

ARTICLE

Colonial Waterbird Predation and Angler Catch of Hatchery Rainbow Trout Stocked in Southern Idaho Fisheries

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Abstract

The abundance of piscivorous colonial waterbirds such as double-crested cormorants *Phalacrocorax auritus* and American white pelicans *Pelecanus erythrorhynchos* has increased dramatically in recent decades in North America, resulting in increased conflict between these birds and fisheries resources, which raises the need to quantify the effects of waterbird predation on fisheries. We estimated avian predation and angler use of two sizes of hatchery-reared Rainbow Trout *Oncorhynchus mykiss* (250 mm and 300 mm on average; termed standard catchables and magnum catchables) at 15 Idaho waters with known cormorant and pelican presence. Fish were tagged with passive integrated transponder (PIT), radio, and T-bar anchor tags prior to release; the tags were subsequently recovered from bird nesting, roosting, and loafing sites. Estimated angler use, which included fish harvested as well as those that were catch-and-release, averaged 17%, while avian predation averaged 35%. Angler catch at study waters declined exponentially as avian predation increased. Predation specifically attributed to double-crested cormorants and American white pelicans was related to their relative abundance at the waterbodies where the fish were stocked. Avian predation rates were similar for standard and magnum catchables, suggesting that larger fish were not able to escape predation any better than smaller ones. Our results add to existing evidence indicating that in some southern Idaho fisheries, piscivorous birds, rather than anglers, are the dominant consumers of hatchery trout. This study further contributes to the larger issue of competition between humans, wildlife, and fisheries populations.

The abundance of large colonial waterbirds such as double-crested cormorants *Phalacrocorax auritus* (hereafter, “cormorants”) and American white pelicans *Pelecanus erythrorhynchos* (hereafter, “pelicans”) was depressed throughout much of the 20th century due to human persecution and the widespread use of organochlorine pesticides such as DDT (Taylor and Dorr 2003; Knopf and Evans 2004). Since the 1970s, cormorant and pelican population abundance has increased dramatically throughout North America due to the curtailment of environmental contaminants, additional protection gained from the U.S. Migratory Bird Treaty Act (as well as provincial legislative protection in Canada), and the birds’ use of augmented nesting habitat that is associated with man-made impoundments (Weseloh et al. 1995; King and Anderson 2005). The resurgence of these fish-eating birds

has resulted in increasing resource conflicts, especially with the aquaculture industry and agencies that are responsible for managing sport fisheries (e.g., Meyer et al. 2016; Dorr and Fielder 2017).

Studies quantifying the effects of predation on wild and hatchery-supported fisheries as well as nongame fish populations have increased concurrently with the heightened conflict between fish-eating colonial waterbirds and fisheries resources. For example, along the Columbia River, gulls *Larus* spp., Caspian terns *Sterna caspia*, and cormorants feed heavily on out-migrating juvenile salmon *Oncorhynchus* spp. and steelhead *O. mykiss*, some of which are threatened or endangered (Collis et al. 2002; Sebring et al. 2013; Hostetter et al. 2015). In lakes of the upper Klamath River basin, pelicans and cormorants prey upon endangered Lost River Sucker *Deltistes luxatus* and

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Shortnose Sucker *Chamistes brevirostris* (Evans et al. 2016). In Lake Huron, cormorant predation on Yellow Perch *Perca flavescens* has negatively affected fisheries by reducing angler catch rates (Fielder 2008; Seefelt and Gillingham 2008; Hundt et al. 2013). And in the intermountain western United States, pelicans and cormorants regularly target wild and hatchery-reared trout (Modde et al. 1996; Derby and Lovvorn 1997; Skiles 2008; Teuscher et al. 2015; Meyer et al. 2016) as well as nongame fish (Scoppettone et al. 2014). In the southeastern United States, aquaculture practices for Channel Catfish *Ictalurus punctatus* have been heavily impacted by cormorant predation (Glahn and Brugger 1995).

A commonly used method for estimating avian predation involves tagging a proportion of the fish population and recovering the tags at bird nesting, roosting, or loafing areas (e.g., Evans et al. 2012). However, estimating total predation also requires estimating tag recovery efficiency because not all of the consumed tags are recovered. The probability that a consumed tag is recovered depends on the probabilities that (1) the fish is eaten, (2) the consumed tags are deposited at the locations that are being searched, and (3) the deposited tags are successfully recovered at the searched location (Hostetter et al. 2015). The difficulty of accounting for all of these probabilities has led some investigators to estimate minimum rather than total predation (e.g., Evans et al. 2012; Sebring et al. 2013). Recently, researchers have estimated tag recovery efficiency by implanting fish with passive integrated transponder (PIT) tags and feeding them directly to birds; tags deposited by birds at nesting and roosting sites are subsequently recovered to estimate the recovery rate of tags that are known to have been consumed by birds (e.g., Osterback et al. 2013; Scoppettone et al. 2014; Teuscher et al. 2015; Meyer et al. 2016). The ability to feed tagged fish directly to birds reduces uncertainty because those fish are known to have been consumed by the bird in question. Thus, as long as some tags from fish that have been fed to birds are recovered, the recovery rates of tags implanted in fed fish relative to tags implanted in fish at large generates total predation estimates (e.g., Osterback et al. 2013; Scoppettone et al. 2014; Teuscher et al. 2015; Meyer et al. 2016). However, feeding fish directly to cormorants is ineffective because they are too wary to feed in appreciable numbers (Meyer et al. 2016). In this study, we used radio tags with mortality signals as substitutes for direct feeding to account for most (but not all) of the consumed, deposited, and recovered probabilities mentioned above, a portion of tags deposited off-colony, and unrecovered tags deposited on the colony.

Stocking catchable-sized hatchery-reared trout (i.e., about 250 mm TL; hereafter termed “catchables”) into put-and-take fisheries creates recreational fisheries in waters that cannot support wild trout or can support so

few that no trout fishery would exist without the stocking program. While such fisheries are popular among anglers (Park 2007; Hunt et al. 2017), raising catchables is expensive (Hunt et al. 2017; Losee and Phillips 2017); therefore, maximizing the proportion of stocked fish that anglers catch is of paramount importance to such programs. Fish-eating colonial waterbirds compete directly with hatchery-trout anglers for stocked fish (Derby and Lovvorn 1997; Meyer et al. 2016), but few studies have directly compared bird predation and angler catch of stocked fish. For catchables, size at stocking can be an important factor influencing return-to-creel rates, with larger stocked fish returning to creel at higher rates than smaller fish (Yule et al. 2000; Cassinelli and Meyer 2018). Based on this relationship, the Idaho Department of Fish and Game (IDFG) recently switched much of their put-and-take hatchery production from trout averaging ~250 mm TL (hereafter, “standard catchables”) to trout averaging ~300 mm TL (hereafter, “magnum catchables”). However, while larger catchables may be caught more often by anglers in a general sense, size-specific avian predation could either mask or enhance this relationship. For example, if larger catchables are better able to avoid avian predators (Fuiman and Magurran 1994), avian predation should be higher on smaller fish, thus augmenting angler catch of magnum catchables relative to standard catchables. Alternatively, if cormorants and pelicans target larger prey, then anglers and birds are both competing for the largest trout. Great cormorants *P. carbo* have shown a preference for larger fish (Radhakrishnan et al. 2010), but double-crested cormorants (DeBruyne et al. 2013) and American white pelicans (Scoppettone et al. 2014; Teuscher et al. 2015) have not.

To better understand the effects of colonial waterbird predation (especially by cormorants) in put-and-take fisheries in southern Idaho, we implanted hatchery-reared fish with various tags and stocked them in waters known or suspected to have considerable avian predation pressure. The specific objectives of this study were to (1) estimate the total avian predation of hatchery-reared Rainbow Trout that were stocked into select Idaho fisheries, (2) assess whether predation by cormorants and pelicans was correlated to their relative abundance at specific waters, (3) evaluate whether avian predation was influenced by the size of the stocked fish, and (4) evaluate whether elevated avian predation negatively influenced angler catch.

METHODS

Study areas.—The study waters consisted of 14 lentic waters ranging in size from 2 to > 22,000 ha and one lotic water, the Snake River from river kilometer (rkm) 1,247 to rkm 1,262 in southeastern Idaho (Table 1). All of the study waterbodies are stocked at least annually with Rainbow Trout that are raised at IDFG hatcheries to provide

and sustain sportfishing opportunities. Stocking typically occurs in late spring when ice has melted, reservoirs are full, and angler activity increases, but it also coincides with the time when piscivorous colonial waterbirds are nesting and foraging for their young. Potential recovery locations for tags that are implanted in fish and subsequently eaten by avian predators were identified based on known bird colonies and loafing/roosting areas, while others were discovered based on radio tag signals.

Fish tagging and stocking.—All of the Rainbow Trout that were used in this study were reared at hatcheries that are operated by the IDFG. Rearing groups were designated as either standard or magnum catchables. Tagged hatchery-reared Rainbow Trout were stocked in all of the study waters during the month of May from 2015 to 2017. The tagged fish were generally released concurrently with a larger group of nontagged fish. Fish were collected for tagging by crowding them within raceways (to ensure a representative sample was collected for each tagging event) and capturing them with dip nets. The fish were sedated and measured to the nearest mm TL prior to tagging.

Most of the fish were tagged externally with fluorescent orange T-bar anchor tags and internally with PIT tags; the subset of fish that were radio-tagged were also PIT-tagged but received no T-bar anchor tag (Table 1). T-bar anchor tags (Floy Tag & Mfg., Inc., Seattle) were placed on the fish by inserting the T-bar into the base of the dorsal fin according to standard methods (Dell 1968). All

anchor tags were printed with a unique number and the website/phone number where anglers can report tags to IDFG's "Tag! You're It!" tag reporting system. This system is designed to track angler exploitation and what is herein termed total use of fish by anglers in statewide waters (see *Angler exploitation estimates* below). We assumed that the fluorescent orange color of the anchor tag did not increase a tagged fish's vulnerability to predation based on the results of Meyer et al. (2016), who found that pelican and cormorant predation was equivalent for catchables tagged with fluorescent orange and dull green colored anchor tags.

Half-duplex PIT tags (23 × 3 mm) were inserted into the body cavity of fish using a 6-gauge hypodermic needle (Prentice et al. 1990). In 2015, only standard-sized catchables were tagged and stocked. In 2016 and 2017, equal numbers of standard- and magnum-sized catchables were tagged with anchor and PIT tags.

Prior to radio tag surgery, the fish were anesthetized in a static immersion bath of AQUI-S 20E (10–100 mg/L) for approximately 5 min. Radio tags (Lotek MST-930-M; 9.5 × 32 mm; 4.5 g; 245 d life) were surgically implanted into the body cavity of the fish by making a small incision into the ventral wall anterior to the pelvic girdle (Hart and Summerfelt 1975). A grooved needle shield was inserted posteriorly past the pelvic girdle and a 6-gauge needle was inserted between the pelvic girdle and the anal vent by using the shielded needle technique to protect

TABLE 1. Tag types and the numbers of fish that were stocked into study waterbodies each year, 2015–2017.

Release location	Surface area (ha)	Year	T-bar anchor only	PIT only	T-bar anchor + PIT	Radio + PIT	Total
American Falls Reservoir	22,364	2016			400	30	430
		2017			398	30	428
Chesterfield Reservoir	504	2016			400	30	430
Deep Creek Reservoir	66	2015	100	100	200	0	400
East Harriman Pond	12	2017			150	20	170
Emerald Lake	14	2016		99	100	30	229
Foster Reservoir	52	2015	100	101	200	29	430
		2016			200	30	230
Frank Oster Pond #4	2	2017			200	17	217
Glendale Reservoir	82	2015	100	100	200	0	400
		2016			400	30	430
Jensens Grove Pond	26	2017			397	30	427
Johnson Reservoir	17	2015	101	100	199	30	430
Lamont Reservoir	34	2015	102	100	198	0	400
Riley Creek Pond	12	2017			200	16	216
Rupert Gravel Pond	4	2016		50	50	16	117
Snake River	NA	2017			399	30	429
Treasureton Reservoir	61	2015	102	100	198	30	430
		2016			200	30	230
		Total	605	950	4,790	428	6,473

internal organs and direct the needle under the pelvic girdle and through the incision on the body wall (Ross and Kleiner 1982). The radio antenna was threaded through the needle so that the antenna exited the opening made by the needle. While threading the antenna, the tag was inserted into the body cavity along with a PIT tag. The incision was closed using two sutures. During the surgery, flowing water was pumped over the gills of the fish. Radio-tagged fish were placed in recovery water and monitored for at least 24 h prior to release; no mortality occurred. Only magnum catchables were implanted with radio tags in 2016 and 2017. All of the tagged fish were stocked in each waterbody along with a larger group of nontagged fish as part of the regular stocking schedule.

Radiotelemetry.—To monitor fish presence and potential removal by predators of radio-tagged fish, fixed radio receivers (Lotek SRX-400) were installed at each waterbody where fish with radio tags were stocked, except at Emerald and Rupert Gravel ponds due to vandalism concerns. At those two waters, mobile radio tracking was conducted in conjunction with bird surveys (see below). Fixed radio receivers were also installed at cormorant and pelican colonies at Walcott, Blackfoot, and Island Park reservoirs to detect the arrival of depredated tagged fish. Receivers were programmed to scan tag-specific frequencies (150.180, 150.300, 150.340, 150.320, 150.360, and 150.380 MHz) every six seconds. Each fixed telemetry station consisted of a radio receiver that was powered by a 12V battery and housed in a lockable steel box. Two Yagi antennae with four elements mounted on a T-post and connected to the receiver with coaxial cable were oriented with the elements perpendicular to the ground and aimed in directions that maximized the scanning area. The radio tags were equipped with internal motion sensors that would emit a mortality signal if the tag had not moved for 12 h, allowing identification of fish mortalities due to predation or other causes, depending on location and detection history.

Bird surveys.—To gather data on the relative bird abundance at each stocked waterbody and to relate these data to specific predation, nonrandom bird counts ($n=10$) were conducted at Foster and Treasureton reservoirs in 2015 when technicians were present for radiotelemetry tracking or radio receiver maintenance. In 2016 and 2017, random bird counts were conducted at each of the waters once per week from May 31 to October 3. Survey days and times (between 0800 and 1800 hours) were randomly assigned to the waterbodies. For efficiency, waterbodies that were close to each other were surveyed for birds on the same day. Using binoculars either from shore or from a boat, we counted the four most prominent avian predators at the study waters including cormorants, pelicans, great blue heron *Ardea herodias*, and osprey *Pandion haliaetus*.

Tag recovery.—PIT tags deposited by birds were recovered at a variety of nesting, roosting, and loafing locations

in the fall after most of the birds had migrated south. When scanning these areas, we detected PIT tags using Oregon RFID HDX (Oregon RFID, Portland, Oregon) backpack PIT tag readers attached to a PVC pole (2 m in length) with a PVC hoop antenna (0.5 m in diameter) on the end that provided a detection range of approximately 0.5 m from the edge of the hoop. The recovery area was searched systematically by walking 2-m transects while sweeping the antenna from side to side until all of the ground at each recovery location was scanned. Bushes and small trees (e.g., willows) with bird nests were also scanned, but nests in tall trees (e.g., cottonwoods) were not; nests in tall trees comprised <5% of all nests in the recovery locations. We strived to maintain equal scanning effort at each recovery area by using the same methods and personnel.

When the PIT tags were detected, their locations were marked with a survey flag. Biomark 601 handheld PIT tag readers (Biomark, Boise, Idaho) were used to locate tags more precisely. The tags were individually recovered by digging and scanning small amounts of material using trowels and sieves when necessary (Teuscher et al. 2015; Meyer et al. 2016). The recovery and removal of individual PIT tags was necessary for two reasons: (1) removing a detected tag in one year prevented confusion the following year regarding whether a tag was consumed in the present or previous years, and (2) signals from one tag could have interfered with the detection of other tags at the same location. Additionally, T-bar anchor tags were visually identified and recovered during this process.

If possible we deduced which bird species ate consumed fish based on the location where the PIT tags were recovered. For example, tags were often found in or directly adjacent to nests, so they were assumed to have been eaten by the related bird species. Tags found in ambiguous locations (i.e., areas used by multiple bird species) around the colonies or recovery areas were not assigned to a specific avian predator.

Upon detection of a mortality signal outside of the stocked waterbody, we recovered deposited radio tags using a mobile Lotek SRX-800 telemetry receiver and handheld Yagi antenna. Sometimes the presence of nesting birds precluded recovery until they left the colony. After completion of the 2015 and 2016 bird surveys and manual tag recoveries at colonies, we completed a single-pass sweep above all of the study waterbodies via a fixed-wing aircraft that was outfitted with three-directional telemetry antennae. In 2017, four flights were conducted along the Snake River and the tags that were detected aurally were marked with GPS waypoints and subsequently located on foot or by boat. Tags with mortality signals that were located in the water where they were stocked were assumed to have died of causes other than avian predation.

Data analysis.—Minimum avian predation estimates from recovered PIT tags and radio tags were calculated by dividing the number of tags recovered by the number of tags stocked at each location. Variances for these minimum predation estimates were calculated using the equation

$$\text{Var}(\text{proportion}) = (P[1 - P]) / (n - 1),$$

where P is the proportion of recovered tags and n is the number of stocked tags. Ninety-five percent confidence intervals for these proportions were calculated using the equation

$$P \pm t\sqrt{\text{Var}(P)},$$

where t is the upper $\alpha/2$ point of the t distribution with $n - 1$ degrees of freedom (Thompson 2012).

Because some proportion of consumed PIT tags go unrecovered, because either they were not deposited in the searched areas or we failed to detect them, we estimated deposition and detection probabilities from radio tag data. Deposition probability (ϕ), which is the probability that a tag was deposited at the searched colony, given that it was eaten, was calculated as the number of consumed radio tags deposited at the searched colony divided by the total number of known radio tags that were consumed. Detection probability (ψ), which is the probability that a PIT tag was detected, given that it was deposited on the colony, was estimated as the proportion of PIT tags that were found with their respective radio tags on the colony. In calculating these estimates, we assumed that PIT and radio tags were deposited on the colony at equal rates. We then calculated total predation (Pred_{Tot}) as

$$\text{Pred}_{\text{Tot}} = \frac{\text{Pred}_{\text{PIT}}}{(\phi\psi)},$$

where Pred_{PIT} is minimum PIT tag predation, ϕ is deposition probability, and ψ is detection probability. PIT tags that were recovered from radio-tagged fish were excluded from minimum PIT tag predation estimates to avoid including them twice in total PIT tag predation estimates. Because radio tag recovery from fish consumed by avian predators was unlikely to have been 100%, we recognize that even the corrected estimates of predation based on PIT tag recoveries may still not account for all consumed tags.

To evaluate the influence of size selectivity in predation, we used individual fish length rather than the size category of the fish because some overlap existed in the ranges of lengths for fish that were reared as either standard or magnum catchables. We performed a linear mixed-effects logistic regression to evaluate the effect of fish length on the binary response variable of individual trout predation

(eaten/not eaten) based on PIT tag recoveries. Length was scaled to a standard normal distribution. In recognizing that the probability of predation may vary among specific waterbody and year, those factors were included as random effects with varying intercepts. We had no hypotheses about whether variation associated with these random effects was related to fish length; therefore, varying slopes were not included in the model. We used R package lme4 (Bates et al. 2015; R Core Team 2016) for this analysis.

Angler exploitation estimates.—As mentioned above, a subsample of stocked fish were implanted with T-bar anchor tags to estimate total angler use (i.e., harvested fish + caught-and-released fish) and exploitation (i.e., harvested fish only). Only nonreward tags were used in this study, but US\$50 rewards are released throughout the state of Idaho each year as part of our overall anchor-tagging program to estimate an annual nonreward tag reporting rate by anglers; during this study, the tag reporting rate was estimated to be 45, 45, and 51% in 2015, 2016, and 2017, respectively (P. R. Branigan, IDFG, unpublished data). This statewide program also double tags some fish (i.e., two anchor tags implanted in the same fish) to estimate an annual anchor tag loss rate, which was 2.5, 0, and 0% for the same years, respectively, during our study. Angler use and exploitation estimates were adjusted to account for tag reporting and tag loss rates (for more details see Meyer et al. 2012 and Meyer and Schill 2014). Avian predation was related to angler catch by using regression analyses.

RESULTS

A total of 6,473 fish were tagged with various combinations of T-bar anchors, PIT tags, and radio tags and released into 15 waterbodies over 21 separate stocking events to estimate avian predation as well as angler exploitation and use of stocked, hatchery-reared Rainbow Trout (Table 1). Of these, a total of 134 anchor tags, 780 PIT tags, and 104 radio tags were later recovered or detected in bird nesting, roosting, or loafing areas.

We conducted 94 randomized bird counts at 10 waters from May 31 to October 3, 2016, and from May 16 to September 5, 2017 (Table 2). Cormorants were the most abundant bird species that was observed at the four reservoirs. Chesterfield Reservoir had the highest daily average number of cormorants (12) and pelicans (9). At Glendale Reservoir, herons were most numerous, while pelicans were most abundant at Treasureton Reservoir. Ospreys were observed at most waters, but they were the least abundant of the four piscivorous species.

Avian Predation

Minimum predation estimates based on recovered PIT tags (not adjusted for tag recovery efficiency) averaged 16.0% (range: 0–58%; Table 3). Minimum predation

estimates based solely on radio tags averaged 27.0% and ranged from 0% to 69% across all release events. The percentage of all consumed radio tags that were deposited in the colonies that were scanned for PIT tags (deposition probability) averaged 75.1% (range: 14–100%). The percentage of PIT tags found with their respective radio tags (detection probability) averaged 62.9%. Total predation estimates from recovered PIT tags (accounting for tag detection probability and deposition probabilities) averaged 35.3% (range: 0–100%). The water with the highest predation using all three estimation methods was Rupert Gravel Pond.

Radiotelemetry data yielded the categorization of eight distinct radio tag fates (Table 4). Of all radio tags that were stocked, 76 (17.8%) were physically recovered, while another 28 (6.5%) were deemed predation events based on radiotelemetry detections in bird use areas. Six tags (1.4%) were detected throughout the telemetry period of that respective season (2016), which lasted until the fall. After which, telemetry efforts ceased because the life of the tags for that year were nearing their end. Tags with unknown fates consisted of 127 (29.7%) that were never detected and 108 (25.2%) that were detected at some point but not again. Mortality signals from the waterbodies where the fish were stocked came from 64 (15.0%) tags. Angler caught-and-reported tags numbered 6 (1/4%). Thirteen tags (3.0%) were not detected, but they were deemed predation events because their corresponding PIT tags were found.

Minimum predation from recovered PIT tags on magnum- and standard-sized catchable trout was 15.2% and 15.8%, respectively. No difference was observed between the length distributions of released vs. depredated fish

(Figure 1); the logistic regression model fit to individual fish data indicated that length was not a significant predictor of predation. For every 1 mm increase in length, the odds of a fish's being eaten decreased by 0.92 (95% confidence interval [CI] 0.84–1.01). The predicted probability of being preyed upon was 0.11 (95% CI, 0.02–0.21) for 250 mm fish (standard catchables) and 0.10 (95% CI, 0.02–0.19) for 300 mm fish (magnum catchables). The variances of the random effects of stream and year were 2.21 and 0.19, respectively.

Of the 715 recovered PIT tags (not including those from radio-tagged fish and used for tag detection probability estimates), 207 (29%) were recovered in unambiguous locations (i.e., in or directly adjacent to nests), so they were attributed to specific avian predators. Cormorants and pelicans were responsible for most of the tags that were recovered in or near nests (Table 5). At waterbodies where bird surveys were conducted, the proportion of cormorants to pelicans was related to the proportion of PIT tags recoveries assigned to each species ($y = 0.8748x$, $R^2 = 0.58$; Figure 2).

The foraging distances, inferred as the distances between recovery locations and the waterbodies where the fish were stocked, varied among species (Figure 3). These distances are only reported for tags with known predators (i.e., those found in or directly under identifiable nests). Cormorant foraging distances ($N = 169$) averaged 28.6 km and ranged from 0 to 133 km. Pelican foraging distances ($N = 150$) averaged 52.2 km and ranged from 14 to 150 km. Heron foraging distances ($N = 19$) ranged from 10 to 19 km.

Angler Use and Exploitation

Total angler use averaged 15.7% (range: 0–26%) for magnum catchables and 14.3% (range: 0–35%) for

TABLE 2. Number of surveys conducted (N) and daily mean and range of number of double-crested cormorants (DCC), American white pelicans (AWP), great blue herons (GBH), and ospreys (OSP) that were counted at each waterbody from June 10 to September 23 in 2015 and from May 31 to October 3 in 2016 and 2017.

Waterbody	Year	N	DCC		AWP		GBH		OSP	
			Mean	Range	Mean	Range	Mean	Range	Mean	Range
Chesterfield Reservoir	2016	26	12.4	0–46	9.2	0–24	1.6	0–7	0.2	0–4
East Harriman Pond	2017	15	1.6	0–4	0.0		0.1		0.6	0–2
Emerald Lake	2016	17	1.6	0–9	0.3	0–3	0.1	0–1	0.1	0–2
Foster Reservoir	2015	10	5.5	0–19	0.0		1.6	0–5	0.0	
	2016	26	7.5	2–31	0.5	0–8	2.0	0–9	0.2	0–2
Frank Oster Pond #4	2017	13	0.5	0–4	2.2	0–14	0.1		0.0	
Glendale Reservoir	2016	24	1.3	0–7	0.0		1.5	0–6	0.3	0–2
Jensens Grove Pond	2017	12	0.0	0–0	0.0		0.0		0.3	0–2
Riley Creek Pond	2017	13	1.5	0–5	2.8	0–10	0.0		0.1	0–1
Rupert Gravel Pond	2016	18	0.6	0–4	0.2	0–4	0.3	0–2	0.2	0–1
Treasureton Reservoir	2015	10	5.8	0–16	2.8	0–10	1.6	0–4	0.0	
	2016	30	4.7	0–14	6.8	0–31	1.1	0–2	0.1	0–1

TABLE 4. Fates of all stocked radio tags as determined by fixed station, aerial (fixed-wing flight), and mobile (auto or on foot) radiotelemetry tracking, presented as frequencies. An asterisk (*) indicates one additional tag stocked in this water was tracked to a North American river otter *Lontra canadensis* burrow, so it was excluded from this table, in which the depredation refers to avian activity.

Water	Year	Depredated recovered	Depredation inferred from telemetry	Apparently survived	Never detected	Angler returned	Dead in water	Detected but fate unknown	Predation from PIT only	Total
American Falls Reservoir	2016		3		27					30
	2017				28			2		30
Chesterfield Reservoir	2016	8	4	1	1		2	14		30
East Harriman Reservoir	2017	7					11	2		20
Emerald Lake	2016	9	3		13	1		2	2	30
Foster Reservoir	2015	14			7	1	3	1	3	29
	2016	9	1		2	1	2	13	2	30
	2017	1	6		2		5	3		17
Frank Oster #4	2016	4	1	3	1	1	3	16	1	30
Glendale Reservoir	2017		1		11			18		30
Jensens Grove	2015	6			2		20		2	30
Johnson Reservoir	2017	1	1		7			7		16
Riley Creek Pond	2016	7	4		2	1		1	1	16
Rupert Gravel Pond										
Snake River	2017	2	2*		12	1	12			30
Treasureton Reservoir	2015	3			11		6	8	2	30
	2016	5	1	2	1			21		30
Grand total		76	28	6	127	6	64	108	13	428

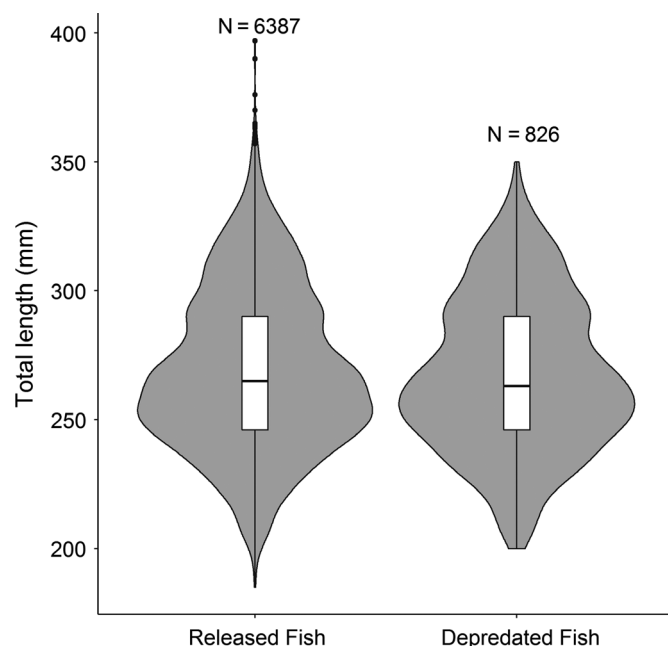


FIGURE 1. Kernel density plots of length distributions for the numbers (N) of released and depredated fish. The boxes show the interquartile ranges (IQR, first to third quartiles); the whiskers extend to $1.5 \times$ IQR (or to minimum/maximum values); and the dots represent outliers of fish lengths (mm).

standard catchables (Table 6). Angler exploitation averaged 11.8% (range: 0–25%) for magnums and 10.2% (range: 0–35%) for standards. A significant relationship was detected between avian predation and angler

exploitation among water bodies and stocking groups (Figure 4; $y = 0.1609^{-1.852x}$, $F_{1, 30} = 10.29$, $P = 0.003$), in which angler exploitation declined exponentially as avian predation increased.

DISCUSSION

In our study, a combination of tagging methods allowed for the estimation of minimum and total avian predation as well as angler use of hatchery-reared Rainbow Trout in Idaho. Although our approach to adjusting minimum estimates differed from previous studies, our estimates of predation by cormorants and pelicans are similar to those that have been reported for inland resident fisheries (Modde et al. 1996; Derby and Lovvorn 1997; Teuscher et al. 2015; Meyer et al. 2016). Total predation rates on adfluvial Yellowstone Cutthroat Trout *O. clarkii bouvieri* by pelicans in Idaho's Blackfoot River averaged 26% over four years and ranged from 6% to 70% (Teuscher et al. 2015). In another study of avian predation on Idaho fisheries, hatchery-stocked Rainbow Trout were preyed upon at an average rate of 18% by pelicans (range: 0–65%), with additional predation attributed to cormorants (range: 2–38%) and total bird predation often exceeding angler use (Meyer et al. 2016).

To estimate total avian predation, we first estimated minimum predation from recoveries of PIT and radio tags that had been implanted in fish. The radio tag estimates allowed us to estimate deposition rates for tags on the colonies, which were then applied to a much larger sample

TABLE 5. Numbers of PIT tag recoveries assigned to specific predators based on recovery location (i.e., in or near nests). Tags that were recovered in ambiguous areas (i.e., areas used by multiple bird species) were assigned to the unknown category.

Water	Year	Cormorant	Pelican	Heron	Osprey	Unknown	Total
American Falls Reservoir	2016	5	13			7	25
	2017	1	4			5	10
Chesterfield Reservoir	2016	5	14			44	64
Deep Creek Reservoir	2015						0
East Harriman Pond	2017	25	1				26
Emerald Lake	2016	31	13			30	74
Foster Reservoir	2015		2			108	110
	2016					49	49
Frank Oster Pond #4	2017	2	9	12		1	24
Glendale Reservoir	2015					55	55
	2016					36	36
Jensens Grove Pond	2017	2	1				3
Johnson Reservoir	2015					39	39
Lamont Reservoir	2015	2	5			56	63
Riley Creek Pond	2017	7	2	1			10
Rupert Gravel Pond	2016	22	8			28	58
Snake River	2017	1	2				3
Treasureton Reservoir	2015	6	11			24	41
	2016					25	25

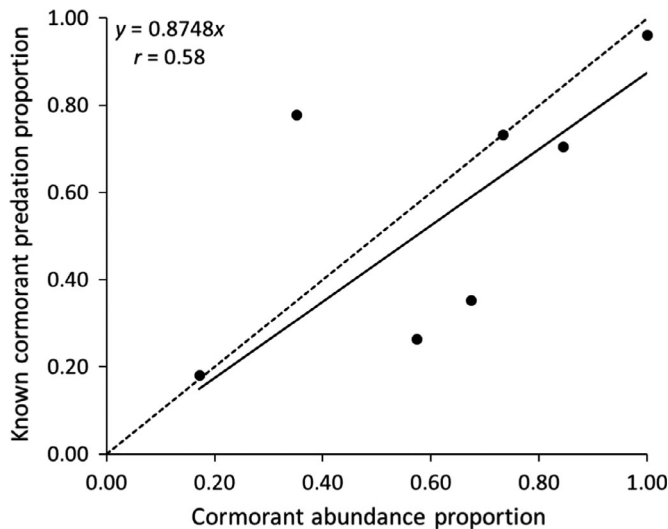


FIGURE 2. Scatterplot of the proportion of cormorant abundance (based on bird surveys) and proportion of cormorant predation (based on tags recovered in or near nests) for waters where the bird surveys were conducted and tags were subsequently recovered. The solid line and equation denote a linear relationship fitted to the data. The hashed line is a 1:1 line that would indicate a direct relationship between cormorant abundance and predation.

size of PIT tag recoveries. Relative recoveries from a subset of fish that had been implanted with both PIT and radio tags informed detection probabilities, which were then applied to overall PIT tag recoveries. This allowed us to adjust for the proportion of tags that had been deposited off-colony as well as unrecovered tags that had been deposited on the colony. An advantage to this approach was that it did not require directly feeding tagged fish to birds, which is not feasible for cormorants (Meyer et al. 2016). A limitation is that our total estimates may still be biased somewhat downward because not every radio tag was accounted for. Some radio tag signals ceased to be detected over time, indicating that those tags had been removed from the water by a predator or angler, but possibly that the tag simply had ceased functioning properly. In addition, a small proportion of PIT tags were found without the corresponding radio tag, which would result in an underestimate of deposition probability based on radio tags. Our average PIT tag detection and deposition probabilities of 63% and 75% were much higher than those reported in an earlier avian predation study that was conducted in Idaho (21%; Meyer et al. 2016). This discrepancy is likely explained by the fact the distance between the study waterbodies where avian predators were foraging and the nesting/roosting/loafing areas where tags were recovered was on average much shorter in our study than in the earlier study and that as foraging distance increases, tag recovery decreases (Meyer et al. 2016). The impetus for our study was to gain more knowledge about

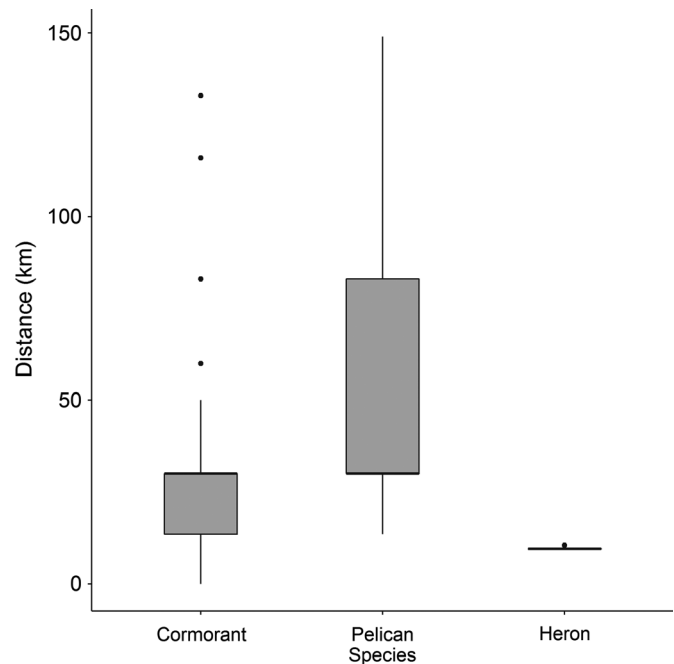


FIGURE 3. Foraging distances of the avian predators: double-crested cormorants ($N=169$), great blue herons ($N=19$), and American white pelicans ($N=150$). Distances were based on locations between where PIT-tagged fish were stocked and those from which they were recovered. The boxes represent the interquartile ranges (IQR; first to third quartiles); the horizontal lines represent median values; and the dots represent outliers of foraging distances (km) for each avian predator.

the effects on fisheries of predation by cormorants, which inherently have shorter foraging distances than pelicans. Given our observed predation rates and the associated foraging distances attributed to cormorants, the higher tag recovery is not a surprising result.

Assigning total avian predation to separate bird species was tenuous because about 71% of the tags that we recovered in nesting/roosting/loafing areas were found in ambiguous locations that were occupied by cormorants, pelicans, and in some instances other avian predators as well. However, we showed that the ratio of cormorant to pelican abundance at the waterbodies where those tags were stocked was related to the ratio of tags that were found in cormorant nests with respect to those that were found in pelican nests. Although we were not able to assign a predator species to a large proportion of our recovered tags, it is not unreasonable to infer a parsing of predation from cormorants and pelicans similar to those observed from nest recoveries. While it is well known that energetic demands differ between these avian predators (Hall 1925; Ferguson et al. 2011; Seefelt and Gillingham 2008), prey selection or vulnerability may also differ (DeBruyne et al. 2013). In our study, the number of PIT tags that were found specifically in cormorants nests at the Minidoka colony exceeded the numbers that were found in pelican

TABLE 6. Estimates of angler exploitation (harvested fish only) and total angler use (proportion of stocked fish that were caught and released or harvested) with 90% confidence intervals (CI) for standard- and magnum-sized hatchery-reared Rainbow Trout that were stocked in southern Idaho waters. The estimates for angler exploitation and use were adjusted to account for year-specific tag loss and tag reporting rates (Branigan, unpublished data). NA refers to estimates for which CIs could not be estimated.

Water body	Year	Standard-sized catchables				Magnum-sized catchables			
		Angler exploitation		Angler total use		Angler exploitation		Angler total use	
		Estimate	±90% CI	Estimate	±90% CI	Estimate	±90% CI	Estimate	±90% CI
American Falls Reservoir	2016	0.03	0.03	0.06	0.04	0.13	0.06	0.18	0.08
	2017	0.05	0.04	0.06	0.04	0.06	0.04	0.08	0.05
Chesterfield Reservoir	2016	0.19	0.08	0.28	0.10	0.09	0.05	0.14	0.07
Deep Creek Reservoir	2015	0.11	0.05	0.21	0.07				
East Harriman Pond	2017	0.05	0.06	0.11	0.09	0.16	0.11	0.21	0.13
Emerald Lake	2016	0.27	0.17	0.31	0.19	0.09	0.10	0.18	0.14
Foster Reservoir	2015	0.11	0.05	0.11	0.05				
	2016	0.14	0.09	0.16	0.10	0.25	0.12	0.24	0.12
Frank Oster Pond #4	2017	0.06	0.07	0.06	0.07	0.06	0.07	0.06	0.07
	2017	0.18	0.16	0.29	0.21	0.06	0.10	0.12	0.14
Glendale Reservoir	2015	0.07	0.04	0.19	0.07				
	2016	0.09	0.05	0.09	0.05	0.18	0.08	0.22	0.09
Jensen Grove Pond	2017	0.19	0.08	0.22	0.09	0.26	0.10	0.26	0.10
Johnson Reservoir	2015	0.07	0.04	0.16	0.06				
Lamont Reservoir	2015	0.01	0.01	0.02	0.02				
Riley Creek Pond	2017	0.35	0.23	0.35	0.23	0.18	0.17	0.24	0.19
	2017	0.12	0.10	0.18	0.12	0.18	0.12	0.24	0.14
Rupert Gravel Pond	2016	0.00	NA	0.00	NA	0.00	NA	0.00	NA
Snake River	2017	0.05	0.04	0.06	0.04	0.07	0.05	0.12	0.06
Treasureton Reservoir	2015	0.00	NA	0.02	0.02				
	2016	0.00	NA	0.07	0.06	0.00	NA	0.07	0.06

ests by 24%, suggesting that cormorants simply consumed more Rainbow Trout than pelicans did, regardless of lower daily energy requirements. Because total avian predation estimates were unhampered by these limitations, we acknowledge that these estimates were more rigorous than the estimates for each bird species.

Regardless of the species that is responsible for predation, the estimate for total avian predation of stocked catchables in our study was higher than that for angler use, and higher predation was associated with reduced angler catch among locations. This concurs with previous research comparing angler exploitation and bird predation in Idaho (Meyer et al. 2016). In the Great Lakes region, predation by cormorants on Yellow Perch reduced angler catch over several years (Fielder 2008). Because the waterbodies that we assessed are managed as put-and-take fisheries, one could argue that the monetary cost of predation on these hatchery-reared fish is significantly higher than that of predation on fish that are born in the wild. Not only are catchable-sized fish expensive to raise and stock but also loss of angler opportunities and

their associated monetary expenditures comprise additional costs of predation. However, it should be noted that avian predation varied widely among the waterbodies, and occasionally, among years at the same water. Substantial variation in fish predation by colonial waterbirds among waterbodies or years has been observed in previous studies, which have ascribed such variation to differences in foraging distance from the colony (Meyer et al. 2016) and environmental conditions that affected the vulnerability of prey (Teuscher et al. 2015; Graham et al. 2019). Also, in some waterbodies with substantial numbers of colonial waterbirds (e.g., American Falls Reservoir; also see Meyer et al. 2016), avian predation of stocked catchables was consistently low, suggesting that birds were targeting other prey. Taken collectively, these results suggest that avian predation diminishes catchables, consequently influencing angler catch of stocked fish, which will likely vary between years and waterbodies depending on a variety of biotic and abiotic factors, some of which may be exacerbated or diminished in the future by climate change.

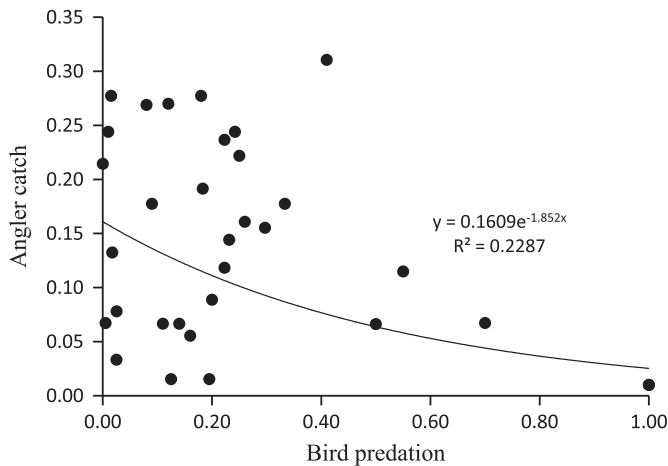


FIGURE 4. Scatterplot of the total angler use (proportion of stocked fish that were caught and harvested or released) and total avian predation (proportion of stocked fish that were eaten by birds) across all stocking events for catchable-sized Rainbow Trout that were stocked in select southern Idaho waterbodies. The line and equation denote an exponential relationship fitted to the data.

Although we observed a slight trend of smaller catchable's being consumed more often than larger fish, this trend was not significant after accounting for variation in waterbody size and stocking numbers. Previous studies provide equivocal evidence on size selectivity for various species of predatory colonial waterbirds, with some studies demonstrating selection of smaller-sized fish (Evans et al. 2016), larger-sized fish (Radhakrishnan et al. 2010), or no size selectivity (Hostetter et al. 2012; Scoppettone et al. 2014; Teuscher et al. 2015). Double-crested cormorants can consume fish that are up to 430 mm in length (Dorr et al. 2014), which is larger than any of the fish that were used in our study. American white pelicans can consume even larger fish (up to 570 mm; Teuscher et al. 2015). It is possible that the tendency for larger fish to be caught at higher rates by anglers simply left a disproportionately high number of smaller fish available to avian predators.

Although T-bar anchor tags were used to estimate rates for angler use and exploitation of stocked Rainbow Trout, many anchor tags were also recovered in and around bird nests. These included 134 anchor tags that came from depredated fish from this study as well as 124 anchor tags that were unrelated to this study. The latter tags were originally implanted in Rainbow Trout, crappie *Pomoxis* spp., and Channel Catfish *Ictalurus punctatus* from 18 different waterbodies (up to 190 km from recovery locations) dating back to the year 2006, demonstrating the spatiotemporal scope of avian predation beyond the waterbodies that were investigated in this study.

The foraging distance that we observed for cormorants greatly exceeded those that have been found in previous studies. Double-crested cormorants typically have been

shown to forage within 20 to 30 km of their colony (e.g., Hobson et al. 1989; Custer and Bunck 1992; Bugajski et al. 2013), but they have been documented traveling over 40 km for food (Anderson et al. 2004). The maximum cormorant foraging distance in our study (133 km), generated from tags found either directly in cormorant nests or other unambiguous cormorant depositional areas (e.g., under a cottonwood tree filled with cormorant nests, with no nests of any other bird species nearby), is more than double those that have been reported in the aforementioned studies. The reason for these extreme foraging distances is not clear, but they may be related to the expanding cormorant population in Idaho. Central place foraging theory predicts that birds should forage within the immediate vicinity of their colony, thereby minimizing energy expenditures (Ashmole 1963). However, if density-dependent feeding or competition is occurring or if males feed at greater distances (Anderson et al. 2004; Glahn et al. 1995), perhaps to avoid direct competition with females, the birds may need to travel farther to obtain food. Another possibility is that these distances were traveled during migration; birds were not simply making foraging trips from the colony. While these occurrences are noteworthy, their low frequency made them outliers among the tags recovered. The foraging distances measured in our study for pelicans and herons concur with those reported previously in the literature (Johnson and Sloan 1978; O'Malley and Evans 1982; Dowd and Flake 1985).

The burgeoning abundance in recent decades of fish-eating colonial waterbirds such as double-crested cormorants and American white pelicans are positive signs of the results of modern wildlife conservation efforts that date back to the 1960s. However, their recovery has led to increasing conflict with aquaculture and recreational angling stakeholder groups. Such conflicts have spurred a growing body of evidence that highlights the increased colonial waterbird predation pressure on free-swimming fish populations throughout North America (e.g., Fielder 2008; Carey et al. 2012; Evans et al. 2012, 2016; Scoppettone et al. 2014; Teuscher et al. 2015) and parallels other examples of the negative effects on important fisheries of overly abundant and expanding wildlife, such as pinniped predation on imperiled salmon and steelhead stocks in the Columbia River (Wargo Rub et al., in press). While several nonlethal management actions to reduce such conflicts can be implemented by some management agencies under their direct authority (e.g., hazing and habitat alteration), such actions are time consuming, expensive to implement, and often ineffective at achieving meaningful long-term reductions in bird abundance or predation effects. In contrast, actions that result in directly taking eggs or birds must be authorized by the U.S. Fish and Wildlife Service via a depredation permit under guidelines developed by individual flyway councils (e.g., Pacific Flyway Council

2012, 2013). Striking a balance between conservation and recreation interests for birds and fish will continue to challenge fisheries and wildlife managers, and this research offers methods to study such conflicts and provides critical data to inform decision makers of the extent to which cormorants and pelicans disrupt popular hatchery-trout fisheries.

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