

## High predation on small populations: avian predation on imperiled salmonids

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**Abstract.** Generalist predators can contribute to extinction risk of imperiled prey populations even through incidental predation. Quantifying predation on small populations is important to manage their recovery, however predation is often challenging to observe directly. Recovery of prey tags at predator colonies can indirectly provide minimum estimates of predation, however overall predation rates often remain unquantifiable because an unknown proportion of tags are deposited off-colony. Here, we estimated overall predation rates on threatened wild juvenile steelhead (*Oncorhynchus mykiss*) by generalist adult Western Gulls (*Larus occidentalis*) in six central California (USA) watersheds. We estimated predation rates by gulls from the recapture of PIT (passive integrated transponder) tags that were originally inserted into steelhead and were subsequently deposited at a Western Gull breeding colony, Año Nuevo Island (ANI). We combined three independent datasets to isolate different processes: (1) the probability a tagged steelhead was consumed during predation, (2) the probability a consumed tag was transported to ANI, and (3) the probability a transported tag was detected at ANI. Together, these datasets parameterized a hierarchical Bayesian model to quantify overall predation rates while accounting for tag loss between when prey were tagged and subsequent tag detection at ANI. Results from the model suggest that low recovery rates of PIT tags from steelhead at ANI were mostly driven by low probabilities of transportation ( $\leq 0.167$ ) of consumed tags to ANI. Low transportation probabilities equate to high per-capita probabilities of predation ( $\geq 0.306/\text{yr}$ ) at the three watersheds in closest proximity to ANI, whereas predation rates were uncertain at watersheds farther from ANI due to very low transportation rates. This study provides the first overall estimate of Western Gull predation rates on threatened wild juvenile steelhead and suggests gull predation on salmonids is a larger source of mortality than was previously estimated from minimum predation rates. This study thus represents an important example of high rates of incidental predation by a generalist consumer on an imperiled prey and provides a quantitative framework to inform robust estimates of predation rates on small populations that can be applied to other systems where direct observation of predation is not feasible.

**Key words:** Bayesian modeling; California, USA; central-place forager; food web; incidental predation; *Larus occidentalis*; *Oncorhynchus mykiss*; PIT tag; steelhead; stream; Western Gull.

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## INTRODUCTION

Predation on imperiled populations may contribute to extinction risk or limit their recovery. In some cases, small prey populations may be relatively buffered from predation when refuges are available or if predators switch to target more abundant prey (Holling 1959, Ackerman 2002, Twardochleb et al. 2012). Furthermore, if predators are specialists, their populations may decline following the decline of their prey, thereby reducing predation rates (Elton and Nicholson 1942, Hanski et al. 2001). Alternatively, if generalist predators continue to prey on small populations, these prey populations may suffer local extinction (Spiller and Schoener 1998) or may experience further population decline even when predation is incidental (Vickery et al. 1992). In these scenarios, there may be few prey individuals relative to the number of predators, and even incidental predation can result in high predation rates (Wittmer et al. 2005). Therefore, the role of predation by generalist predators can be an important factor in the dynamics of small prey populations.

Quantifying predation rates on imperiled populations is often difficult as predation is a rare event with few prey relative to predators. For this reason, researchers have applied a variety of approaches to estimate predation rates indirectly. Estes et al. (1998) estimated predation rates on sea otters (*Enhydra lutris*) by comparing long-term population trends in locations with and without predatory killer whales (*Orcinus orca*). Visual observations and bioenergetics models were combined to quantify the impact of killer whale predation on sea otter populations (Estes et al. 1998, Williams et al. 2004). Alternatively, Fernández-Olalla et al. (2012) combined long-term monitoring of population decline of a vulnerable grouse species (*Tetrao urogallus*) with the removal of mesopredators to quantify the

impact of predation on the grouse population growth rate which guided management strategies for population recovery. In both studies, long-term datasets and natural or intentional experiments facilitated quantification of the impact of predators on the decline of native prey. However, long-term population data are rare, especially in conjunction with manipulations of predator populations. Therefore, estimating predation in the absence of long-term data may be necessary to identify significant sources of mortality for populations at risk of extirpation.

In systems with central-place foragers, the return of predators with prey items to their roosting or nesting sites can be used to estimate rates of predation. Specifically, where prey can be uniquely marked with identification tags, recovery of regurgitated or defecated prey tags at predator roosting or breeding sites can be used to quantify minimum predation rates. This method has been applied in freshwater and marine systems where fish tags were recovered within colonies of piscivorous avian predators (e.g., Evans et al. 2011, Frechette et al. 2012). For example, passive integrated transponder (PIT) tags are often used to individually mark juvenile salmonids (*Oncorhynchus* spp). These tags can be subsequently detected at piscivorous avian predator colonies once predators have regurgitated or defecated the consumed tag. For example, by using the recovery of PIT tags, Evans et al. (2012) estimated that predation by Caspian Terns (*Hydroprogne caspia*) and Double-crested Cormorants (*Phalacrocorax auritus*) constitute between 2.5% and 16% of juvenile salmonid mortality in the Columbia River. Because PIT tags are passive and therefore cannot be detected remotely, estimates of predation rates using recoveries of prey tags require that tags are (1) consumed during predation, (2) transported to the predator colony, and then (3) successfully detected at the colony with a mobile PIT tag antenna (Fig. 1).

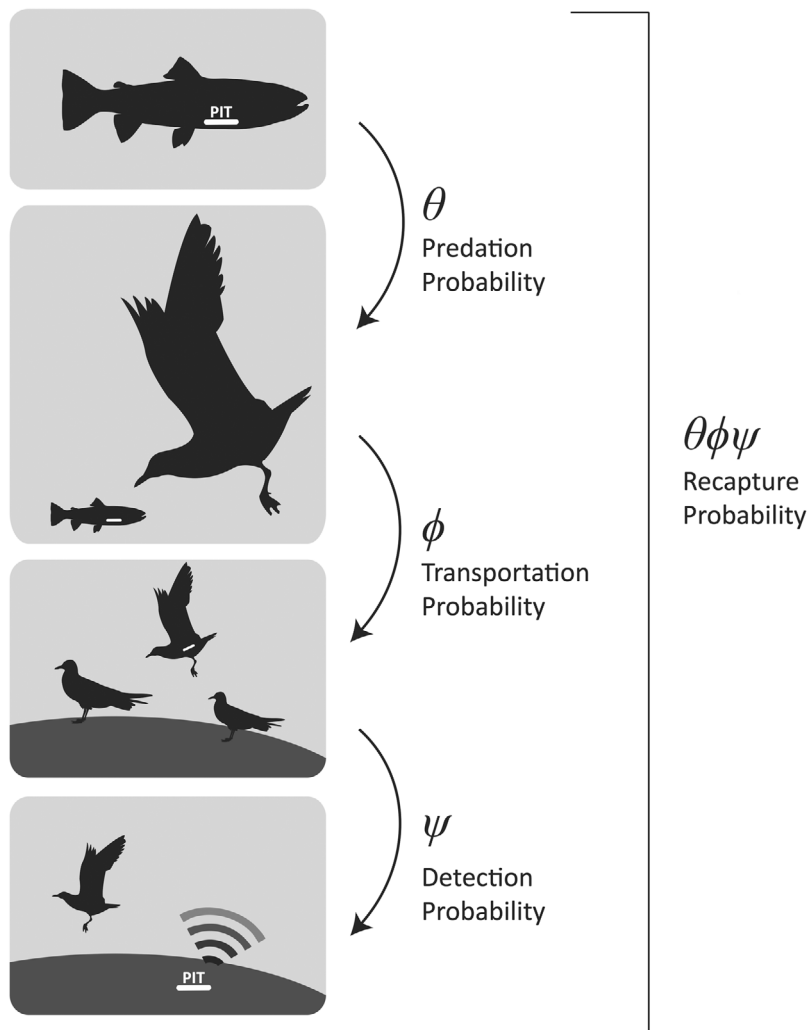


Fig. 1. The three-step process for how PIT tags from tagged juvenile salmonids are recaptured on avian predator colonies, where each step has its own probability of occurrence. For a PIT tag to be recaptured at an avian predator colony, a PIT-tagged salmonid first has to be consumed by an avian predator (with probability  $\theta$ ), transported to the predator colony (with probability  $\phi$ ), and then detected on the colony (with probability  $\psi$ ). Therefore, the probability of recapturing a PIT tag from a tagged salmonid is the probability, or product, of all three steps occurring (with probability  $\theta\phi\psi$ ).

Successful recoveries of tags, therefore, only represent consumed tags that undergo all three steps and therefore do not include tags that were lost between steps. Thus, as acknowledged by previous studies, predation estimates from tag recoveries only represent minimum predation rates (Evans et al. 2012, Frechette et al. 2012). To this point, no peer-reviewed study has incorporated estimates of these three processes and their uncertainty to estimates of predation.

Pacific salmon and steelhead (*Oncorhynchus mykiss*) populations along the west coast of North America have declined over the last century due to destruction of habitat, climate change, artificial propagation from hatcheries, construction of dams, over-harvest, and other anthropogenic and natural factors (Ruckelshaus et al. 2002, Gustafson et al. 2007). Consequently, approximately half of the unique Pacific salmon populations in the United States (managed as

Evolutionary Significant Units for salmon or Distinct Population Segments for steelhead) have been listed as threatened or endangered under the Endangered Species Act (Good et al. 2005). Whereas anthropogenic factors have substantially reduced many salmon populations (Sheer and Steel 2006, Selbie et al. 2007), the added impacts of predation may drive further population decline or impede recovery. Concerns regarding the impact of avian predation on salmonid populations has resulted in extensive research in large river systems such as the Columbia River Basin (Collis et al. 2001, Antolos et al. 2005, Good et al. 2007, Evans et al. 2012) and the Sacramento-San Joaquin River Basin (Evans et al. 2011, Adrean et al. 2012), whereas relatively little is known about the impact of avian predators on salmonids in the many small coastal watersheds along the coast of California (but see Frechette et al. 2012). California salmon populations are at the southern extent of the species' ranges and are of particular concern as many populations are declining (Moore et al. 2011). For example, coastal populations of endangered coho salmon in small central California watersheds are nearing extinction (Miller 2010). Due to a lack of data on natural sources of mortality, the recently released central coast coho salmon recovery plan recommended an assessment of avian predation on coho salmon to determine the impact predation has on salmon mortality (National Marine Fisheries Service 2012). Therefore, quantifying predation on imperiled populations of salmon may identify a critical factor that influences their recovery or extirpation.

Here we estimate predation rates on imperiled populations of threatened wild juvenile steelhead by adult Western Gulls (*Larus occidentalis*) in central California watersheds. Western Gulls are abundant generalist predators that feed on trash, carrion, and are known to prey on outmigrating juvenile salmonids (Frechette et al. 2012). In this study, we ask: what are overall predation rates by Western Gulls on wild juvenile steelhead and how do predation rates by these central-place foragers vary among watersheds and years? We use a large dataset of tagged juvenile steelhead and associated recaptured tags at Año Nuevo Island (ANI) where a large Western Gull colony is located to provide estimates of predation. We develop a Bayesian model that integrates three

datasets to provide estimates of gull predation that account for tag loss between the initial PIT tagging of juvenile steelhead and the subsequent detection of PIT tags at ANI. These methods provide the first overall estimate of adult Western Gull predation rates on threatened populations of central California coast steelhead. From a methodology perspective, this research highlights the importance of estimating multiple processes of unobserved tag loss and using a robust quantitative framework to accurately estimate predation rates.

## METHODS

### Study system

We studied six coastal watersheds within San Mateo and Santa Cruz counties (California, USA) and Año Nuevo Island (ANI), a small island (10 ha) located 1.6 km off Point Año Nuevo (Fig. 2). ANI provides habitat to many species of seabirds and marine mammals, and is one of the three largest Western Gull colonies in central California (Carter et al. 1992, Capitolo et al. 2009). All six study watersheds (Gazos Creek, Waddell Creek, Scott Creek, San Lorenzo River, Soquel Creek, and Aptos Creek) drain directly into the Pacific Ocean and support wild populations of threatened central California coast steelhead. The populations of steelhead in the study watersheds are small; for instance, the abundance of adult steelhead in Scott Creek from 2004 through 2012 ranged from only 109 to 440 individuals (S. A. Hayes, *unpublished data*). We focused on wild juvenile steelhead for this study because they are the only salmonid species present at all six study watersheds. It is worth noting that Scott Creek also supports hatchery-raised steelhead and a small run of wild and hatchery-raised endangered coho salmon (*Oncorhynchus kisutch*). The Scott Creek population of coho salmon is generally recognized as the southernmost population of coho (Federal Register 2005) and although they are also likely exposed to gull predation, their numbers are too small to quantify predation.

The study region is dominated by a Mediterranean climate with warm dry summers and mild wet winters. Stream flow in the study creeks varies with episodic rainfall in the winter, whereas in the late summer and fall the

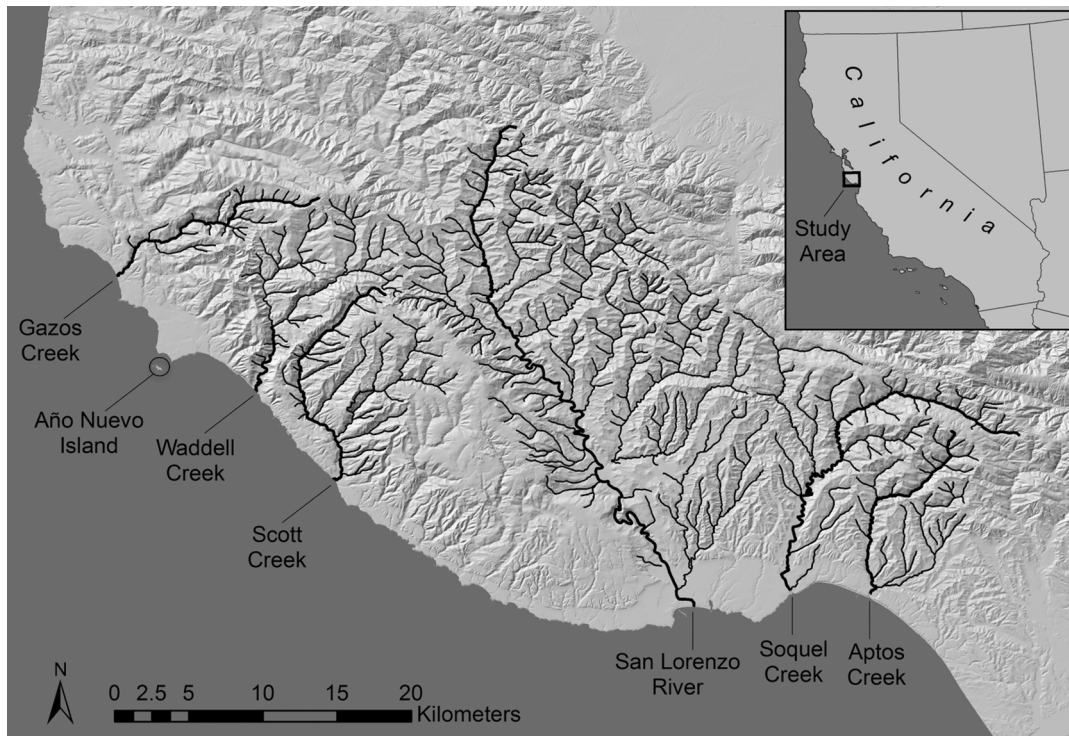


Fig. 2. Location of the six central California (USA) watersheds (Gazos Creek, Waddell Creek, Scott Creek, San Lorenzo River, Soquel Creek, and Aptos Creek) and the seabird breeding colony (Año Nuevo Island) that compose the study area.

combination of low stream flow and oceanic wave action at creek mouths result in a bar-built estuary that creates a freshwater lagoon. Typically, sand bar formation creates a barrier between creek surface flow and the ocean, thereby restricting the timing of juvenile salmonid outmigration to the winter and spring seasons when the creeks are connected to the ocean (Bond et al. 2008, Hayes et al. 2008, 2011).

During the juvenile salmonid outmigration period (typically December through June), Western Gulls use shallow creek mouths to drink, bathe, and opportunistically prey on outmigrating juvenile salmonids as they migrate to the ocean (Fig. 3). Therefore, Western Gulls prey primarily on juvenile steelhead after steelhead survived the mortality bottlenecks within their first year of life and completed the freshwater rearing phase of their lifecycle. The number of adult Western Gulls breeding at ANI increased by almost an order of magnitude from 1976 to 2003 (Thayer and Sydeman 2004). This increase is possibly due to accessibility of anthropogenic

food sources, including local waste management facilities (i.e., landfills), which may subsidize the gull population and could contribute to incidental predation and local extinction of steelhead populations (A.-M. K. Osterback, *unpublished data*).

There is both direct and indirect evidence that Western Gulls are predators of juvenile salmonids in the study region. First, we directly observed both juvenile and adult Western Gulls feeding on outmigrating juvenile salmonids at the shallow mouth of Scott Creek (Frechette 2010). These predation events were infrequent or sporadic enough that quantifying predation rates through direct observation alone was not feasible. Second, we previously documented that between 0.1 and 4.6% of all PIT tags from juvenile salmonids from each of the six study watersheds were detected at ANI (Frechette et al. 2012). Although other species of piscivorous birds and mammals use ANI for breeding and roosting habitat, we identified adult Western Gulls as the primary predator species and age



Fig. 3. A photo taken at the mouth of Scott Creek, just before the creek enters the ocean. Hundreds of Western Gulls congregate at shallow creek mouths to bathe, drink, and opportunistically feed on items that are transported downstream by stream flow, including outmigrating juvenile salmonids.

class responsible for deposited PIT tags at ANI (Frechette et al. 2012, Hayes et al. 2012). The predation rate estimates reported by Frechette et al. (2012) represent minimum estimates because PIT tags were recaptured after being consumed during predation by a gull, transported to ANI, and subsequently detected at ANI (Fig. 1). As a result, overall predation rates are potentially much higher than the reported minimum predation rate estimates.

#### *Data collection and modeling*

We combined three independent datasets to parameterize the variables required to estimate overall predation rates of juvenile wild steelhead by adult Western Gulls at each of the six study watersheds. We describe the first two datasets in turn. The third dataset is from a previous study (Frechette et al. 2012) and is incorporated in the model parameters. We then detail a model for estimating predation rates from these data.

Therefore this study evaluates all three steps of tag recapture at ANI, and quantifies the probability tagged steelhead were preyed on, transported to, and detected at ANI (Fig. 1).

*Steelhead tag recapture study.*—We and the National Marine Fisheries Service (NMFS) PIT-tagged wild juvenile steelhead in the six study watersheds and subsequently scanned ANI annually to detect any deposited PIT tags that were regurgitated or defecated by Western Gulls. This component of the study represents the recapture probability, which is the net probability of predation, transportation, and detection probabilities (Fig. 1). PIT tagging of juvenile steelhead in the study watersheds was conducted by the NMFS between 2003 and 2011. Fish were captured through a combination of downstream migrant trapping, beach seining, and backpack electrofishing. At Gazos Creek, San Lorenzo River, and Aptos Creek, juvenile steelhead were captured exclusively in the lagoon by beach

seining. Although fish were also captured with beach seining in the lagoons of the other three watersheds (Waddell, Scott, and Soquel Creeks), steelhead were also captured in downstream migrant traps in the creek mainstem (Waddell and Scott Creeks only) and during electrofishing surveys in the upper watershed (Scott and Soquel Creeks only). Individuals tagged in the lagoon are predominately age 0+ and age 1+ steelhead, whereas individuals tagged in the creek mainstem and upper watershed include the entire range of age classes, some of which may never attempt to out-migrate (Hayes et al. 2008). Therefore, our estimates reflect Western Gull predation on the entire tagged wild juvenile steelhead population in each watershed as they migrate out to the ocean. All juvenile steelhead were handled according to Hayes et al. (2004), where date, time, watershed, and morphometric features (fork length and weight) were recorded for each fish. We quantified watershed distance as the linear distance of the creek mouth to Año Nuevo Island (ANI). Beginning in 2006, we scanned ANI annually to recapture deposited PIT tags. We conducted scans by traversing the entire island with a mobile PIT antenna (for equipment specifications, see Bond et al. 2007) and GPS to mark location and identification of deposited tags (for more details, see Frechette et al. 2012). Because annual scans at ANI did not begin until 2006, we excluded from our analysis all steelhead PIT-tagged prior to 2005. This was done to avoid the complication of potential loss of tags to wave action or burial in years prior to annual scanning that could skew recapture rates for those years.

To account for the variation in outmigration timing of juvenile steelhead, we assigned each steelhead an outmigration year based on the date each fish was last handled and the date of lagoon closure at Scott Creek. For example, tagged juvenile steelhead last handled prior to lagoon closure (January until lagoon closure) were assumed to out-migrate that same calendar year before low stream flow resulted in lagoon closure. Tagged juveniles last handled after lagoon closure were categorized as outmigrants in the following year because outmigration cannot resume until the following winter when adequate rainfall opens the lagoon and reconnects the creek with the ocean. The date of lagoon

closure at Scott Creek was applied to the other five watersheds because consistent data are lacking on the timing of lagoon closure at other sites.

*Transportation ("hotdog") experiment.*—In 2010, we fed between 43 and 586 PIT tags to adult Western Gulls at each creek mouth and then subsequently scanned ANI to quantify the proportion of experimental tags that were successfully transported and detected on the island. Therefore this experiment evaluated the last two steps of tag recapture at ANI: transportation and detection (Fig. 1). From 18 March 2010 through 7 July 2010, we fed gulls at two watersheds on each sampling day using stratified sampling to randomly select watershed and order (first or second site of the day). Stratified sampling was conducted to minimize effects of season and time of day on transportation rates by ensuring that all sites were visited at least once before any one site was revisited, and all sites were visited with a similar representation of first or second feedings of the day. PIT tags were fed to gulls at creek mouths using two different vehicles of delivery. For the first method, PIT tags were inserted into miniature hotdogs (Hillshire Farm Beef Lit'l Smokies) and tossed out with a folding slingshot to maximize the number of different individual gulls that ingested tags. Hotdogs were used as an economical way to deliver PIT tags to gulls. We also inserted PIT tags into pre-thawed Icelandic capelin (*Mallotus villosus*) in a paired experiment to evaluate whether hotdogs were appropriate substitutes for PIT-tagged fish. The Icelandic capelin is a pelagic fish similar in size and shape to juvenile steelhead. The two delivery methods (hotdogs and capelin) were used as proxies for juvenile steelhead since feeding tagged juvenile steelhead to avian predators was not permitted due to the threatened status of these fish. A primary observer directly observed tag consumption by gulls with the unaided eye and a second observer confirmed each consumption event using 8 × 42 binoculars. Species and age class were recorded for each bird that consumed an experimental tag, and the total count of each species and age class of all birds at the creek mouth were recorded at each site after all tags were fed.

To evaluate whether feed type, time of day, or season influenced transportation rates of PIT tags

to ANI, we conducted paired analyses at the three most northern watersheds: Gazos Creek, Waddell Creek, and Scott Creek. We evaluated these comparisons at the northern watersheds only because we postulated watersheds closer to ANI would have the highest transportation rates and therefore yield a larger sample size to adequately address these comparisons. We evaluated the influence of feed type on transportation rates by feeding both hotdogs and Icelandic capelin at all three of these watersheds. To evaluate whether time of day influences transportation rates, we also conducted paired evening (between 18:00 and 19:00) and subsequent morning (between 07:00 and 11:00) feedings at Gazos Creek. We also compared transportation rates between seasons at Waddell Creek in order to capture variation in transportation rates due to different periods of juvenile salmonid outmigration activity, such as (1) the peak outmigration period (March–May), and (2) after the completion of outmigration (June–July). To reflect these different outmigration periods, seasonal feedings were categorized into Spring (2 April 2010 through 7 May 2010) and Summer (16 June 2010 through 6 July 2010) at Waddell Creek. After completion of the feeding experiments, we scanned Año Nuevo Island for PIT tags from hotdogs and Icelandic capelin. The entire colony was scanned twice, once during 2010 and once during early 2011, to increase our probability of detecting deposited experimental tags.

We restricted our analysis of predation and transportation rates to experimental PIT tags eaten by adult Western Gulls only, because they overwhelmingly represent the dominant species and age class of gulls that use ANI for breeding and roosting habitat and were identified as the dominant species and age class responsible for tag deposition at ANI (Frechette et al. 2012). If an adult Western Gull was uniquely identifiable (e.g., natural external markings or location during feeding) and ate more than one tag during a single feeding event, we only included one tag in the analysis to preserve sample independence. Additionally, we restricted the analysis to fed PIT tags where the observers were confident of bird species identification, age classification, and confirmation that the tag was consumed. Therefore, we excluded tags from our analysis that were either out of the observers'

sight before being consumed by a gull or when gull species and age class were uncertain. We used a Fisher's exact test to evaluate whether adult Western Gulls exhibited significantly different transportation and detection rates depending on differences in feed type, time of day, or season of each feeding.

*Estimating transportation and predation.*—In this section, we present a hierarchical Bayesian method to combine all three datasets to estimate the annual predation rate of adult Western Gulls on wild juvenile steelhead at each watershed, and when possible, each year. We assigned  $\theta_{iy}$  as the probability that a wild PIT-tagged juvenile steelhead is consumed by an adult Western Gull in outmigration year  $y$  at watershed  $i$ . Let  $\phi_i$  be the probability that a tagged steelhead is transported to ANI given it was consumed at watershed  $i$ , and  $\psi$  be the probability that a PIT tag is detected at ANI given it was transported to the island. The parameters  $\theta_{iy}$ ,  $\phi_i$ , and  $\psi$  are bounded between 0 and 1. Assuming independence among the three steps of predation ( $\theta_{iy}$ ), transportation ( $\phi_i$ ), and detection ( $\psi$ ), the probability of recapturing a PIT tag from a steelhead tagged at a given site and year is the product of these three probabilities:  $\theta_{iy}\phi_i\psi$ . Similarly, the probability of observing a PIT tag from a tagged hotdog or capelin at ANI that was fed to an adult Western Gull is  $\phi_i\psi$  because all PIT tags included in the analysis were consumed by a gull in this experiment and therefore  $\theta_{iy} = 1$ . For the probability of detecting a PIT tag that had been deposited at ANI ( $\psi$ ), we used the estimated probability of tag capture ( $0.644 \pm 0.083$  SE) reported by Frechette et al. (2012). Briefly, this detection probability was generated using the POPAN variant of the Jolly-Seber model within Program MARK, for combined PIT tag recapture data from all six study watersheds during scans of ANI conducted between 2006 and spring 2009 (see Frechette et al. 2012 for detailed methods). From surveys of ANI, we observed  $k_{iy}$  PIT tags from tagged steelhead out of  $n_{iy}$  deployed during steelhead tagging (see Table 1 for sample sizes) and observed  $l_i$  PIT tags from tagged hotdogs or capelin out of  $m_i$  that were fed to adult Western Gulls during the transportation experiment (see Table 2 for sample sizes).

We assume the probability of transportation is a smooth function of the distance of each site from ANI in kilometers  $d_i$ , and can be modeled as



Table 1. Sample sizes for the steelhead tagging experiment during each outmigration year from 2005 through 2011 at each of the six study watersheds.

Watershed	Outmigration year							Total
	2005	2006	2007	2008	2009	2010	2011	
Waddell								
Tagged	...	153	...	556	631	192	...	1532
Detected	...	10	...	5	22	24	...	61
Gazos								
Tagged	474	68	...	...	...	...	...	542
Detected	16	3	...	...	...	...	...	19
Scott								
Tagged	947	1199	1204	1856	1501	1981	940	9628
Detected	5	26	9	5	21	31	37	134
San Lorenzo								
Tagged	252	9	...	...	...	...	...	261
Detected	1	0	...	...	...	...	...	1
Soquel								
Tagged	823	1068	850	680	185	274	524	4404
Detected	1	1	1	0	0	0	0	3
Aptos								
Tagged	222	112	...	...	...	...	...	334
Detected	0	0	...	...	...	...	...	0
Totals								
Tagged	2718	2609	2054	3092	2317	2447	1464	16701
Detected	23	40	10	10	43	55	37	218

Notes: “Tagged” is the total number of wild juvenile steelhead PIT-tagged at each watershed and outmigration year, which corresponds with values of  $n$  in the model. “Detected” is the number of PIT tags from wild juvenile steelhead that were subsequently detected at Año Nuevo Island (ANI), which correspond with values of  $k$  in the model.

a logistic function

$$\phi_i = \frac{1}{1 + \exp(-(\alpha + \beta d_i))}. \tag{1}$$

We estimated the predation rate hierarchically at the two sites for which we have at least four years of salmonid PIT tags detected at ANI (Waddell Creek and Scott Creek) and only estimated a single  $\theta_i$  at the remaining four sites. For hierarchical sites, we modeled the predation rate in each year as a draw from a site-specific beta distribution,  $\theta_{iy} \sim \text{Beta}(\gamma_i \delta_i)$ . This formulation allows for inference about among-year variation in predation at each site.

We were interested in estimating the joint posterior distribution of all of the parameters given the observed data. Throughout, bold symbols indicate vectors. For notational simplicity let  $\Omega$  indicate the set of non-hierarchical parameters,  $\Omega = \{\alpha, \beta, \psi\}$  and  $x$  indicate the observed data,  $x = \{k, n, l, m, d\}$ . Then  $p(\Omega, \theta, \gamma, \delta|x)$  is the joint posterior distribution of the parameters given the data,  $p(x|\Omega, \theta, \gamma, \delta)$  is the joint likelihood, and  $p(\Omega, \theta, \gamma, \delta)$  is the joint prior distribution for the parameters. By Bayes’ theorem,

$$p(\Omega, \theta, \gamma, \delta|x) \propto p(x|\Omega, \theta, \gamma, \delta)p(\Omega, \theta, \gamma, \delta) \propto p(x|\Omega, \theta)p(\theta|\gamma, \delta)p(\Omega, \theta, \gamma, \delta) \tag{2}$$

with the second line in Eq. 2 showing how the likelihood can be factored into two components. The second term,  $p(\theta|\gamma, \delta)$ , is the beta likelihood for the hierarchical parameters. For a single site  $i$ ,

$$p(\theta_i|\gamma_i, \delta_i) \propto \prod_{y=1}^Y \frac{\Gamma(\gamma_i + \delta_i)}{\Gamma(\gamma_i) + \Gamma(\delta_i)} (\theta_{iy})^{\gamma_i-1} (1 - \theta_{iy})^{\delta_i-1} \tag{3}$$

where  $\Gamma(\cdot)$  indicates the gamma function and  $Y$  is the number of years observed. For the sites where we do not estimate hierarchical parameters and assume  $p(\theta|\gamma, \delta)$  is proportional to 1.

The first component of the likelihood,  $p(x|\Omega, \theta)$  is the product of two binomial likelihoods corresponding to the steelhead tag recaptures and transportation experiments, respectively, where  $I$  indicates the total number of sites,

$$p(x|\Omega, \theta) \propto \prod_{i=1}^I \prod_{y=1}^Y \left[ (\theta_{iy} \phi_i \psi)^{k_{iy}} (1 - \theta_{iy} \phi_i \psi)^{n_{iy} - k_{iy}} \right] \times \prod_{i=1}^I \left[ (\phi_i \psi)^{l_i} (1 - \phi_i \psi)^{m_i - l_i} \right]. \tag{4}$$

Table 2. Sample sizes for the 2010 transportation experiment for each feed type (hotdogs and capelin). All data are from spring morning (AM) feedings unless otherwise indicated (i.e., PM, summer).

Watershed and feed type	Tags fed	Tags detected
Waddell (5.5)		
Hotdog	253	14
Hotdog (summer)	78	6
Capelin	131	9
Capelin (summer)	124	14
Gazos (6.6)		
Hotdog	209	1
Hotdog (PM)	159	1
Capelin	35	0
Capelin (PM)	22	0
Scott (12)		
Hotdog	228	8
Capelin	21	3
San Lorenzo (33)		
Hotdog	71	0
Soquel (38)		
Hotdog	96	0
Aptos (41)		
Hotdog	43	0
Totals	1470	56

*Notes:* Values in parentheses following the watershed names are the linear distances (km) between the mouth of a given watershed and Año Nuevo Island (ANI). “Tags fed” indicate the total number of PIT tags fed to adult Western Gulls for a given feed type, season, and time of day. For a given watershed, sample sizes for season and time of day were combined (hotdog data only) and correspond with values of  $m$  in the model. Capelin were excluded from the model (see text for more details). “Tags detected” indicate the number of PIT tags fed to adult Western Gulls that were subsequently detected on Año Nuevo Island (ANI). For a given watershed, sample sizes for season and time of day were combined (hotdog data only) and correspond with values of  $l$  in the model. Capelin were excluded from the model (see text for more details).

Finally, we specified independent prior distributions for parameters. Because previous research estimated detection probabilities for PIT tags at ANI (Frechette et al. 2012), we used a strongly informative independent beta prior distribution for  $\psi$ ,  $p(\psi) \sim \text{Beta}(21.05, 11.65)$ ; this is the methods-of-moments estimator for  $\psi$  derived from the detection probabilities reported in Frechette et al. (2012). For all other parameters we used diffuse priors. The deposition parameters of  $\alpha$  and  $\beta$  exist on the real line, so we used normal distributions with very large variances:  $p(\alpha) \sim N(0, 10000^2)$ ,  $p(\beta) \sim N(0, 10000^2)$ . These priors are effectively uniformly distributed. The hierarchical parameters  $\gamma$  and  $\delta$  must be positive, so we used uniform priors for both sites:  $p(\gamma) \sim \text{Unif}(0, 25)$ ,  $p(\delta) \sim \text{Unif}(0, 25)$ . Alternate priors

had negligible effects on the estimated posterior.

We estimated all parameters for the model using standard Markov chain Monte Carlo (MCMC) approaches in R (v. 2.15.0; R Development Core Team 2012). MCMC sampling was conducted with 1,020,000 draws; the first 20,000 iterations were removed as burn-in. We retained every 200th posterior sample to provide 5,000 independent draws from the posterior distribution. We ran three replicate chains and confirmed model convergence using Gelman-Rubin diagnostics (Gelman and Rubin 1992).

*Model assumptions.*—Estimated predation rates are based on assumptions made during our individual parameter estimates and our comparisons of tagged fish between watersheds. We mention the major assumptions of the model here and refer readers to the appendix for a thorough justification of the model. The above model assumes (1) the probability of detecting tags is constant across all years; (2) transportation probabilities are constant among years; (3) experimental transportation rates are comparable to transportation rates of consumed steelhead, (4) PIT tags recovered at ANI were transported by adult Western Gulls, and (5) PIT-tagged steelhead are representative of the outmigrating steelhead population. In most cases, our assumptions are necessary and will tend to slightly under-estimate gull predation rates (see *Discussion* and Appendix).

## RESULTS

### *Steelhead tag recapture study*

We recaptured PIT tags at ANI that were originally inserted into wild juvenile steelhead. In total, we PIT-tagged 16,701 wild juvenile steelhead in the six study watersheds combined and 218 of these were recaptured at ANI (Table 1). We observed a higher proportion of recaptured PIT tags from fish from watersheds with increasing proximity to ANI (Fig. 4). For Waddell Creek, the watershed in closest proximity to ANI, the observed proportion of recaptured tags for all years combined was 3.98%, whereas zero tags were recovered from the furthest watershed from ANI, Aptos Creek (Fig. 4). The proportion of recaptured PIT tags at ANI represent the proportion of all PIT tags from juvenile steelhead that were recaptured at ANI from predation,

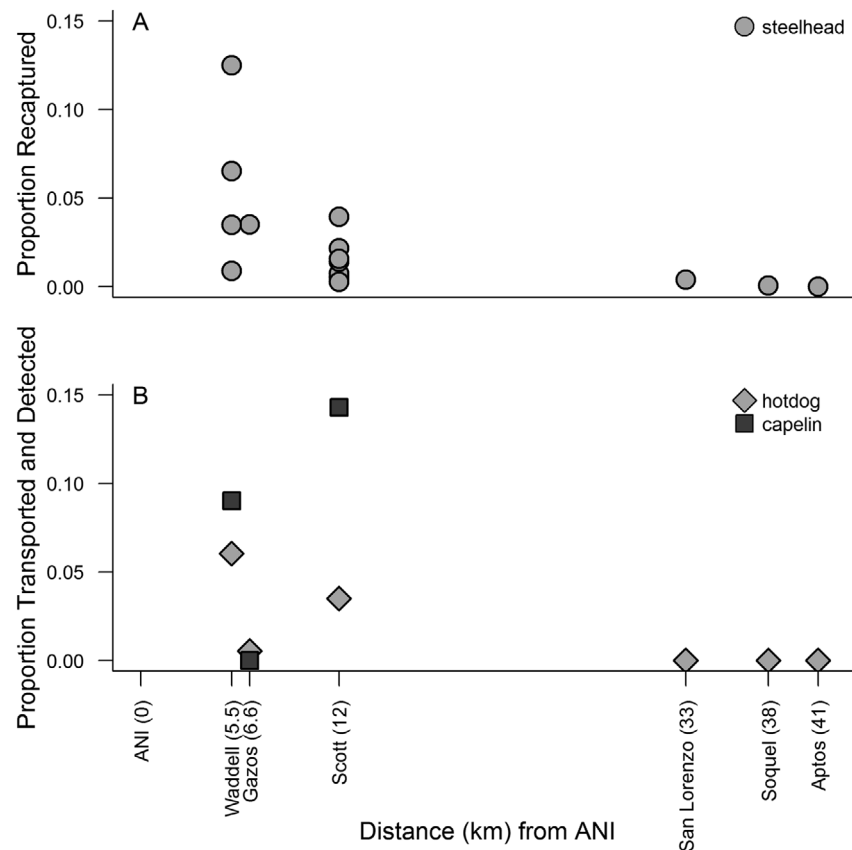


Fig. 4. The observed proportion of PIT tags detected at Año Nuevo Island (ANI) during the steelhead tagging study (A) and the transportation experiment (B) for each watershed. The proportion recaptured (A) is based on the proportion of PIT tags recaptured at Año Nuevo Island (ANI) relative to the number of tagged wild juvenile steelhead at each site, where multiple years of recapture data are available for Waddell ( $N = 4$  years) and Scott Creeks ( $N = 7$  years). The proportion of tags transported and detected (B) is based on the proportion of PIT tags from PIT-tagged hotdogs and capelin detected at ANI relative to the number fed to adult Western Gulls at each site during the transportation experiment.

after accounting for tag loss from transportation, and detection (Fig. 1).

#### Transportation (“hotdog”) experiment

From visual counts, we observed variation in gull species composition and Western Gull age class composition between sites. Of all gulls counted at creek mouths ( $N = 5,403$ ), Western Gulls were the most abundant species (85.4%), with fewer (14.3%) California Gulls (*Larus californicus*) and a very small percentage of other gull species (0.3%) including Heermann’s Gulls (*Larus heermanni*) and Glaucous-winged Gulls (*Larus glaucescens*). Adult Western Gulls were the most abundant species and age class at the three

watersheds closest to ANI, whereas they accounted for less than one-third to one-tenth of the species composition at the three watersheds furthest from ANI (Fig. 5).

The transportation (hotdog) experiment revealed low but spatially variable probabilities of transportation. The vast majority of PIT tags deposited at ANI from the transportation experiment were originally fed to adult Western Gulls (95%), further supporting the hypothesis that adult Western Gulls are the primary species and age class responsible for PIT tag deposition at ANI (see Appendix for more details). Of 1,470 PIT-tagged capelin and hotdogs fed to adult Western Gulls during the transportation experi-

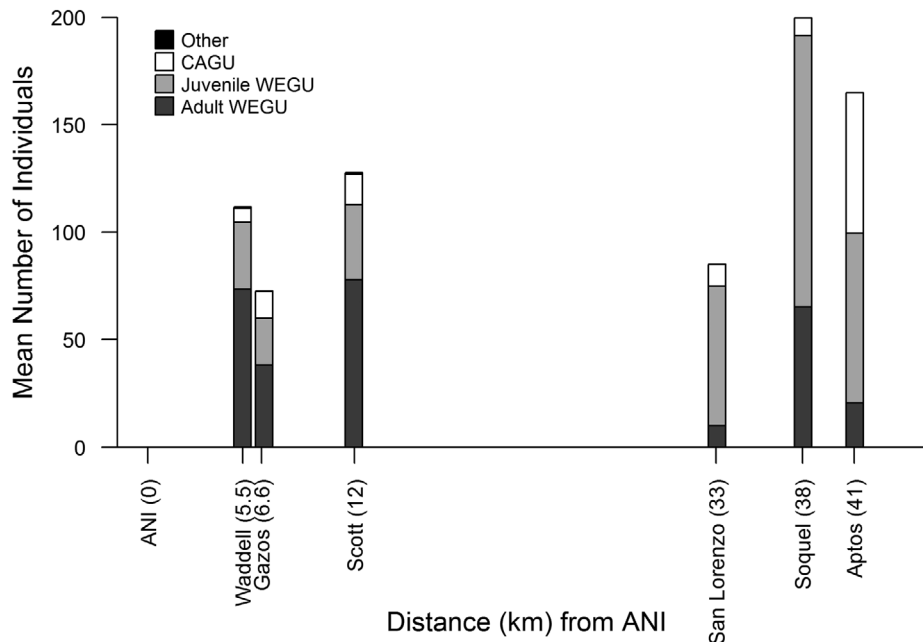


Fig. 5. Mean number of birds present at each watershed during the transportation experiment, separated by species and by age class (for Western Gull species only). Data were restricted to counts conducted during the spring and morning surveys only to be comparable among sites. Abbreviations: CAGU, California Gull; WEGU, Western Gull; Other, all other species combined.

ment, 56 tags were subsequently detected at ANI (Table 2). All of the detected tags were from one of the three watersheds closest to ANI, whereas no PIT tags were recovered at ANI from gulls that were fed at the San Lorenzo River, Soquel Creek, or Aptos Creek (Fig. 4). Thus, watersheds in closer proximity to ANI had higher transportation probabilities.

Feed type, season, and time of day had variable influence on the transportation rates of PIT tags fed to gulls during the transportation experiment. Although feed type did not result in statistically significant differences in transportation rates (Waddell Creek,  $p = 0.208$ ; Scott Creek,  $p = 0.070$ ), capelin were almost always transported at higher rates than hotdogs to ANI (Table 2, Fig. 4). When compared to hotdogs, capelin transportation rates were 1.5 times higher at Waddell Creek and 4.1 times higher at Scott Creek, which results in a weighted average where capelin were transported 2.3 times the rate of hotdogs. Therefore, in order to compare transportation rates among all study watersheds, we removed capelin and only used hotdog data

for subsequent analyses because they were the only feed type used at all six study watersheds. After removing capelin from the analysis, we detected no significant differences in hotdog transportation rates for season at Waddell Creek ( $p = 0.589$ ). Gazos Creek had too few tag recoveries to conduct statistical analyses on whether time of day influenced hotdog transportation rates, however given similar sample sizes, transportation rates were similar for morning ( $1/209 = 0.005$ ) and evening feedings ( $1/159 = 0.006$ ). Therefore we combined the data for both seasons and time of feeding for all hotdog tags fed at each watershed ( $N = 1,137$ ; Table 2) to inform the transportation portion of the following model.

#### Estimating transportation and predation

We estimated the posterior probability distributions for transportation rates as a component of the Bayesian model. Due to the differences in transportation rates between hotdogs and capelin, we restricted the model to include hotdog data only to provide among site comparisons. Estimated transportation rates based on hotdog

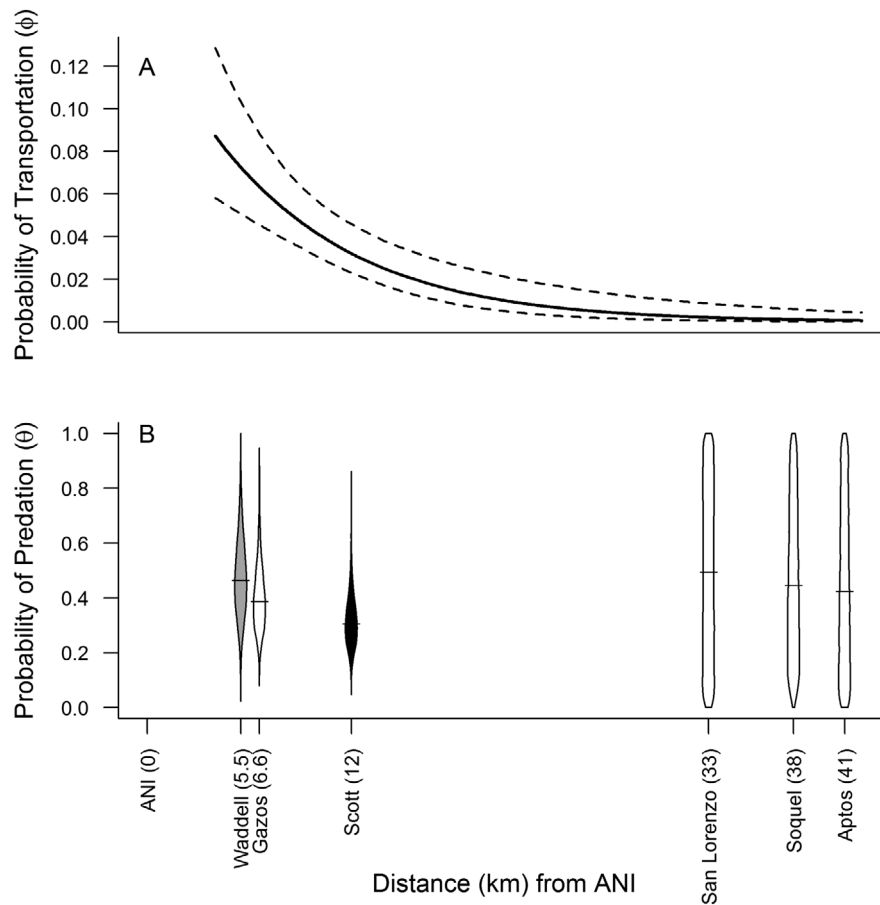


Fig. 6. Site-specific parameter estimates for (A) posterior estimates of the probability of transportation ( $\phi$ ) of a consumed PIT tag to ANI (median  $\pm$ 90% CI), before incorporating the capelin correction factor of 2.3 and (B) posterior estimates of probability of predation ( $\theta$ ) of a PIT-tagged steelhead, including sites with a single year of data (white) and the across-year mean predation rate from the hierarchical model for sites with  $>3$  years of data, which includes Waddell Creek (grey) and Scott Creek (black). Beanplots show the full posterior distribution for each quantity after incorporating the capelin correction factor of 2.3. Horizontal lines indicate median estimates.

data were low and declined as a function of distance from ANI. At the three watersheds closest to ANI, the median probability that a tagged hotdog consumed by an adult Western Gull was transported to ANI each year was 0.073 (0.051–0.103, this and the following represent 90% CI), 0.063 (0.045–0.088), and 0.032 (0.023–0.046) at Waddell Creek, Gazos Creek, and Scott Creek, respectively (Fig. 6A). Median estimates of transportation probability declined sharply at the three watersheds furthest from ANI, where less than 0.003 of all consumed tagged hotdogs were predicted to be transported to the island. To convert hotdog transportation rates into correct-

ed transportation rates more representative of consumed steelhead, we incorporated a correction factor of 2.3 into the model, which multiplied hotdog transportation estimates by the average relative difference from capelin transportation rates. This is equivalent to replacing  $\phi_i$  in Eq. 4 with  $c\phi_i$  and letting  $c = 2.3$ . As a result, the corrected transportation rates remain low, but increased to 0.167, 0.146, 0.074 at Waddell Creek, Gazos Creek, and Scott Creek, respectively, whereas transportation rates were less than 0.005 at all other watersheds. We conducted analyses using both the corrected and uncorrected transportation rates but present only the

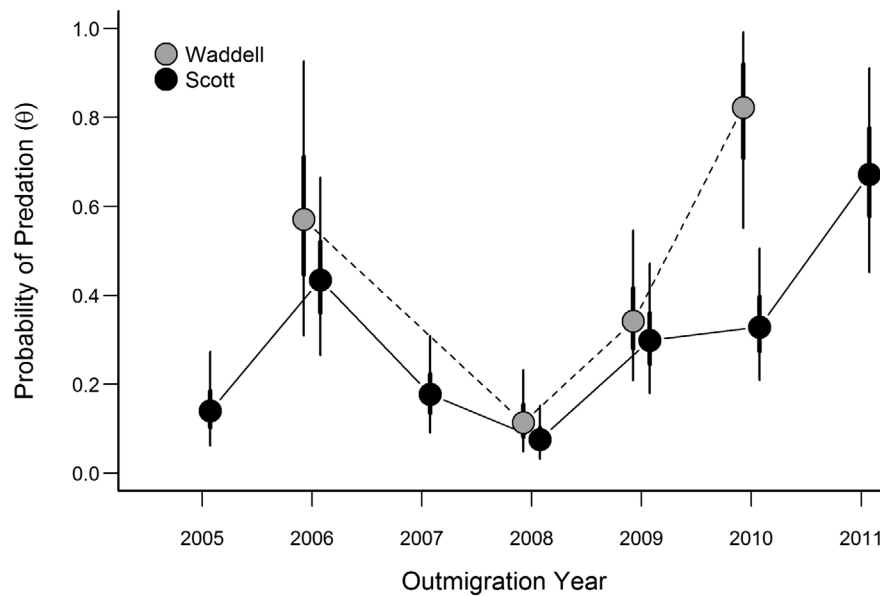


Fig. 7. Posterior estimates for the probability of predation ( $\theta$ ) of wild juvenile steelhead by adult Western Gulls for individual years at two sites: Waddell Creek (grey) and Scott Creek (black). Points show median estimates, thick vertical lines show interquartile range, and thin lines show 90% CI.

predation results using the corrected transportation rates below.

Low transportation rates translate into high predation rates because tags detected at ANI represented a relatively small proportion of the total number of consumed tags. Overall, the probability that a wild juvenile steelhead was consumed as it passed the gauntlet of Western Gulls at the watershed mouth was highest in watersheds closest to ANI (median hierarchical estimates for Waddell = 0.464 [0.260–0.726 90% CI] and Scott 0.306 [0.183–0.480]; non-hierarchical median for Gazos = 0.387 [0.234–0.616]; Fig. 6B). Predation rates at the southernmost watersheds farther from ANI were highly uncertain (Fig. 6B) due to the relatively few recaptures of steelhead tags at ANI from these watersheds (Table 1) and the lack of transported PIT tags from the transportation experiment (Table 2).

For sites with multiple years of wild steelhead recaptures at ANI, gull predation rates were highly variable among years. Median predation rates at Scott Creek ranged from 0.075 to 0.673, over the seven years estimated (Fig. 7). At Waddell Creek, median predation rates ranged from 0.113 to 0.823 across the four years estimated. Patterns of interannual variation were

similar between the two watersheds for the four years that both watersheds were sampled (Fig. 7). Specifically, in both Waddell and Scott Creeks, the median probability of predation was relatively high in 2006 and 2010, average in 2009, and relatively low at both creeks in 2008 (Fig. 7). Comparisons of predation rates between watersheds were not possible for 2005, 2007, and 2011 because no steelhead were tagged in Waddell Creek during those years.

## DISCUSSION

We developed a robust quantitative framework to better understand the impact of predation by an abundant generalist predator, adult Western Gulls, on populations of threatened wild juvenile steelhead in central California watersheds. Our results suggest predation rates at the three watersheds closest to ANI are high (median probability of predation  $\geq 0.306$ ) and variable, ranging from 0.075 to 0.823 depending on the watershed and year. Predation rate estimates increase with proximity to the breeding colony for the three sites closest to ANI and grow increasingly uncertain at watersheds furthest from ANI ( $\geq 33$  km), driven in part by spatial

patterns of transportation rates. Annual patterns of predation varied similarly among years at the two sites where time-series data were available. With the approach and model developed in this study we are able to generate overall Western Gull predation rates on juvenile steelhead and further understand the spatial and temporal influence of a central-place forager on threatened prey populations.

The predation rates estimated in this study provide the first estimate of overall predation rates of adult Western Gulls on juvenile wild steelhead. Predation rate estimates are almost an order of magnitude higher than minimum predation rates from tag recoveries (Fig. 4A), mark-recapture methods at ANI (Frechette et al. 2012), and avian predation estimates on salmonids in other California watersheds (Evans et al. 2011, Adrean et al. 2012). Therefore, our study reveals minimum estimates from tag recovery may considerably underestimate predation rates and suggests predation by avian predators is a more significant source of mortality for juvenile salmonids than previously recognized. In addition, PIT tags from critically endangered coho salmon from Scott Creek have also been observed on ANI (Frechette et al. 2012) and while populations were too small to quantify gull predation rates during this study, we expect gull predation is a significant source of mortality for coho populations as well. Furthermore, because we estimate predation for a single colony of the most common species and age class of avian predator (adult Western Gulls), we have not quantified overall predation by avian predators, including those species and age classes that do not breed or roost at ANI. Thus the total avian predation is likely higher than the already substantial rates reported here.

We observed that transportation rates are low and declined with increased distance from the Western Gull breeding colony (Fig. 4B), controlling the spatial scale of inference. Specifically, our model estimated the median transportation probability was highest at Waddell Creek, the watershed in closest proximity to ANI, and transportation probabilities declined rapidly for the three locations furthest from ANI (Fig. 6A). Because tags from distant sites are rarely transported to ANI, our estimates of predation grow increasingly uncertain as distance from

ANI increases, and we could not make strong inference about predation rates at those sites (Fig. 6B). One possible explanation for the decline in transportation rates with distance from ANI is the increased time between predation and return to ANI may result in higher rates of tag loss. Alternatively, gulls that forage at watersheds further from ANI may be more likely to be non-breeders (Fig. 5) or may use breeding and roosting locations other than ANI, which would reduce transportation rates from these more distant watersheds. Low transportation rates by Western Gulls may also be influenced by species-specific behavior while on the colony, including how adults provision their chicks, where Western Gulls feed chicks through regurgitation whereas other avian predators (e.g., terns) may feed whole fish to their chicks. Thus, different predator foraging behaviors such as generalists (i.e., gulls) versus piscivorous specialists (e.g., terns) may likely control the spatial scale of inference for this type of tag-recapture study. Our results thus provide the first example that low transportation probabilities may dramatically alter estimates of predation rates.

Estimated predation rates varied similarly across years at Scott and Waddell Creeks (Fig. 7). In other systems, variation in predation rates over time by visual predators has been attributed to changes in regional environmental variables such as stream flow (Antolos et al. 2005, Hostetter et al. 2012), ontogenetic requirements that trigger diet switching (Annett and Pierotti 1989), or change in the abundance of prey (Type II or III functional response [Holling 1959], Keefer et al. 2012). These factors may have contributed to temporally coherent predation rates at Scott and Waddell creeks. Furthermore, annual variation in tagging effort at different locations of the watershed (i.e., upper watershed vs. lagoon) could be contributing to variation in estimates of predation rates. The effect of tagging effort on predation rates is supported by an observed negative correlation between annual predation rates and the number of steelhead tagged in the upper watershed in Waddell Creek (Pearson's correlation,  $p = 0.028$ ) and Scott Creek (Pearson's correlation,  $p = 0.150$ ). Therefore, we hypothesize years with higher estimated predation rates were driven, in part, by the fact that a larger proportion of steelhead were PIT-tagged in

the lagoon. Lagoon-reared steelhead are more susceptible to gull predation because they are more likely to attain the size threshold needed to survive the ocean phase of life and as a result are more likely to out-migrate (Bond et al. 2008, Hayes et al. 2011). High predation rates of wild steelhead that utilize lagoon habitat are of particular concern because lagoon-rearing individuals constitute over 87% of the returning adult steelhead population (Bond et al. 2008) and are therefore a critical component of the population for recovery of local steelhead.

High predation rates such as those observed in this study have significant implications for small populations because the loss of a few individuals can dramatically affect the probability of extirpation (Brook et al. 2008). At small population sizes, rare and random events contribute to driving population variability (Lande 1998). The effect of stochastic predation on small prey populations has been shown to decimate specific cohorts; for instance predation events by mountain lions (*Felis concolor*) resulted in significant mortality of desert tortoises in 2003 and 2007 (Medica et al. 2012). In more severe cases, stochastic predation may lead to the extirpation of populations. For example, there is a greater than 50% chance that unpredictable mountain lion predation events may result in the extirpation of isolated bighorn sheep populations (*Ovis canadensis*) (Festa-Bianchet et al. 2006) and a greater than 23% chance that striped bass (*Morone saxatilis*) predation will result in the quasi-extinction of winter-run Chinook salmon populations (*Oncorhynchus tshawytscha*) (Lindley and Mohr 2003). Similar to these examples, we documented high but variable predation rates by gulls on juvenile salmonids. Although salmonid predation is likely rare from the perspective of the gulls, incidental and stochastic predation can account for a large proportion of mortality for small salmonid populations and may contribute to salmon decline or potential extirpation.

The impact of predation is likely exacerbated in this system by anthropogenic subsidies to a generalist predator (Harrington et al. 1999, Kristan and Boarman 2007, Esque et al. 2010). Previous research on Western Gulls has shown that landfills provide one of the most important foraging habitats for most age classes of Western Gulls (Spear 1988), and in other systems anthro-

pogenic subsidies have been identified as the source of increased gull populations (Duhem et al. 2008), gull reproductive success (Weiser and Powell 2010), and juvenile and adult gull survival (Mudge 1978, Mudge and Ferns 1982). On-going research is investigating the linkages between anthropogenic subsidies and Western Gulls to better understand the role of subsidies in limiting the recovery of imperiled salmonid populations (A.-M. K. Osterback, *unpublished data*).

Small populations are particularly challenging to manage and are also the most at risk of extirpation. Effective management of small populations requires quantification of mortality sources, such as predation, that may contribute to further population decline. Although directly quantifying predation on small populations is difficult, here we have demonstrated how managers can estimate multiple sources of tag loss to result in indirect, yet realistic, estimates of predation rates. Our approach of combining a Bayesian model with experimental and monitoring data can be broadly applied to other systems to estimate predation rates by central-place foragers. Predation rates, such as those presented in this study, are critical to inform an ecosystem management approach for fisheries, which depend on accurate estimates of the role of predation and other trophic interactions in fisheries population dynamics (Mangel and Levin 2005, Naiman et al. 2012, Ward et al. 2012).

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## SUPPLEMENTAL MATERIAL

## APPENDIX

## ASSUMPTIONS OF THE MODEL

This study likely provides the most robust accounting to date of potential sources of uncertainty to estimate avian predation rates on salmon. Through propagating uncertainty of the various processes, we generated realistic posterior probability estimates of predation. Below we present and discuss assumptions.

*Detection probability*

We held the probability of detection constant across all years for the consumption model even though detection probability was somewhat variable among years. We investigated the sensitivity of model results to changes in the tag detection rate and found predation rates varied minimally (<0.002 change in median probability of predation) with fairly substantial changes ( $\pm 0.23$ ) to the published estimates for detection probability ( $0.644 \pm 0.083$  SE; reported by Frechette et al. [2012]). The marginal effect of detection probabilities on estimated predation rates is primarily driven by low transportation rates, such that increases in detection rate have little impact on transportation rates, and subsequently have minimal effects on estimates of predation. In the following two paragraphs, we discuss how detection rates varied depending on the year, however given the results of the model sensitivity analysis such slight differences in detection probabilities among years likely have little to no effect on our estimated predation rates.

The model assumed scanning effort on Año Nuevo Island (ANI) was constant among years. Although standardized scanning effort resulted in constant detection probabilities for most years (i.e., 2006 through spring 2009; Frechette et al. 2012), deviations from typical scanning effort in 2005, 2010, and 2011 likely affected the true detection probabilities during those years. Detection probability was likely lower for PIT tags deposited in 2005 because tags may have been washed away or buried before the first full scan of ANI in November 2006. In contrast, detection probability was higher in 2010 and 2011 when scanning effort increased to ensure tag detections from the transportation

experiment. As a result, these variations in detection effort may result in slightly under-estimated predation rates in 2005 (due to reduced scanning effort) and over-estimated predation rates for 2010 and 2011 (due to increased scanning effort).

Because the transportation experiment was conducted during a year with increased detection probability (i.e., 2010), our transportation estimates are inflated for years with less scanning effort (2006 through spring 2009) which would therefore under-estimate predation rates for those years. As a result, the accurate median predation rate may be higher than the estimated predation rates for watersheds with recapture data only prior to 2009 (Gazos Creek, Aptos Creek, and the San Lorenzo River), and may be less variable than the estimated predation rates for watersheds that spanned all years of scanning effort (Waddell Creek, Scott Creek, and Soquel Creek).

*Transportation probability*

We assumed transportation probabilities were the same across years even though it is possible that annual differences in foraging patterns may differ among years, thereby influencing estimates of predation. Since it is impossible to retrospectively quantify transportation rates, we are constrained by the reality of the system and applied 2010 transportation rates to all years of the study. This unaccounted for variation in transportation probabilities among years may also be reflected in the coherent annual variation in predation rates between Scott and Waddell Creeks. For example, if transportation rates varied systematically across years, the assumption would generate greater variation in the estimated annual predation rates between both creeks.

Transportation estimates also assume PIT tagged hotdogs or Icelandic capelin are consumed, processed, and transported to ANI in a way that represents eating a PIT tagged steelhead. Results from the transportation experiment demonstrate that capelin were consistently transported to ANI at a higher rate than hotdogs. Although no paired experiment was possible to compare capelin and steelhead transportation rates due to the threatened status of steelhead, we

assume the difference in transportation rates between capelin and steelhead is minimal. This is supported by a study of Herring Gulls that reported minimal differences in mean gut retention time (<7% difference) when fed three different species of fish prey (Hilton et al. 1998). Therefore, it is likely that fish species such as capelin and steelhead are processed similarly by gulls in our system, and we therefore assume capelin transportation rates are representative of steelhead transportation rates. Because we did not feed capelin at all six study watersheds, we were constrained in using hotdog data only to compare transportation rates among sites. We then multiplied the hotdog transportation rates by a capelin correction factor of 2.3 to result in transportation rate estimates more comparable of consumed steelhead. This multiplier increased the transportation rates, and therefore resulted in lower, and hence more conservative, estimated probabilities of predation at all study watersheds.

In our model, we assume the majority of steelhead PIT tags deposited on ANI were transported by adult Western Gulls, which was supported by the results of the transportation experiment. Of the 2707 PIT tagged hotdogs and Icelandic capelin fed to birds present at creek mouths, an overwhelming majority of these were consumed by Western Gulls, where 54.3%, 17.2%, and 23.6% were consumed by adult, subadult, and juvenile Western Gulls, respectively, and the remaining 4.9% were consumed by California Gulls and other avian species. Of these consumed tags, 59 tags were subsequently detected on ANI, mostly from adult Western Gulls (N = 56) and a small number from subadult Western Gulls (N = 3). However, two of the three tags eaten by subadults were likely eaten by the same individual because both tags were fed at the same location and day and were detected next to each other on ANI. These results suggest PIT tag transportation by other age classes of Western Gulls or other avian species is rare, therefore supporting our assumption that the majority of deposited PIT tags are from adult Western Gulls.

#### *Recapture probability: steelhead tagging*

Our model assumptions include PIT tagged steelhead are representative of all out-migrating steelhead within each watershed. Although lethal and non-lethal effects of PIT tagging are of

concern when applying results to a greater non-tagged population, mortality of juvenile salmonids from PIT tagging is considered to be low (less than 2%) and retention of PIT tags is considered to be high (95%; Sogard et al. 2009). Additionally, over 27% of all PIT tagged steelhead in Scott Creek steelhead were handled multiple times in the creek between the initial PIT tag event and their subsequent recapture on ANI, suggesting tagging was not the source of mortality for these individuals. Therefore, it seems unlikely that tagging biases our estimates of predation rates.

The model estimates predation rates on the tagged population of steelhead, and it is important to note that the characteristics of the tagged population vary by watershed. Specifically, tagging location and time may have an effect on survival before individuals are exposed to gull predation, and therefore predation rates represent different subsets of the wild juvenile steelhead population depending on when and where fish were tagged for a given watershed. For example, individuals tagged in the lagoon are predominately age 0+ and age 1+ steelhead, whereas individuals tagged in the creek mainstem and upper watershed include the entire range of age classes, some of which may never attempt to out-migrate (Hayes et al. 2008). As a result, a smaller proportion of juveniles PIT tagged in the upper watershed may out-migrate to the ocean where they are ultimately exposed to gull predation. Therefore, predation rates may be diluted at watersheds where some juveniles were PIT tagged in the upper watershed (e.g., Waddell, Scott, and Soquel Creeks) when compared to watersheds where juveniles were tagged exclusively in lagoon habitat (Gazos Creek, San Lorenzo river, and Aptos Creek). Although survival of juvenile steelhead is typically higher in the upper watershed when compared to the lagoon environment (Satterthwaite et al. 2012), most out-migrating individuals eventually use the lagoon habitat to rear before entering the ocean (Hayes et al. 2011) and possibly experience greater cumulative mortality. These potential biases are difficult to correct for individual cases. Regardless, these biases result in conservative estimates of predation of out-migrating steelhead at some sites and likely do not affect the overall magnitude nor the negative relationship between consumption rates and distance from ANI.