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Avian Predation on Juvenile and Adult Lost River and Shortnose Suckers: An Updated Multi-Predator Species Evaluation

Allen F. Evans,*  Quinn Payton, Nathan Banet, and Bradley M. Cramer

Real Time Research, Inc., 1000 Southwest Emkay Drive, Bend, Oregon 97702, USA

Caylen Kelsey¹ and David A. Hewitt²

U.S. Geological Survey, Western Fisheries Research Center, Klamath Falls Field Station, 2795 Anderson Avenue, Suite 106, Klamath Falls, Oregon 97603, USA

Abstract

Previous research suggests that predation by piscivorous colonial waterbirds may negatively influence the survival of Lost River Suckers (LRS) *Deltistes luxatus* and Shortnose Suckers (SNS) *Chasmistes brevirostris* in the Upper Klamath Basin (UKB), USA. However, estimates of predation from past studies, which were based on suckers with PIT tags, represent minimum estimates of sucker mortality because analyses did not account for the proportion of tags that were consumed by birds and deposited beyond their breeding colony. To address this uncertainty, we fed PIT-tagged suckers to American white pelicans *Pelecanus erythrorhynchos* to estimate deposition probabilities. A hierarchical Bayesian model was then used to estimate predation rates (percentage of available tagged fish that were consumed) on juvenile suckers that were released as part of the Sucker Assisted Rearing Program (SARP) and on wild juvenile and adult LRS and SNS during 2009–2020. Pelican deposition probabilities were estimated to be 0.47 (95% credible interval = 0.36–0.60), indicating that for every 100 tags consumed, 47 tags on average were deposited on breeding colonies by birds. Deposition-corrected estimates of predation rates were approximately two times greater than those previously reported and ranged annually from 4.3% (95% credible interval = 2.9–6.7%) to 8.5% (6.3–12.7%) on SARP juvenile suckers, from 4.3% (0.9–13.2%) to 10.5% (3.8–24.5%) on wild juvenile suckers, and from 0.1% (<0.1–0.3%) to 7.2% (2.8–16.4%) on adult suckers, depending on species and location. Results suggest that predation by colonial waterbirds, although not the original cause of sucker declines, was a substantial source of sucker mortality in some years. Future studies should consider models that jointly estimate both predation and survival and models that include environmental factors that potentially influence sucker susceptibility to avian predators in the UKB.

Piscivorous colonial waterbirds are an integral part of the Upper Klamath Basin (UKB) ecosystem, with breeding colonies of American white pelicans *Pelecanus erythrorhynchos* (hereafter, “pelicans”), double-crested cormorants *Nannopterum auritum* (hereafter, “cormorants”), Caspian terns *Hydroprogne caspia* (hereafter, “terns”), and other

native species present in the region (Shuford 2010). Although western pelican and cormorant populations have been in decline for more than a century, colonies in the UKB are some of the largest in North America when breeding conditions are favorable (King and Anderson 2005; Shuford 2010). Pelican colonies in the UKB

*Corresponding author: allen@realtimeresearch.com

¹Present address: U.S. Fish and Wildlife Service, Alaska Regional Office, 1011 East Tudor Road, Anchorage, Alaska 99503, USA.

²Present address: U.S. Fish and Wildlife Service, Deepwater Horizon Gulf Restoration Office, 341 North Greeno Road, Suite A, Fairhope, Alabama 36532, USA.

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consisting of more than 2,000 breeding adults have been present in Clear Lake Reservoir, California, and cormorant colonies of more than 1,500 adults have been documented in Upper Klamath Lake, Oregon (Shuford 2010; Evans et al. 2016). Large colonies of terns have also been documented in recent years, with more than 1,000 breeding adults observed in Sheepy Lake, California (Roby et al. 2021).

Two long-lived catostomid species, the Lost River Sucker (LRS) *Deltistes luxatus* and the Shortnose Sucker (SNS) *Chasmistes brevirostris*, are also found in the UKB and are listed as endangered under the U.S. Endangered Species Act (ESA; USFWS 1988). Historical accounts indicate that both LRS and SNS were once extremely abundant throughout the UKB and were harvested in both a Native American subsistence fishery and a recreational fishery (Rasmussen 2011). Spawning populations for both species in Upper Klamath Lake, however, have declined by more than 50% since the early 2000s (Hewitt et al. 2018). Most of the suckers in Upper Klamath Lake were spawned in the early 1990s, meaning that most of the individuals of both species, but especially SNS, have been mature for many years and are now beyond the average expected life span for the species (Janney et al. 2008; Terwilliger et al. 2010). Some of the spawning populations may now consist of fewer than 10,000 individuals (Childress et al. 2019). Numerous factors have been identified as limiting the recovery of sucker populations, including habitat loss, poor water quality, low water levels, and a lack of juvenile recruitment into spawning populations (Janney et al. 2008; USFWS 2012; Burdick et al. 2015, 2020; Hewitt et al. 2018, 2021). Recent data also suggest that impacts from colonial waterbirds may be limiting sucker survival based on the number and percentage of PIT tags implanted into suckers that were subsequently recovered on bird colonies in the UKB during 2009–2014 (Evans et al. 2016).

To monitor the behavior and survival of LRS and SNS, fish have been PIT-tagged in Upper Klamath Lake and Clear Lake Reservoir for over two decades (Janney et al. 2008; Hewitt and Hayes 2013; Burdick et al. 2015; Hewitt et al. 2018, 2021). Passive integrated transponder tags link species, size, age-class (adult, juvenile), release/recapture location, and other demographic information to individual fish. Until recently, most PIT-tagged suckers have been adults, as fewer than 1,000 juveniles have been captured and tagged since 2009. This is due in part to poor summer survival of juveniles, particularly in Upper Klamath Lake, which has resulted in a prolonged lack of recruitment into adult spawning populations (Bart et al. 2020; Burdick et al. 2020). As part of an effort to recover imperiled LRS and SNS populations and to address concerns regarding juvenile survival, the Sucker Assisted Rearing Program (SARP) was developed by the U.S. Fish

and Wildlife Service (USFWS) and its partners in 2015 (Groves et al. 2017). The program operates under the hypothesis that poor water quality conditions in Upper Klamath Lake reduce the survival of young-of-the-year and juvenile suckers (Day et al. 2020). Beginning in 2016, wild-origin sucker larvae have been captured annually at spawning locations in Upper Klamath Lake and its tributaries and reared at off-site facilities for 1–3 years or until they reach a size that has been determined to offer the best chance of survival in Upper Klamath Lake. Since 2018, thousands of juvenile suckers have been PIT-tagged and released in Upper Klamath Lake once they reach their target age or size (Childress et al. 2019).

A portion of PIT-tagged suckers are consumed by avian predators, and their corresponding tags are deposited (regurgitated or defecated) at nesting sites (colonies), where the tags can be detected by researchers after the breeding season (Evans et al. 2016). To address concerns over the potential impact of avian predators on ESA-listed suckers, research involving the recovery of sucker PIT tags on bird colonies in the UKB has been ongoing since 2009 (Evans et al. 2016). However, not all PIT tags that are ingested by colonial waterbirds are subsequently deposited on their breeding colony; a portion of the PIT tags consumed by birds are damaged and rendered unreadable after digestion or are regurgitated off-colony at loafing, staging, or other areas used by birds during the breeding season (Evans et al. 2012; Osterback et al. 2013; Hostetter et al. 2015; Teuscher et al. 2015; Meyer et al. 2016). Evans et al. (2016) measured minimum predation rates (percentages of available tagged fish that were consumed) on LRS and SNS. Those estimates were adjusted to account for the proportion of tags that were detected by researchers after the breeding season (i.e., detection probabilities) but not for the proportion of ingested tags that were deposited by birds during the breeding season (i.e., deposition probabilities). Despite being minimum estimates, annual predation rates on adult and juvenile suckers were documented to be as high as 4.6% and 8.4%, respectively (Evans et al. 2016). These data were collected on naturally reared or wild juveniles, while the impacts on suckers reared in captivity were unknown. Given the greater susceptibility of hatchery-reared fish to bird predation as observed in other systems (Fritts et al. 2007; Hostetter et al. 2012), predation impacts on SARP fish released into Upper Klamath Lake could be substantial but were previously unknown.

Prior research indicates that the probabilities of PIT tag deposition by colonial waterbirds can be low and vary by predator species. For instance, in a study of cormorant, tern, and California gull *Larus californicus* predation on PIT-tagged Pacific salmon *Oncorhynchus* spp., Hostetter et al. (2015) estimated that average annual PIT tag deposition probabilities varied considerably among predator

species, with estimates of 0.15 (95% credible interval = 0.11–0.21) for gulls, 0.51 (0.34–0.70) for cormorants, and 0.71 (0.51–0.89) for terns. Integrating deposition probabilities increased the predation rate estimates by a factor of 1.4–6.7 depending on the predator species; thus, accurate estimates of predation rely on accurate estimates of species-specific deposition probabilities (Hostetter et al. 2015). Although recent studies have suggested that not all PIT-tagged fish consumed by pelicans are deposited on their breeding colonies (Teuscher et al. 2015; Meyer et al. 2016), no parameter estimates of pelican deposition probabilities were available for use in mark–recapture–recovery predation models (Evans et al. 2016). A lack of deposition probabilities for pelicans was thus identified as a critical uncertainty in estimating the impacts of predation on juvenile and adult sucker survival in the UKB (Evans et al. 2016).

Accurate assessment of cause-specific mortality may be paramount to evaluating the efficacy of management actions aimed at increasing the survival of ESA-listed suckers in the UKB. Thus, the primary goals of this study were to (1) estimate deposition probabilities for pelicans to generate more accurate estimates of predation rates on LRS and SNS and (2) evaluate the extent to which avian predation is limiting sucker survival, including the survival of hatchery-reared suckers released as part of the SARP management plan.

METHODS

Study Area

During 2009–2020, we investigated predation on PIT-tagged suckers by pelicans, cormorants, and terns nesting on colonies located in Upper Klamath Lake, Oregon; and Clear Lake Reservoir, Tule Lake, and Sheepy Lake, California (Figure 1). These three species of piscivorous colonial waterbirds were previously identified as posing a potential risk to sucker survival in the region (Evans et al. 2016). All colonies included in the study were located on islands within the USFWS Klamath Basin National Wildlife Refuge Complex (Figure 1).

Availability of PIT-Tagged Sucker

The methods of Evans et al. (2016) were used to determine the availability of PIT-tagged suckers to predation by breeding pelicans, cormorants, and terns. In brief, the number of suckers available to birds was based on the number of tagged suckers released or re-encountered (previously tagged) between September 1 and August 31, the presumed end of the breeding season (Evans et al. 2016). Adult suckers were identified to species (LRS or SNS), sexed (Markle et al. 2005), measured (FL; mm), and PIT-tagged (12-mm long × 2-mm wide, 134-kHz, full-duplex tag; Biomark). In keeping with recent research that demonstrated a lack of genetic distinctiveness between

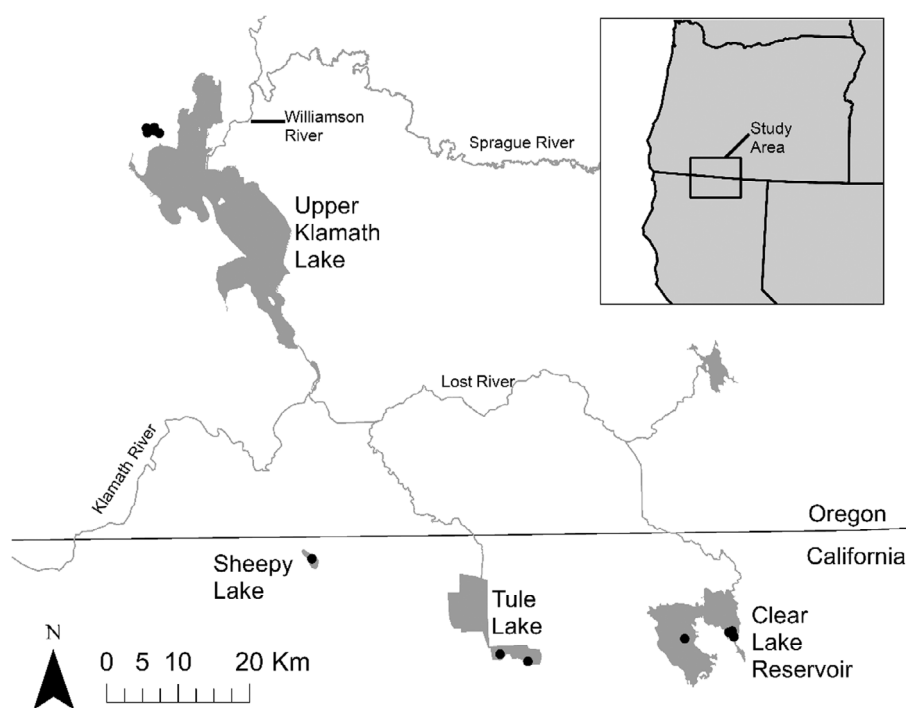


FIGURE 1. Breeding sites (dots) used by colonies of American white pelicans, double-crested cormorants, and Caspian terns in Upper Klamath Lake, Clear Lake Reservoir, Tule Lake, and Sheepy Lake during 2009–2020.

SNS and Klamath Largescale Suckers (KLS) *Catostomus snyderi* in Clear Lake Reservoir (Dowling et al. 2016; Smith et al. 2020), individuals that were identified as either SNS or KLS were combined into a single “SNS–KLS” species designation. Juvenile suckers were defined as individuals less than 300 mm FL based on age and growth information (Terwilliger et al. 2010) and observations of the smallest individuals that joined spawning migrations. Juvenile suckers cannot be identified to species in the field (Burdick and Martin 2017), and genetic markers were only recently developed (Smith et al. 2020); therefore, juvenile suckers were not identified to species in our analyses. Only juveniles larger than 72 mm were PIT-tagged, based on the minimum tagging size used in the region (Burdick 2011). Releases and re-encounter histories of wild juveniles and adult suckers in Upper Klamath Lake and Clear Lake Reservoir were provided by the U.S. Geological Survey (USGS) Klamath Falls Field Station (KFFS; see also Hewitt et al. 2010, 2018, 2021). Release and re-encounter histories of wild juveniles and adults date back to 2009, the first year in which bird colonies were scanned for tags in the UKB. Releases and re-encounter histories of SARP juveniles date back to 2018, the first year in which SARP fish were released into Upper Klamath Lake (data were provided by the USFWS). Prior to 2005, suckers were tagged with 125-kHz PIT tags, but only 134-kHz tags were used in subsequent years. Due to the small numbers of 125-kHz tagged fish available (re-encountered) during 2009–2020 and because detection probability estimates were only available for 134-kHz tags, only suckers tagged with 134-kHz tags were included in the study. In addition to PIT tags, radiotelemetry tags were also inserted into some SARP and adult suckers (i.e., fish were double-tagged) as part of other studies, but since these fish were captured, tagged, handled, and released in a different way than PIT tag-only fish, they were not included in the present study.

Bird Colony Locations and Sizes

The methods of Adkins et al. (2014) were used to determine the location and approximate size (number of adults) of pelican, cormorant, and tern colonies that were subsequently scanned for sucker PIT tags after each breeding season. In brief, estimates were based on the number of adult birds visible on-colony in oblique aerial photographs taken during the breeding season (March–August), with one to three aerial surveys conducted each year during 2009–2020. Colony size was based on the total number of adults present during the late egg incubation/early chick rearing period (early June), the stage of the nesting cycle when the greatest number of breeding adults is generally found on-colony (Gaston and Smith 1984). For cases in which birds at a given nesting site failed (i.e., abandoned the site) prior to the June aerial survey (conducted in all

years), photographs taken of the colony earlier in the breeding season, if available, were used to estimate the colony size. Photographs were taken with a high-resolution digital single-lens reflex camera from a fixed-wing aircraft (see Adkins et al. 2014 for additional details).

Recovery of PIT Tags

Electronic recovery (detection) of sucker PIT tags was conducted at all active colony sites included in the study during each year (Figure 1). Recovery of sucker PIT tags on bird colonies followed the methods of Evans et al. (2016). In brief, PIT tags deposited by birds on nesting colonies were recovered in situ after the birds dispersed from their colonies following the breeding season (September–November). Colony sites were scanned using pole-mounted PIT tag antennas and portable transceivers. The PIT tags were detected by scanning the entire area occupied by birds during the breeding season, with two passes or complete sweeps of the nesting site conducted in each year. The area occupied by birds was determined from aerial photographs taken of the colony during the breeding season. Although recovery efforts were focused on pelican, cormorant, and tern nesting sites, other piscivorous waterbird species (e.g., California gulls, ring-billed gulls *L. delawarensis*, and great blue herons *Ardea herodias*) were also present at some of these nesting sites in some years. In most cases, the nesting habitat of these other colonial waterbird species was readily identifiable from aerial imagery, but small numbers of these other species could have deposited PIT tags that were included in the study.

Predation Rate Estimates

A hierarchical Bayesian model was used to estimate predation rates on suckers based on the number of PIT-tagged fish available and the number of tags recovered on the Upper Klamath Lake, Clear Lake Reservoir, Tule Lake, and Sheepy Lake bird colonies each year (Hostetter et al. 2015). The probability of recovering a sucker tag on a bird colony was the product of three stochastic processes: (1) the probability that a tagged fish is consumed (predation probability), (2) the probability that the tag is deposited on the nesting colony (deposition probability), and (3) the probability that the tag is detected by researchers following the breeding season (detection probability; Figure 2).

Tag detection probabilities.—Not all PIT tags deposited by birds on their nesting colony are subsequently detected by researchers after the breeding season (i.e., detection probabilities <1.0). For example, tags can be blown off the colony during windstorms, washed away during flood events, or otherwise damaged or lost during the breeding season. Previous research indicates that detection probabilities often vary considerably within and between colonies

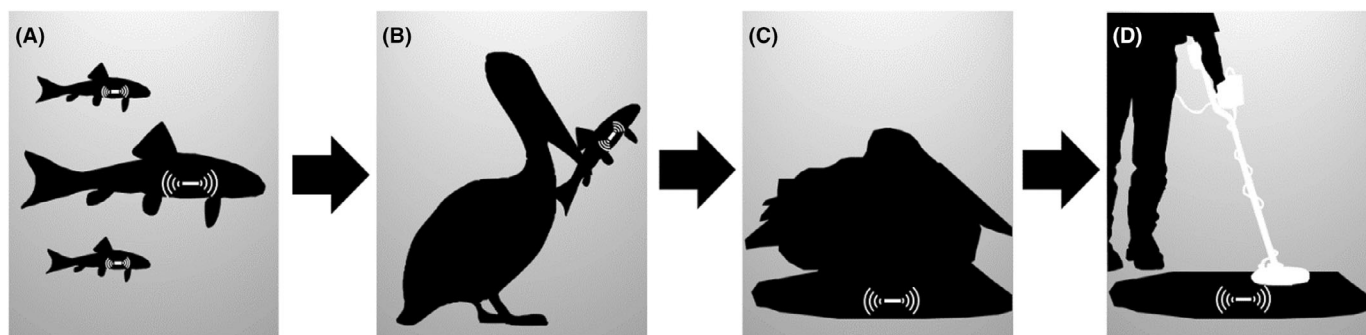


FIGURE 2. Conceptual model of the tag recovery process in capture–mark–recovery studies of avian predation on fish populations: (A) PIT-tagged population of suckers, (B) predation probability (the probability that a tagged sucker is consumed by a breeding bird), (C) deposition probability (the probability that the tag is deposited on the bird’s nesting colony), and (D) detection probability (the probability that the tag is detected by researchers after the breeding season). (Figure modified from Hostetter et al. 2015).

—variation that necessitates a direct measure of detection probabilities for each colony in each year (Evans et al. 2012, 2016; Hostetter et al. 2015; Payton et al. 2019). To address this, PIT tags with known tag codes were intentionally sown by researchers on colonies in Upper Klamath Lake, Clear Lake Reservoir, Tule Lake, and Sheepy Lake each year to estimate PIT tag detection probabilities (hereafter, referred to as “control tags”). Control tags were of the same size and type as those implanted in suckers. Control tags were sown throughout the areas occupied by nesting birds during the breeding season, identified through aerial imagery. Tags were randomly scattered and blindly recovered such that the detections (i.e., recoveries) of control tags during scanning efforts each year could be used to model the probability of detecting tags deposited throughout the breeding season via logistic regression. Roughly equal numbers of control tags were sown on each colony in each year, and sample sizes were selected by considering historical sample sizes (Evans et al. 2016). This approach allows for direct comparisons of independent detection probabilities, with similar precision among years (Payton et al. 2019).

Tag deposition probabilities.—Not all PIT tags consumed by breeding birds are subsequently deposited on their nesting colonies (i.e., deposition probabilities <1.0). Hostetter et al. (2015) previously estimated deposition probabilities of terns and cormorants by intentionally feeding PIT-tagged fish to breeding birds from multiple colonies in multiple years, and the proportion of known ingested tags subsequently recovered was used to estimate predator-specific deposition probabilities. The distribution of the median deposition probability from that study was 0.71 (95% credible interval = 0.51–0.89) for terns and 0.51 (0.34–0.70) for cormorants. Results from Hostetter et al. (2015) indicated that deposition probabilities did not vary considerably within or between years for a given predator species (cormorants or terns). Thus, for the purposes of this study, we assumed that

the deposition probabilities reported by Hostetter et al. (2015) for cormorants and terns were applicable to cormorant and tern colonies in the UKB. However, no previously published PIT tag deposition probability estimate was available for pelican colonies.

To determine the fraction of sucker PIT tags ingested by pelicans that were subsequently deposited on the colony, we followed the methods of Hostetter et al. (2015) by directly feeding dead fish implanted with PIT tags to adult pelicans from multiple colonies. Deposition probabilities were estimated by feeding suckers (FL range = 173–325 mm) and Rainbow Trout *O. mykiss* (FL range = 112–273 mm) with known tag codes to nesting pelicans on Clear Lake Reservoir (UKB) and on Badger Island (Columbia River, Washington), respectively, during the 2020 breeding season. To account for potentially different levels of colony attendance during the breeding season, multiple feeding periods or trials were conducted at each colony, with tagged fish consumed during the nest-building, egg incubation, and chick-rearing stages. Tagged suckers were consumed by adult pelicans throughout the course of each day (range = 0615–2042 hours) during each trial to mimic variable foraging times, and trials were designed to feed as many individual birds as possible. Suckers used in deposition trials were implanted with PIT tags of the same size and type that were implanted into live suckers in the UKB. A camouflaged boat was used to approach nesting birds and to present them with PIT-tagged fish. Only tagged fish that were known to have been consumed by an adult pelican were included in the study. Results from multiple colonies and multiple trials were used to assess whether pelican deposition probabilities varied by colony location (Clear Lake Reservoir or Badger Island), fish species (sucker or Rainbow Trout), and week and to bolster the sample sizes of tagged fish used to estimate pelican deposition probabilities for use in predation analyses. Sample sizes of PIT-tagged fish ($n = 401$; Table 1) were similar to those used in

the cormorant ($n=428$) and tern ($n=456$) deposition trials conducted by Hostetter et al. (2015).

The probability of an experimental deposition PIT tag being deposited on each colony was then inferred from the binomial process of recovering the experimental tag. That is, for each colony studied (Badger Island and Clear Lake Reservoir), we assumed

$$k_{ci} \sim \text{Binomial}(n_{ci}, \phi_c \times \psi_{ci}),$$

where k_{ci} is the number of PIT tags recovered from among the number of tags observed to be consumed (n_{ci}) on colony c in week i , ϕ_c represents the probability that a tag consumed in week i by a bird from colony c is subsequently deposited on the colony, and ψ_{ci} represents the probability that a tag deposited in week i is detected after the nesting season. Trial-specific deposition probabilities were ascribed a hyperdistribution:

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

where prior distributions of $\mu_\phi \sim \text{Normal}(0, 25)$ and $\sigma_\phi^2 \sim \text{Half-normal}(0, 25)$ were assigned. The colony-specific weekly probability of detection, ψ_{ci} , was assumed to be a logistic function of week:

$$\text{logit}(\psi_{ci}) = \beta_{c0} + \beta_{c1} \times i,$$

where β_{c0} and β_{c1} are both derived from uninformative priors ($\text{Normal}[0, 1,000]$).

Predation rates.— Following the methodology of Hostetter et al. (2015), predation rates were modeled independently for each year, each bird species (pelican, cormorant, or tern), each nesting location (Upper Klamath Lake, Clear Lake Reservoir, Tule Lake, or Sheepy Lake), and each sucker group (SARP juvenile; wild juvenile; or adult LRS, SNS, or SNS-KLS). The probability of recovering a sucker PIT tag on each colony in each year was modeled as the product of the three probabilities described above: (1) the probability

that the fish was consumed (θ), (2) the probability that the PIT tag was deposited on-colony (ϕ), and (3) the probability that the PIT tag was detected on-colony after the breeding season (ψ_i ; see also Figure 2).

Estimation of the probability that a fish was consumed was complicated by two factors: (1) the highly variable number of fish available to predators and (2) the unknown date of consumption for tags recovered from bird colonies. It is generally assumed that predation probabilities vary across time (Payton et al. 2019). Avian predation studies generally delineate release groups by week, with an assumption of exposure to depredation occurring within the same week of release. However, fish in this study were released/encountered throughout the year with uncertainty as to when they were consumed. We partitioned the year into exposure periods of one or more weeks delineated by weeks in which any fish were released/encountered and included all consecutive subsequent weeks in which no fish were released/encountered. We then estimated the predation probability for each partition. Explicitly, we let $g \in 1, \dots, G$ represent the predation groups and W_1, W_2, \dots, W_G represent the set of weeks, including the week of release/encounter and all subsequent weeks prior to the next release/encounter.

For each release group g , we let the simplex vector $[s_g \ \theta_{g,0} \ \theta_{g,1} \ \dots \ \theta_{g,C}]^T$ represent the probabilities that during the weeks of W_g , a fish alive at the beginning of W_g survived (s_g), died due to some unexplained reason ($\theta_{g,0}$), or was consumed by a bird from a given colony c ($\theta_{g,c}$, for $c \in \{1, \dots, C\}$, where C is the number of colonies assumed to be foraging in the given year).

We further assumed that these survival, predation, and mortality probabilities were similar from week to week, letting

$$\log(\theta_{g+1,c}) - \log(\theta_{g,c}) = \log(\theta_{g,c}) - \log(\theta_{g,C}) + \varepsilon_{c,g},$$

where $\varepsilon_{c,g} \sim \text{Normal}(0, |W_g| \times \sigma_c^2) \forall g \in \{1, \dots, G-1\}$, with $|W_g|$ denoting the number of weeks in group g . Using the recovery parameters described above, the probability of a fish released/encountered in the first week of W_g being consumed by colony c and recovered after the breeding season can be represented by $\gamma_{i,c}$ and enumerated as

$$\gamma_{i,c} = \theta_{g,c} \times \phi_c \times \bar{\psi}_{c,i} + s_g \times \chi_{g+1},$$

where

$$\chi_{g+1} = \theta_{g+1,c} \times \phi_c \times \bar{\psi}_{c,g+1} + s_{g+1} \times \chi_{g+2}$$

and $\bar{\psi}_{g,c}$ represents the arithmetic average probability of detection for tags consumed (and deposited) on colony c across all weeks in period g .

TABLE 1. Sample sizes of PIT-tagged suckers and Rainbow Trout consumed by American white pelicans nesting on an island in Clear Lake Reservoir and on Badger Island (Columbia River), respectively, and the number of tags recovered in 2020.

Colony	Trial (dates)	Consumed	Recovered
Clear Lake Reservoir	1 (May 8–10)	55	16
	2 (May 29–31)	97	48
	3 (Jul 1–3)	10	2
Badger Island	1 (May 17–19)	36	5
	2 (Jun 5–9)	95	33
	3 (Jul 5–10)	108	48
All		401	152

These assumptions allowed for the identification of temporal variation in predation rates across time while maintaining the integrity of the disparate release/encounter dates for each fish. Although survival and probabilities of other mortality are specified in the model, we neither attempted nor expected to precisely identify survival rates throughout the year, which are very weakly identifiable; rather, their presence is included to recognize the uncertainty associated with the indeterminate time of predation for any recovered tag. Furthermore, without recapture opportunities subsequent to the breeding season, s_G and $\theta_{G,0}$ are only jointly identifiable.

This parameterization allows us to simply model the recovery of tags as

$$\bar{h}_i \sim \text{Multinomial}\left(m_i, [\gamma_{i,1} \ \dots \ \gamma_{i,C} \ 1 - \sum_C \gamma_{i,C}]^T\right),$$

where \bar{h}_i is a $C+1$ length vector in which the c th entry enumerated the number of sucker PIT tags recovered from colony c (for $c = 1, \dots, C$) and the final entry was equal to the number of unrecovered tags from the available m_i tags observed/released in week i .

Informative beta priors were used to model deposition probability (ϕ). The shape parameters (α , β) are dependent on the predator species (pelican, cormorant, and tern) and are assumed to be mutually independent from colony to colony. For pelicans, we assumed an α of 6.70 and a β of 7.37 (based on the results of the deposition study presented herein). For cormorants, we assumed an α of 15.98 and a β of 15.29 (based on Hostetter et al. 2015). For terns, we assumed an α of 16.20 and a β of 6.55 (based on Hostetter et al. 2015). Several of the nesting areas were inhabited by multiple avian species in some years, with mixed-species breeding areas of pelicans and cormorants on Upper Klamath Lake and Clear Lake Reservoir and a mixed-species nesting area of pelicans, cormorants, and terns on Sheepy Lake. Without data to inform estimates of the impacts of each species independently, we assumed the probability that a tag was deposited by any species to be approximately equal (i.e., we used an average mixed-species deposition probability).

Annual predation rates were derived as the sum of the estimated number of PIT-tagged suckers consumed each week divided by the total number of PIT-tagged suckers available. Summation of weekly consumption estimates is necessary to accurately reflect variation and autocorrelation of predation rates and thus to create annual rates with accurate assessments of precision (Hamilton 1994).

Models were analyzed using the software STAN (Stan Development Team 2020), accessed through R version 4.1.0 (R Core Team 2014) via RStan version 2.21.2 (Stan Development Team 2020). All estimates presented here represent posterior distribution medians, with 95% credible

intervals representing 2.5% and 97.5% quantiles. To simulate random draws from the joint posterior distribution, we ran four Hamiltonian Monte Carlo–Markov chain processes. Each chain contained 4,000 warm-up iterations followed by 4,000 posterior iterations thinned by a factor of 4. Chain convergence was visually evaluated and verified using the Gelman–Rubin statistic (Gelman et al. 2013); only chains with zero reported divergent transitions were accepted. Posterior predictive checks compared the simulated and observed annual aggregate raw release and recovery numbers to ensure that the model estimates reflected the observed data. Reported estimates represent simulated posterior medians along with 95% highest (posterior) density intervals (95% credible interval) calculated using HDInterval version 0.2.0 (Meredith and Kruschke 2016).

RESULTS

Availability of PIT-Tagged Suckers

The number of PIT-tagged SARP juveniles released into Upper Klamath Lake and its tributaries ranged annually from 2,155 to 3,511 during 2018–2020 (Table 2). Only small numbers of PIT-tagged wild juveniles, however, were available for use in predation analyses, with 100 or more PIT-tagged wild juveniles available in Upper Klamath Lake during 2 years (2009 and 2012) and in Clear Lake Reservoir during 3 years (2017, 2019, and 2020; Table 2). The numbers of released or re-encountered PIT-tagged adult LRS, SNS, and SNS–KLS also varied considerably by location and year during 2009–2020 (Table 2). Sample sizes of available PIT-tagged adult LRS were large in Upper Klamath Lake, ranging annually from 14,211 to 28,278 tagged fish. Sample sizes of adult LRS were smaller in Clear Lake Reservoir, ranging annually from 186 to 1,354 tagged fish (Table 2). Sample sizes of SNS in Upper Klamath Lake and SNS–KLS in Clear Lake Reservoir ranged annually from 1,010 to 6,407 tagged fish (Table 2).

Bird Colony Locations and Sizes

Aerial surveys provided information on where to recover sucker PIT tags after each breeding season (Figure 1), as well as information on the approximate size of the colonies included in the study. Birds typically arrived to breeding colonies in late March to early April and remained on-colony until mid-August, although the exact timing varied each year and depended on colony success (i.e., rearing of young). The species composition (pelican, cormorant, tern) varied by nesting site and year, with pelicans and cormorants nesting on islands in Clear Lake Reservoir and Upper Klamath Lake and pelicans, cormorants, and terns nesting on islands in Sheepy and Tule

TABLE 2. Numbers of PIT-tagged adult Lost River Suckers (LRS), Shortnose Suckers (SNS), Shortnose/Klamath Largemouth Suckers (SNS-KLS), and juvenile suckers (wild and Sucker Assisted Rearing Program [SARP]) available and numbers subsequently recovered (in parentheses) on piscivorous waterbird colonies in the Upper Klamath Basin during 2009–2020. Recoveries represent the total number of suckers consumed from all colonies combined (see Table S.2 [available in the Supplement in the online version of this article] for recoveries by nesting location). Tag recoveries only include those tags that were recovered on colonies during the same year in which the fish was classified as being available to avian predators; the number was not adjusted to account for detection or deposition probabilities and thus represents the minimum number of tagged fish consumed in each year (see Methods). A dash (–) denotes that the sample size of available tagged fish was less than 100 and/or that PIT tag recovery did not occur at a given waterbody (Upper Klamath Lake or Clear Lake Reservoir) in that year. The SARP releases did not commence until 2018.

Sucker group	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
Upper Klamath Lake												
Adult LRS	14,211 (27)	–	–	22,607 (76)	–	26,298 (17)	28,278 (17)	–	16,972 (63)	17,728 (69)	16,423 (9)	17,314 (2)
Adult SNS	4,766 (25)	–	–	5,979 (75)	–	5,603 (18)	6,185 (19)	–	4,526 (61)	4,525 (41)	4,009 (5)	4,011 (2)
Juvenile (wild)	170 (6)	–	–	218 (6)	–	–	–	–	–	–	–	–
Juvenile (SARP)	–	–	–	–	–	–	–	–	–	2,155 (30)	2,750 (50)	3,512 (113)
Clear Lake Reservoir												
Adult LRS	185 (4)	299 (0)	469 (0)	513 (4)	721 (18)	674 (4)	469 (4)	833 (5)	1,080 (1)	889 (5)	1,354 (1)	957 (3)
Adult SNS-KLS	1,010 (16)	2,445 (5)	3,363 (50)	1,220 (9)	2,070 (50)	2,375 (17)	3,153 (17)	5,415 (89)	4,249 (32)	2,887 (12)	4,140 (26)	2,034 (15)
Juvenile (wild)	–	–	–	–	–	–	–	–	148 (1)	–	139 (2)	111 (4)

lakes. Pelican counts ranged annually from 142 to 2,763 breeding adults, cormorant counts ranged annually from 293 to 1,710 breeding adults, and tern counts ranged annually from 498 to 1,094 breeding adults, depending on the colony location and year (Table S.1).

Recovery of PIT Tags

In total, 193 PIT tags from SARP juveniles released into Upper Klamath Lake were recovered from pelican, cormorant, and tern colonies following each breeding season during 2018–2020 (Table 2). The number of tags recovered varied by colony location and year, with the majority of tags recovered on nesting sites located in Upper Klamath Lake ($n = 135$), followed by Sheepy Lake ($n = 53$), Tule Lake ($n = 3$), and Clear Lake Reservoir ($n = 2$; Table S.2). Overall, 12 and 7 tags from wild juvenile suckers released into Upper Klamath Lake and Clear Lake Reservoir, respectively, were recovered on bird colonies after the 2009, 2012, 2017, 2019, and 2020 breeding seasons (Table 2), and all of the tags from each release location were recovered on colonies within the water body of release (Table S.2). A total of 913 tags from adult suckers were recovered on bird colonies following the 2009–2020 breeding seasons (Table 2). Of these, 338 were adult SNS-KLS from Clear Lake Reservoir, 280 were adult LRS from Upper Klamath Lake, 246 were adult SNS from Upper Klamath Lake, and 49 were adult LRS from Clear Lake Reservoir. Of the adult sucker tags recovered, the majority were recovered from nesting sites in Upper Klamath Lake ($n = 561$) and Clear Lake Reservoir ($n = 477$), with only smaller numbers of adult sucker tags recovered on nesting sites in Sheepy Lake ($n = 80$) and Tule Lake ($n = 4$). None of the adult LRS and SNS-KLS from Clear Lake Reservoir was recovered at nesting sites on Upper Klamath, Sheepy, or Tule Lake (Table S.2), suggesting that birds from these colonies did not commute to Clear Lake Reservoir to forage on tagged suckers. Conversely, birds nesting at Clear Lake Reservoir, Sheepy Lake, and Tule Lake foraged on both adult and juvenile suckers in Upper Klamath Lake (Table S.2).

Detection and Deposition Probabilities

Estimated detection probabilities were generally high (often >0.80 , or 80%) at most nesting sites and years (Table S.3). Estimates were also relatively consistent across years at the same nesting site. For instance, despite the presence of multiple nesting sites across 12 breeding seasons, detection probabilities at colonies in UKB ranged annually from 0.85 (95% credible interval = 0.69–0.94) to 0.91 (0.70–0.97). Results suggest that the majority of sucker PIT tags deposited by birds on their nesting colony were subsequently recovered by researchers after the breeding season.

Trial-specific deposition probabilities for pelicans nesting on Clear Lake Reservoir and Badger Island ranged from 0.30 (95% credible interval = 0.10–0.54) to 0.66 (0.47–0.90; Figure 3). There was no evidence that deposition probabilities varied significantly by trial (week), colony (Clear Lake Reservoir or Badger Island), or the species of tagged fish (sucker or Rainbow Trout; statistical significance defined here and throughout as $\alpha = 0.05$; Figure 3). Average annual deposition probabilities (average of all three trials at each colony) were estimated to be 0.43 (0.31–0.59) and 0.50 (0.36–0.69) at the Clear Lake Reservoir and Badger Island colonies, respectively. Average annual deposition probabilities from all trials ($n = 6$) and both colonies (Clear Lake Reservoir and Badger Island) were estimated to be 0.47 (0.36–0.60). Results indicate that for every 100 tagged fish consumed by pelicans, 47 tags (or 47%) on average were deposited on breeding colonies.

Predation Rate Estimates

Predation rates by pelicans, cormorants, and terns on PIT-tagged SARP juvenile suckers, corrected to account for detection and deposition probabilities, ranged annually from 4.3% (95% credible interval = 2.9–6.7%) to 8.5% (6.3–12.7%) during 2018–2020 (Table 3). Of the nesting locations evaluated, the highest predation probabilities were consistently observed for pelicans and cormorants nesting at Upper Klamath Lake, with estimates ranging annually from 3.4% (2.1–5.5%) to 5.0% (3.5–7.6%) during 2018–2020. Higher estimates of predation coincided with the close proximity of nesting sites in Upper Klamath Lake to releases of SARP juveniles in that lake. Predation rates by pelicans, cormorants, and terns nesting on Sheepy Lake were highly variable, ranging annually from 0.2% (<0.1–0.8%) to 3.0% (1.8–6.9%), and indicated that birds were commuting from Sheepy Lake to forage on SARP juveniles released into Upper Klamath Lake, over 30 km away (Figure 1). Predation rates on SARP juveniles by pelicans and cormorants nesting on islands in Clear Lake Reservoir and by terns nesting in Tule Lake were consistently the lowest of those observed (<0.3%) during 2018–2020. Clear Lake Reservoir and Tule Lake were the two nesting areas that were the greatest distance from Upper Klamath Lake at over 50 km away. By year, estimated predation rates on SARP releases were highest in 2020 at 8.5% (6.3–12.7%), but estimates in 2020 were not significantly different from those observed in 2019 at 5.6% (4.0–8.2%); Table 3).

Predation rates by pelicans and cormorants on wild juvenile suckers ranged annually from 4.3% (95% credible interval = 0.9–13.2%) to 10.5% (3.8–24.5) for wild juveniles in Clear Lake Reservoir and from 10.0% (4.8–19.0%) to 10.1% (4.8–19.3%) for wild juveniles in Upper Klamath Lake during 2009–2020 (Table 2); these estimates were similar to, and in some years slightly higher than, those for SARP juveniles. Unlike the results for SARP juveniles,

there was no evidence that birds breeding at Clear Lake Reservoir, Sheepy Lake, or Tule Lake foraged on wild suckers from Upper Klamath Lake, but sample sizes of wild juveniles were small and data were limited to just 2 years (2009 and 2012; Table S.2). Predation on wild juveniles from Clear Lake Reservoir was limited to pelicans and cormorants nesting on islands in that reservoir, with no evidence that breeding birds from nesting sites in Upper Klamath, Sheepy, or Tule Lake were commuting to Clear Lake Reservoir to forage on wild juvenile suckers (Table S.2); however, here too, only small sample sizes of wild juveniles in Clear Lake Reservoir were available for predation analysis (Table 2).

Predation rates by pelicans, cormorants, and terns on adult suckers were consistently lower than predation rates observed for juvenile suckers, with predation rates on adult suckers in Upper Klamath Lake and Clear Lake Reservoir ranging annually from 0.1% (95% credible interval = <0.1–0.2%) to 7.2% (2.8–16.4%) during 2009–2020 (Table 2). Predation rates were consistently the lowest on adult LRS in Upper Klamath Lake, with estimates ranging annually from just 0.1% (<0.1–0.2%) to 1.1% (0.7–1.7%); Table 2). Predation rates on adult SNS in Upper Klamath Lake were higher than those on LRS in Upper Klamath Lake, with estimates ranging annually from 0.4% (0.2–0.9%) to 3.7% (2.6–5.7%); Table 2). Similar to SARP juveniles released into Upper Klamath Lake, predation on adult suckers in Upper Klamath Lake was from nesting colonies at Upper Klamath Lake as well as from colonies at Clear Lake Reservoir and, to a lesser degree, colonies at Sheepy Lake. For instance, 3.7% (2.6–5.7%) of adult SNS from Upper Klamath Lake in 2012 were consumed by birds from all colonies combined (Upper Klamath Lake, Clear Lake Reservoir, Sheepy Lake, and Tule Lake); of this percentage, 2.1% (1.3–3.8%) was associated with colonies on Upper Klamath Lake, 1.4% (0.8–2.6%) was associated with colonies on Clear Lake, and the remaining 0.1% (<0.1–0.3%) was associated with colonies on Sheepy Lake.

The highest estimates of predation on adult suckers were observed for suckers from Clear Lake Reservoir, with estimates ranging annually from 0.6% (95% credible interval = <0.1–1.8%) to 6.2% (4.0–10.2%) for SNS–KLS and from 0.4% (0.1–1.5%) to 7.2% (2.8–16.4%) for LRS during 2009–2020 (Table 2). Estimates were often in excess of 2.0%, with similar levels of predation observed in SNS–KLS and LRS when comparing estimates from the same year. Estimates of predation on adult SNS–KLS and LRS, however, were still consistently lower than those of wild juvenile suckers in Clear Lake Reservoir when comparing estimates from the same year. Unlike adult suckers in Upper Klamath Lake, all predation on Clear Lake Reservoir adult suckers was due to pelicans and cormorants that were nesting on islands within Clear Lake Reservoir.

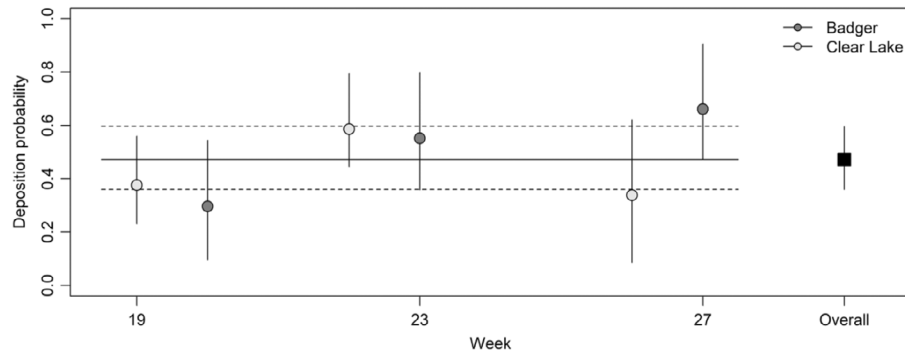


FIGURE 3. Trial-specific deposition probabilities (with 95% credible intervals) for American white pelicans nesting on Badger Island (Columbia River) and on Clear Lake Reservoir during 2020. Weeks are those of the Julian calendar. The solid line and black shaded square denote the average annual deposition probability estimated across all trials and colonies (“Overall”). The dashed lines represent the associated 95% credible interval for all colonies. See Table 1 for sample sizes of consumed PIT-tagged fish for each pelican colony and trial.

TABLE 3. Estimates of predation rates (%; with 95% credible intervals in parentheses) on PIT-tagged Lost River Suckers (LRS), Shortnose Suckers (SNS), Shortnose/Klamath Largescale suckers (SNS–KLS), and juvenile suckers (wild and Sucker Assisted Rearing Program [SARP]) by piscivorous colonial waterbirds nesting at colonies in Upper Klamath Lake, Clear Lake Reservoir, Tule Lake, and Sheepy Lake combined (i.e., cumulative predation effects). Predation estimates are adjusted to account for PIT tag detection and deposition probabilities that were unique to each predator species, colony, and year (see Methods). A dash (–) denotes that the sample size of available tagged fish was less than 100 or that PIT tag recovery did not occur at that site in that year. The SARP releases commenced in Upper Klamath Lake in 2018. Estimates update the minimum estimates of predation reported by Evans et al. (2016) during 2009–2014.

Year	Upper Klamath Lake suckers				Clear Lake Reservoir suckers		
	Adult LRS	Adult SNS	Wild juveniles	SARP juveniles	Adult LRS	Adult SNS–KLS	Wild juveniles
2009	0.5 (0.3–0.9)	1.5 (1.0–2.6)	10.1 (4.8–19.3)	–	7.2 (2.8–16.4)	4.6 (2.6–8.4)	–
2010	–	–	–	–	0.7 (<0.1–3.8)	0.6 (<0.1–1.8)	–
2011	–	–	–	–	0.8 (0.1–3.2)	4.0 (2.6–7.0)	–
2012	1.1 (0.7–1.7)	3.7 (2.6–5.7)	10.0 (4.8–19.0)	–	4.7 (1.8–10.8)	3.8 (1.8–7.6)	–
2013	–	–	–	–	6.7 (3.7–12.8)	6.2 (4.0–10.2)	–
2014	0.2 (0.1–0.4)	0.9 (0.5–1.8)	–	–	2.1 (0.8–4.9)	1.8 (1.0–3.7)	–
2015	0.2 (0.1–0.3)	0.8 (0.4–1.4)	–	–	2.5 (<0.1–5.5)	1.4 (0.7–2.7)	–
2016	–	–	–	–	1.2 (<0.1–3.0)	4.0 (2.8–6.5)	–
2017	1.0 (0.7–1.8)	3.6 (2.4–5.7)	–	–	0.4 (0.1–1.5)	1.9 (1.2–3.5)	4.3 (0.9–13.2)
2018	1.0 (0.7–1.7)	2.5 (1.6–4.0)	–	4.3 (2.9–6.7)	2.2 (0.9–5.0)	1.4 (0.7–2.7)	–
2019	0.2 (0.1–0.4)	0.6 (0.3–1.2)	–	5.6 (4.0–8.2)	0.5 (0.1–1.7)	1.7 (1.0–3.1)	5.6 (1.5–14.7)
2020	0.1 (<0.1–0.2)	0.4 (0.2–0.9)	–	8.5 (6.3–12.7)	1.2 (0.4–3.2)	2.0 (1.0–4.2)	10.5 (3.8–24.5)

DISCUSSION

Results of this study provide the first estimates of PIT tag deposition probabilities for breeding colonies of pelicans. Pelican deposition probabilities, coupled with previously published cormorant and tern deposition probabilities, as well as colony-specific detection probabilities provided the necessary data to estimate predation rates on SARP juvenile suckers and to update the minimum estimates of predation on wild juvenile and adult LRS and SNS as reported by Evans et al. (2016). Deposition-corrected estimates of predation rates reported herein were approximately two times greater than those previously reported by Evans et al. (2016). Collectively,

these results provide a more accurate and comprehensive assessment of piscivorous colonial waterbird predation effects on imperiled LRS and SNS in the UKB.

Results of this study indicated that for every 100 PIT tags consumed by pelicans, 47 on average were deposited on breeding colonies, where researchers could potentially recover them after the breeding season. Teuscher et al. (2015) also investigated pelican predation and fed PIT-tagged fish with known tag codes to pelicans, but estimates of detection probabilities from that study were unavailable, so the proportion of consumed tags that were lost due to off-colony deposition versus the imperfect detection of tags on bird colonies by researchers after the

breeding season was unknown. Although estimates of detection probabilities in this study were generally high (>0.80), the results of this and other studies indicate that detection probabilities can vary by colony, year, and week, necessitating a direct measure of detection probability at each colony in each year (Evans et al. 2012, 2016; Osterback et al. 2013; Hostetter et al. 2015; Payton et al. 2019). Similar to the results of the cormorant, tern, and gull deposition study conducted by Hostetter et al. (2015), pelican deposition probabilities did not vary significantly by colony or by period or trial within the breeding season. Small sample sizes of consumed tagged fish during some trials, however, resulted in imprecise weekly estimates of pelican deposition probabilities, and results were limited to a single year (2020). Despite these caveats, due to the lack of intra-annual variation in estimates of deposition and the similar estimates of deposition from two different pelican colonies on two different groups of tagged fish (salmonids and catostomids), results suggest that the pelican deposition estimate derived from this study is applicable or appropriate for use in other pelican predation studies utilizing PIT-tagged fish.

Deposition probability estimates for pelicans (0.47; 95% credible interval = 0.36–0.60) were similar to those for cormorants (0.51, 0.34–0.70; Hostetter et al. 2015). Deposition probability estimates for pelicans and cormorants were, however, lower than those for terns (0.71, 0.51–0.89; Hostetter et al. 2015). Several of the nesting areas that were scanned for sucker PIT tags in the UKB were from mixed-species breeding sites, where the avian species responsible for depredation on a given tag (pelican, cormorant, or tern) was unknown. Results suggested that the assumption of equal deposition via use of an average deposition probability for pelicans and cormorants (0.50, 0.27–0.69) at breeding sites on Clear Lake Reservoir and Upper Klamath Lake had little influence on estimates of predation probabilities because the estimates of pelican and cormorant deposition were so similar. However, use of an average deposition probability for pelicans, cormorants, and terns (0.56, 0.25–0.82) at nesting sites in Sheepy Lake could (1) slightly underestimate predation if most of the tags were deposited by pelicans and cormorants or (2) slightly overestimate predation if most of the tags were deposited by terns. For instance, a predation rate of 5% based on a deposition probability for a mixed pelican–cormorant–tern colony would be closer to 4% if most of the recovered tags were consumed and deposited by terns; conversely, the predation rate would be closer to 6% if most of the tags were consumed and deposited by pelicans or cormorants.

Across all nesting colonies, predation by pelicans, cormorants, and terns on SARP juveniles released into the Upper Klamath Lake system accounted for an estimated 4.3–8.5% of available suckers annually. Given the imperiled status of these fish and efforts to bolster recruitment

through SARP, these impacts may be considered substantial by some managers. Suckers from SARP appear to suffer high mortality within the first year of release, which is consistent with the poor survival observed for wild juvenile suckers (Burdick and Martin 2017). Of the SARP suckers released as part of this study, less than 1% were subsequently detected alive on remote PIT tag antennas in the Upper Klamath Lake system more than 5 months after their release (through spring 2021). Results of a radiotelemetry study conducted on SARP suckers released in the spring during 2018 and 2019 also suggested that substantial mortality occurred, with the majority of suckers presumably dead by the end of the summer each year after release (M. Shaffer, USFWS, personal communication). As such, despite predation rates as high as 8.5% annually, evidence suggests that predation by pelicans, cormorants, and terns likely represented a small component of the apparently high total mortality experienced by SARP suckers during 2018–2020.

There was some evidence that predation impacts on wild juvenile suckers were slightly higher than impacts on hatchery-reared SARP juvenile suckers. Small sample sizes of wild suckers, however, resulted in imprecise estimates of predation, so relative differences in predation between wild and SARP suckers should be interpreted cautiously. Comparisons do provide evidence that suckers reared in captivity were not substantially more susceptible to predation than their wild counterparts, as some other studies have demonstrated (Fritts et al. 2007; Hostetter et al. 2012). Mortality of SARP suckers associated with factors other than avian predation could also influence the number of SARP fish available to predators compared with naturally reared suckers. Thus, larger sample sizes of PIT-tagged wild juvenile suckers and comparisons of predation on a known number of wild and SARP juvenile suckers at the same location and time would enhance our understanding of sucker susceptibility to colonial waterbird predation based on rearing history.

Results of this study indicated that predation on adult suckers was consistently lower than that observed on juvenile suckers. The greater susceptibility of juvenile suckers to avian predation is likely due, in part, to the gape width and size of terns, cormorants, and pelicans: terns are capable of consuming fish upwards of 280 mm, cormorants can consume fish upwards of 450 mm, and pelicans can consume fish upwards of 730 mm (Hatch and Weseloh 1999; Hostetter et al. 2012; Evans et al. 2016). As such, juvenile suckers are subject to predation by all three predator species (terns, cormorants, and pelicans), but terns are not capable of consuming adult-sized suckers, and many of the larger-sized adult suckers—particularly LRS—exceed the gape width of cormorants. On the other hand, pelicans can consume all but the largest individuals of LRS (Evans et al. 2016). The smaller size of juvenile suckers may also increase their

susceptibility to other piscivorous waterbird species that were not investigated as part of this study but have been documented in the UKB. For instance, Forster's terns *Sterna forsteri*, great blue herons, common mergansers *Mergus merganser*, and grebes *Aechmophorus* spp. may be consuming juvenile suckers, but impacts to adult-sized suckers from these species are likely small or nonexistent (Evans et al. 2016). These species are also less numerous compared with pelicans, cormorants, and terns in the UKB (Shuford 2010). In the case of gulls *Larus* spp., which are not strictly piscivorous but are numerous in the UKB (several-thousand breeding adults annually; Shuford 2010), no sucker PIT tags were recovered as part of this study on colony areas that were exclusively used by nesting gulls, suggesting that gull impacts to both juvenile and adult suckers were negligible. It should also be noted that estimates of predation on both juvenile and adult suckers were from actively nesting or breeding colonies of pelicans, cormorants, and terns, whereas impacts from nonbreeding birds or failed breeders were not included in estimates of predation. In addition to avian species, the impacts to suckers from piscivorous predators, like Rainbow Trout and nonnative Brown Bullheads *Ameiurus nebulosus*, are unknown but could also contribute to juvenile sucker mortality. For instance, Rainbow Trout have been confirmed to feed on sucker eggs and likely consume some larvae in Upper Klamath Lake during the spring (S. Burdick, USGS, personal communication).

Despite lower levels of avian predation on adult suckers compared with juvenile suckers, predation on adults may have a greater overall effect on the population at large. This is because avian predators are removing individuals from the population that are capable of spawning for multiple years, as SNS and LRS reach maturity at ages 5–9 and can live for more than 30 years (Janney et al. 2008; Terwilliger et al. 2010). Avian predation is also one of the largest known causes of adult sucker mortality in the UKB. For instance, despite annual avian predation rate estimates of just 1–7%, annual estimates of total mortality (i.e., 1 – survival) for adult suckers during 2009–2018 were just 6–26% in Upper Klamath Lake and were 5–55% in Clear Lake Reservoir (depending on the sucker species; Hewitt et al. 2018, 2021). Thus, avian predation represented a relatively large proportion of all sources of adult sucker mortality in some years. For instance, in Clear Lake Reservoir during 2018, avian predation accounted for nearly half (49%) of the LRS mortality from all sources. For the other years, across both species and locations, avian predation accounted for 2–35% of the estimated total adult sucker mortality. Predation impacts presented herein were also estimated on a seasonal or annual basis, but the effects of predation across multiple years may be greater than what is implied by annual estimates of predation alone, especially during years with little or no juvenile recruitment into sucker spawning populations.

Recent data suggest that limited or infrequent access to spawning tributaries and an inability to return to Clear Lake Reservoir after spawning are limiting factors for adult suckers, and these factors appear to correspond with higher susceptibility to avian predation (Banet et al. 2021; Hewitt et al. 2021). Predation on suckers in spawning tributaries to Clear Lake Reservoir has also been confirmed (Banet et al. 2021), similar to predation by pelicans and cormorants on Bonneville Cutthroat Trout *O. clarkii utah*, Yellowstone Cutthroat Trout *O. clarkii bouvieri*, Lahontan Cutthroat Trout *O. clarkii henshawi*, and Cui-ui *Chasmistes cujus* during spawning migrations in other systems (Scoppettone et al. 2014; Teuscher et al. 2015; Budy et al. 2016). Lower Clear Lake Reservoir water levels that resulted in limited (2013) or no (2015) access to spawning tributaries also corresponded with higher avian predation (Banet et al. 2021; Hewitt et al. 2021). The large number of pelicans nesting at Clear Lake Reservoir in 2020 was similar to the number present in 2013 (Evans et al. 2016); however, predation rates, on average, were lower in 2020 than in 2013. This may have been due to higher water levels in 2020 relative to 2013, which likely reduced pelican access to spawning suckers in 2020.

Breeding populations of pelicans, cormorants, and terns—all native piscivorous colonial waterbirds—have historically nested at colonies in the UKB (Shuford 2010). Results of this and other studies indicate that colony sizes vary substantially by species, colony, and year (Shuford 2010; Evans et al. 2016; Lawes et al. 2021). This is typical of piscivorous waterbird colonies in high-desert wetland ecosystems, such as those in the Harney Basin and Warner Valley, Oregon, where suitable nesting habitat varies based on fluctuating water levels due to periodic drought and flooding events (Lawes et al. 2021). Given that terns, cormorants, and pelicans are long-lived species (in excess of 20 years; Suryan et al. 2004; Roby et al. 2021) and given that colonies in the UKB show connectivity to other breeding sites in the Pacific Northwest (e.g., Columbia River basin; Roby et al. 2021), variable colony sizes in the UKB are expected in future years, particularly in a region that continues to experience highly variable hydrologic conditions. This, in part, will impact predation pressure on ESA-listed suckers in the UKB.

Finally, although more accurate estimates of predation by breeding colonies of pelicans, cormorants, and terns were generated as part of this study, several uncertainties remain regarding the degree to which predation limits sucker survival in the UKB. More specifically, estimates of survival for SARP-released juvenile suckers are currently lacking but are necessary to determine the proportion of SARP mortality (all sources) that is due to avian predation. Although beyond the scope of this study, recently developed state-space mark–recapture–recovery models, which incorporate tag detections from both live and dead animals

(King 2012; Hostetter et al. 2018; Payton et al. 2019), could be used to jointly estimate predation and survival in the same group of tagged fish, thus providing a better understanding of predation across space and time as well as the importance of avian predation relative to other sources of mortality experienced by suckers in the UKB. These models could also begin to evaluate the degree to which environmental conditions experienced by suckers (e.g., poor water quality, loss of deepwater refugia, and limited access to spawning tributaries) and/or poor fish condition are associated with sucker susceptibility to bird predation in the UKB (Evans et al. 2016; Banet et al. 2021). Similarly, for SARP-released suckers, the effects of release size, location, and timing (e.g., spring, fall, or winter season) on overall mortality and avian predation could be evaluated if releases are designed to provide contrast in these factors. Addressing these remaining uncertainties would help resource managers to better understand the impacts of predation by piscivorous waterbirds on the survival of ESA-listed sucker populations in the UKB.

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ORCID

Allen F. Evans  <https://orcid.org/0000-0002-9806-9713>

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.