis) by year. RRE = blue circles and RIS = orange circles. The estimated Pearson correlation coefficients are r = 0.91 between the two SAR values and r = 0.97 between the two raw Tag Recovery probabilities. Strong correlation between data sets suggests that RIS-tagging data may be useful for identifying trends in avian predation. Data are from the 19 February 2021 FPC memo, Tables 4 and 5.

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