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ARTICLE

Estimating population abundance with a mixture of physical capture and PIT tag antenna detection data

Mary M. Conner, Phaedra E. Budy, Richard A. Wilkison, Michael Mills, David Speas, Peter D. Mackinnon, and Mark C. Mckinstry

Abstract: The inclusion of passive interrogation antenna (PIA) detection data has promise to increase precision of population abundance estimates ($\hat{N}$). However, encounter probabilities are often higher for PIAs than for physical capture. If the difference is not accounted for, $\hat{N}$ may be biased. Using simulations, we estimated the magnitude of bias resulting from mixed capture and detection probabilities and evaluated potential solutions for removing the bias for closed capture models. Mixing physical capture and PIA detections (p_{det}) resulted in negative biases in $\hat{N}$. However, using an individual covariate to model differences removed bias and improved precision. From a case study of fish making spawning migrations across a stream-wide PIA ($p_{det} \leq 0.9$), the coefficient of variation (CV) of $\hat{N}$ declined 39%–82% when PIA data were included, and there was a dramatic reduction in time to detect a significant change in $\hat{N}$. For a second case study, with modest p_{det} (≤ 0.2) using smaller PIAs, CV ($\hat{N}$) declined 4%–18%. Our method is applicable for estimating abundance for any situation where data are collected with methods having different capture–detection probabilities.

Résumé : L'inclusion de données de détection par antennes d'interrogation passives (AIP) a le potentiel d'accroître la précision des estimations d'abondance de populations ($\hat{N}$). Les probabilités de rencontres sont toutefois plus élevées pour les AIP que pour la capture physique. La non prise en compte de cette différence peut se traduire par un biais des valeurs de $\hat{N}$. En utilisant des simulations, nous estimons la magnitude du biais découlant de probabilités de capture et de détection mixtes et évaluons des solutions possibles pour retirer ce biais pour des modèles de capture fermée. Le mélange de captures physiques et de détections par AIP (p_{det}) produit des biais négatifs de $\hat{N}$. L'utilisation d'une covariable individuelle pour modéliser les différences enlève le biais et améliore la précision. À partir d'une étude de cas de poissons effectuant des migrations de frai captés par des AIP dans tout le cours d'eau ($p_{det} \leq 0,9$), le coefficient de variation (CV) de $\hat{N}$ diminue de 39–82 % quand les données d'AIP sont incluses, et il y a une réduction marquée du temps nécessaire pour détecter un changement significatif de $\hat{N}$. Pour une deuxième étude de cas caractérisée par de modestes p_{det} ($\leq 0,2$) et utilisant de plus petites AIP, le CV ($\hat{N}$) diminue de 4–18 %. Notre méthode peut être appliquée pour estimer l'abondance pour toute situation où les données sont obtenues par des méthodes présentant différentes probabilités de capture–détection. [Traduit par la Rédaction]

Introduction

Estimating abundance remains one of the most challenging and important activities in the conservation and management of animals. Ecologists and managers alike want to know "how many are there" (Williams et al. 2002), and abundance is a key indicator of population dynamics across both space and time, with the potential to also elucidate ecological processes (Murdoch 1994; Kelt et al. 2019). Further, population abundance criteria are often used as guidelines for enacting or adjusting management actions and assessing progress towards recovery of sensitive and imperiled species (Holmes and York 2003; Osmundson and White 2017). However, estimating abundance can be challenging analytically, expensive, time-consuming logistically, and potentially harmful to animals sensitive to handling, which is especially important for threatened or endangered species (Pine et al. 2001; Al-Chokhachy et al 2009; Fraser et al. 2017).

Recent advances in fish marking and detection technology have resulted in dramatically increased recapture rates while not requiring actual physical recapture (e.g., Skalski et al. 1998; Gibbons and Andrews 2004; Budy et al. 2017). In the Columbia River Basin, between 1987 and 2018 over 45 million salmon were tagged with passive integrated transponder (PIT) tags (Pacific States Marine Fisheries Commission 2018), and in the Colorado River Basin, conservative estimates are that between 1990 and 2019, >1.2 million large river desert fish were PIT-tagged in the Upper Colorado River basin (Species Tagging, Research and Monitoring System (STReaMS) 2019). The most recent advances in marking–detection have been the installation of passive interrogation antennas (PIAs), permanent or semipermanent antennas capable of detecting, identifying, and recording an individual PIT-tagged fish (or other organism) as they swim over, through, or near the antennas. The rapidly increasing utilization of these PIAs has dramatically increased the numbers of

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Table 1. Description of the approaches used for combining physical capture data with passive interrogation antenna (PIA) detection data collected concurrently for use in closed capture models to estimate population abundance.

Approach	Description	Model for capture and recapture probability[a]
1. No antenna data	Only fish physically captured and recaptured included in the data set	$p(.)=c(.)$
2. All data no IC	All physical captures and recaptures and passive PIA detections used in the data set, but no accounting for heterogeneity using an individual covariate (IC)	$p(.)=c(.)$
3. All data with IC	All physical captures and recaptures and passive PIA detections used in the data set, and an individual covariate (PrevCap) used to account for fish already PIT-tagged at the start of the sampling period	$p(\text{PrevCap})$ $c(.)$
4. All data with groups	All physical captures and recaptures and passive PIA detections used in the data set, and two groups used to account for fish already PIT-tagged at the start of the sampling period (group 1) and fish not PIT-tagged (group 2)	$p(\text{group})$ $c(.)$

[a]Model notation: p = probability of initial capture, c = probability of recapture, "." = constant p or c for the sampling occasions, PrevCap = individual covariate for each fish that indicates if it was previously captured and PIT-tagged (so initial capture can be from an antenna detection).

fish detected (which can represent a capture or recapture in capture–mark–recapture models) by several orders of magnitude, with the added benefit of minimizing the handling stress on fish, as well as minimizing effort in the field. Although there are potential financial and logistical constraints for PIAs, (Al-Chokhachy et al. 2009), there are many additional advantages of collective PIT tag and PIA technology. PIA detections can be used to estimate demographic vital rates (Roni et al. 2012; Conner et al. 2015; Pearson et al. 2016) and abundance (Dzul et al. 2018; Pearson et al. 2016), delineate fish movement patterns (Bowerman and Budy 2012; Cathcart et al. 2018) and barriers (Pennock et al. 2018), as well as describe habitat use (Roussel et al. 2000; Richer et al. 2017; Stout et al., in press), community distributions (Cathcart et al. 2015, 2019), and spawning behavior (Pearson et al. 2016).

Despite the potential to greatly increase the detection rate and minimize fish handling stress, the data collected with PIAs come with several analytical challenges (Zydlewski et al. 2006; Stout et al. 2019; Stout et al., in press). One unresolved analytical issue associated with PIA data are heterogeneity in capture or detection probabilities, which refers to the variation among individuals in their probability of detection. Most capture–recapture models assume capture probability is constant across individuals within a group. When individuals vary in their capture probabilities, animals with higher "capture" (detection) probabilities are likely to be caught first and more often. This heterogeneity leads to an overestimate in capture probability, which then results in underestimates (i.e., negative bias) of population abundance ($\hat{N}$) (Pollock et al. 1990; Link 2004; Lukacs and Burnham 2005). Differences in capture and detection probabilities, which is a specific type of heterogeneity, can be accounted for within a single closed capture sampling session using models where recapture probability is different from initial capture probability (White et al. 1982). However, with PIT tag technology, captures can be via physical capture or via PIA detection, and more often than not, the PIA detection probability is much higher than the physical capture probability. This is a more general form of heterogeneity, and if the two types of capture probabilities are mixed and not accounted for analytically, the resulting estimates of N will likely be biased. Pearson et al. (2016) presented one sophisticated solution to this problem using multistate models. Their approach was particularly useful for estimating survival, skipped spawning, and assessing the potential to minimize physical capture, but they did not primarily assess bias in $\hat{N}$.

Here, we address the mixing of PIA detection data with physical capture data for estimating population abundance using closed capture models, wherein the same population of fish is sampled by both methods during the closed capture sampling occasions. That is, physical capture sites and PIAs are located such that fish are vulnerable to detection by physical capture (for tagged and untagged) and PIA (for tagged). Our overarching goals were to (i) determine the magnitude of bias resulting from mixed capture and detection probabilities on $\hat{N}$ and its precision and offer a

potential solution and (ii) quantify the improvement in $\hat{N}$ in terms of reduced bias and increased precision resulting from addition of PIA detection data using both simulations and two case studies of real data. With a baseline that used closed capture models to estimate N without PIA detections, we simulated a range of scenarios bracketing low to high probabilities of physical capture and passive detection of PIT-tagged fish at PIAs, across a range of proportions of PIT-tagged fish. For these scenarios, we demonstrate two potential approaches for minimizing the bias in $\hat{N}$ arising from mixed capture probabilities and quantify the improvement in precision from using PIA data. Lastly, we demonstrate the improvement in precision gained from incorporating real PIA detection data for two case studies representing a common set of life history expressions among fishes: adfluvial June sucker (*Chasmistes liorus*) and fluvial bull trout (*Salvelinus confluentus*), both of which are listed as endangered and threatened under the Endangered Species Act (ESA), respectively (US Fish and Wildlife Service 1999, 2015). These two case studies represent common, but quite different, field situations.

Methods

Simulation cases and input parameters

We estimated precision and bias for estimates of N using the Huggins formulation (Huggins 1989, 1991) of closed capture models (Otis et al. 1978) in Program MARK (White 2008) to quantify the effects of combining encounter data from physical captures and passive PIA detections. We took four different approaches for including (or not including) PIA detections in closed capture models to estimate abundance (Table 1). The four approaches dealt with capture heterogeneity that arose because fish that entered the closed capture period with a PIT tag had a higher probability of being initially detected (i.e., captured) than a fish not PIT-tagged. We could have included an approach using the Huggins–Pledger closed capture heterogeneity model (Pledger 2000) for two groups. However, in our situation, where groups related to the heterogeneity are known, the Pledger approach would not be efficient (i.e., the precision would not be as high) because it would predict to which group each encounter history belonged. We knew which group each encounter history belonged to because it depended on whether the individual was PIT-tagged at the start of the closed capture sampling period (e.g., because it was released from a hatchery with a PIT tag or because it had been captured and PIT-tagged in a previous year).

Note that all approaches assume that the same population of fish are sampled physically and by the antenna during the closed capture periods. That is, physical capture location and antenna locations are close enough that fish are vulnerable to detection by physical capture (for tagged and untagged) and PIA (for tagged). Our modeling approaches were as follows: (i) only physical capture data was included in the data set, which avoids the problem of initial capture heterogeneity but discards PIA detections and the potential to increase the precision of estimated abundance;

(*ii*) both physical captures and PIA detections were included, but we did not account for the heterogeneity in the capture probability; (*iii*) both physical captures and PIA detections were included, but we accounted for capture heterogeneity using an individual covariate (IC) to indicate animals that were PIT-tagged at the start of the closed capture period; and (*iv*) both physical captures and PIA detections were included, but we classified animals starting with a PIT tag in one group and animals not starting with a PIT tag in another group. While the group approach is the same underlying model as the IC approach, we included it because we realize that modeling groups is more familiar to practicing biologists and is well described in the Program MARK literature (e.g., Cooch and White 2018).

Because we were focusing on issues with combining capture and detection data to estimate population abundance, we emulated the field situation where physical capture and marking occur during a closed capture period concurrently with PIA detections. In our simulations, a PIT-tagged individual could be initially captured based on the probability of physical capture (p_{phy}), but if not captured physically then it could be initially "captured" based on the probability of PIA detection (p_{det}). Thus, p_{phy} and p_{det} were cumulative, such that overall probability of capture was higher than if only a single method had been used (i.e., $p_{overall} = p_{phy} + p_{det} − p_{phy} × p_{det}$). Recapture (*c*) was simulated the same way (i.e., $p_{overall} = c_{overall}$). However, an individual not having a PIT tag could only be initially captured physically with probability p_{act}. For all approaches, we simulated a range of physical capture probabilities (p_{phy}) and PIA detection probabilities (p_{det}) to represent the range typically observed in field studies. We also simulated a range of the proportion of fish that were PIT-tagged at the start of the sampling period. We varied the proportion of PIT-tagged fish because there can be an increase in numbers of PIT-tagged fish over years of PIT tagging or stocking PIT-tagged fish. Our simulation inputs were as follows:

1. Probability of physical capture and recapture (p_{phy}) = 0.1–0.3 by 0.05 increments
2. Probability of PIA detection (p_{det}) = 0.1–0.6 by 0.05 increments
3. Proportion of fish PIT-tagged at start of sampling period (p_{mark}) = 0.1–0.5 by 0.05 increments

For all simulation scenarios, we used a population abundance (*N*) of 1000, three sampling occasions (e.g., river surveys or detection probabilities), a closed population during the sampling period (no births, death, immigration or emigration were included in the generating model), and assumed 100% tag retention.

We generated all encounter histories in program R (R Core Team 2018) using a random Bernoulli detection process. For fish not having a PIT tag at the start of the sampling period, we used a random Bernoulli test for each sampling occasion to determine whether an individual was initially captured based on p_{phy} first. If the individual was not captured, we moved to the next sampling occasion and repeated the process. In the encounter occasions following initial capture, we first tested to see whether the fish was physically recaptured. If it was, we moved to the next sampling occasion. If not, we used a second random Bernoulli test to determine whether the fish was recaptured via a PIA detection, based on p_{det}. For fish with a PIT tag at the start of the sampling period, we followed the recapture procedure for each encounter occasion. That is, we first tested to see whether the fish was physically recaptured. If it was, we moved to the next sampling occasion. If not, we used a second random Bernoulli test to determine whether the fish was recaptured from a PIA detection, based on p_{det}.

For each simulation, we generated one data set and then manipulated it for three of the four approaches. For the first approach, we omitted all encounters that were antenna detections and utilized only the physical encounters. For the second approach, we did not manipulate the data. For the third approach, we added an individual covariate to the data set that indicated whether a fish started the sampling period with a PIT tag or not, which we call PrevCapIC (Table 1). For the fourth approach, we added groups to the data set, with one group for fish with a PIT tag and another for fish without a PIT tag, at the start of the sampling period. To estimate population abundance, we analyzed the data using the Huggins formulation (Huggins 1991) of a closed capture model (Otis et al. 1978; White 2008). All estimating models had constant *p* and *c*, with models appropriate to the approach (Table 1). We note that *c* is not used in the estimation of *N* in closed capture models and so could be any value (including 0 as in a removal model); because the modeling of *c* was not important for this purpose, we used simple models (Table 1). For all simulations, we ran each data set using Program MARK (White and Burnham 1999, 2001), via R package RMARK (Laake 2013), and output the estimated *N* and its standard error (SE). For each simulation, we calculated percent CV($\hat{N}$) as SE($\hat{N}$)/$\hat{N}$ × 100 to represent precision and percent relative bias [($\hat{N} − N$)/N] × 100 to represent bias. We ran 500 iterations for each scenario; we report the mean of the estimates and their CV($\hat{N}$) and relative bias across the simulations.

Case studies and empirical data

We evaluated the impact of PIAs for two case studies where fish were physically captured and detected passively by PIAs during a closed capture period and abundance was estimated. The two studies represent very different scenarios; case study 1 had low physical capture probabilities and very high PIA detection probabilities, while case study 2 had low physical capture probabilities and similarly low PIA detection probabilities.

Data for case study 1 are for endangered June sucker (USFWS 1999) in three tributaries to Utah Lake, Utah, USA, with data collected 2008–2016. However, for simplicity we only used data for the Provo River tributary in this example. Some fish were PIT-tagged at the time of stocking, while others were PIT-tagged the first time they were captured (physically) during the closed capture sampling period (see online Supplemental Information[1] for details of marking and sampling). Fish were physically captured using trap nets, trammel nets, and spotlighting and passively detected at PIAs in each sampled tributary of Utah Lake as part of the June Sucker Recovery Program (USFWS 1999). All physical captures occurred at the confluence of Provo River, and the antenna was located ~2.9 km upstream. Although not in exactly the same location, operationally the physical captures and antenna detections were both sampling the same population of June suckers going upstream to spawn. That is, over the 2-week closed capture sampling occasions, all fish were assumed to be vulnerable to detection by physical capture and PIA, although only tagged fish could be detected at the PIA. Data were for adult fish (95% CI of total length was 361–545 mm) that make a targeted migration into tributaries of Utah Lake in the spring (June–July), presumably to spawn. The data used in the models were for a total of 2788 suckers physically captured and recaptured (8%) and (or) passively detected at PIAs (92%) for 3 years where physical capture data alone (no PIA detection data) were adequate to estimate *N* (years 2011, 2014, 2015). Because more fish were stocked with PIT tags than were captured and PIT-tagged over the study period, proportions of fish initially "captured" at the PIA during the closed capture sampling period increased and were relatively high from 2012 onward.

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Fig. 1. Simulation results illustrating coefficient of variation (CV) and estimates of population abundance ($\hat{N}$) for different approaches of incorporating passive interrogation antenna (PIA) detections with physical capture data for closed capture models. Results are shown for a population abundance = 1000, sampling occasions = 3, proportion of PIT-tagged fish at the start of the closed capture sampling period (p_{mark}) = 0.2, probability of physical capture (p_{act}) = 0.1, and (*a*) probability of passive antenna detection (p_{det}) = 0.2 and (*b*) p_{det} = 0.6. Relative bias as a percentage of the true (input) value is shown above abundance estimates for each method; vertical bars represent 95% confidence intervals. The four approaches (Table 1) are the *y*-axis labels, moving from approach 1 on the left to approach 4 on the right; IC stands for individual covariate. [Colour online.]
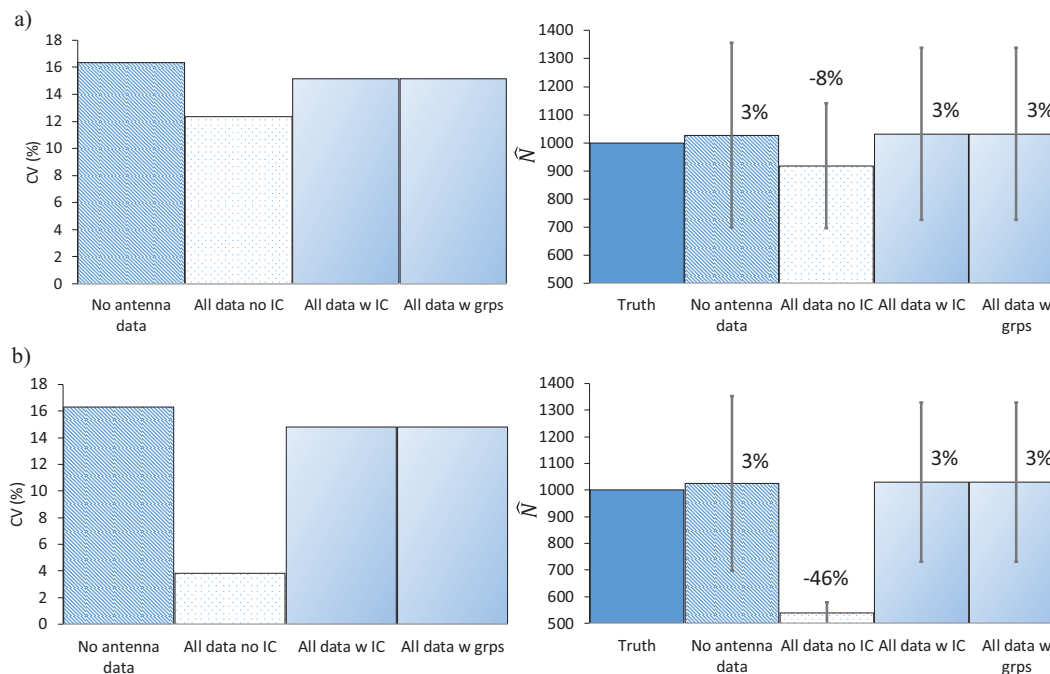
Data for case study 2 are for federally threatened bull trout (USFWS 2015) in Hells Canyon of the Snake River, Idaho, USA, with data collected 2016–2018 (Idaho Power). In this case, bull trout were physically captured via angling on their winter range during January and February (and into early March for 2018) and passively detected on portable 36-inch (1 inch = 2.5 cm) circular submersible (wagon-wheel) PIAs (BioMark Inc., Boise, Idaho) at 15–18 physical sampling sites across the winter range over 31 river miles (1 mile = 1.609 km; see online Supplemental Information[1] for details of marking and sampling). Data were for adult fish (95% CI of total length was 270–560 mm). During the closed capture sampling period, bull trout were not making targeted migrations to or from their winter range. The data used in the models were for a total of 274 bull trout physically captured and recaptured (56%) and (or) passively detected at PIA (44%) across 3 years (see Supplemental Information[1] for details of marking and sampling).

For both case studies, we used a Huggins formulation (Huggins 1991) of the robust-design closed capture model (Pollock et al. 1990; Kendall et al. 1995) to analyze the data. We modeled fish entering closed capture sampling periods with a PIT tag using an IC, analogous to approach 3 in our simulations (Table 1). To evaluate the impact of PIA data for each case study, we omitted all encounters in the data set that were passive PIA detections, analogous to approach 1 in our simulations (Table 1), and then re-ran that data set through the same models that were run for the combined data in Program MARK. We used the top model (based on minimum AIC$_c$) with and without PIA detections (there were different, simpler, top models after encounters from PIA detections were removed) to compare estimates of *N* and its precision for each case study.
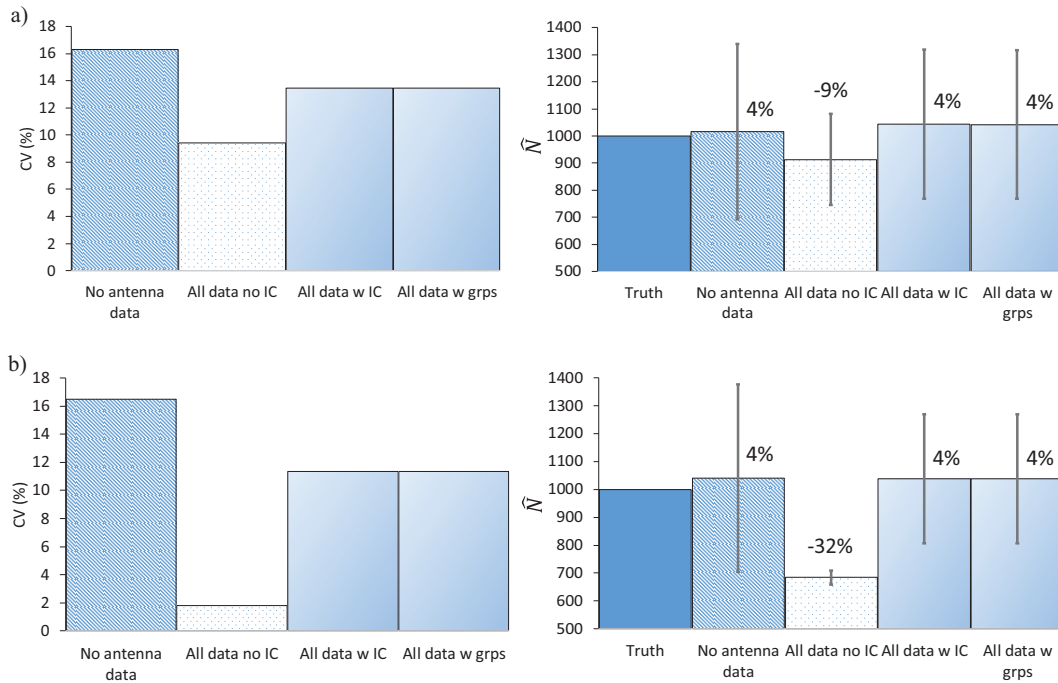
Results

There were several common patterns across all approaches and simulation scenarios. First, results for approach 3 (PrevCapIC was used to account for differences in initial capture probabilities) and approach 4 (groups were used to account for differences in initial capture probabilities) were virtually identical; thus, for brevity we only discuss results for approach 3 (all simulation results are available in the Supplemental Information[1]). Here we show an example of the patterns for probability of physical capture (p_{phy}) at a low but realistic p_{phy} = 0.1 and a relatively low and high proportion of marked fish at the start of the sampling period (p_{mark}) of 0.2 and 0.5, respectively (e.g., Al-Chokhachy and Budy 2008; Bowerman and Budy 2012; Pearson et al. 2016).

In all scenarios, incorrectly including all the PIA detection data without correction (approach 2) resulted in a negative bias in $\hat{N}$. When p_{mark} was relatively low and probability of PIA detection (p_{det}) was close to p_{phy} (Fig. 1*a*), the negative bias was not as large as when p_{det} was much larger than p_{phy} (Fig. 1*b*). Estimates of *N* were negatively biased for the uncorrected case (approach 2), and at a relatively low p_{det} = 0.2, $\hat{N}$ had a bias of −8% (Fig. 1*a*). These biases were larger when p_{det} = 0.6 (Fig. 1*b*). Bias in $\hat{N}$ had a nonlinear change as p_{mark} increased. That is, when p_{det} = 0.2, the bias in $\hat{N}$ was similar for low and high p_{mark} (Fig. 1*a* and Fig. 2*a*). However, as p_{mark} increased, the bias increased and then decreased (see Supplemental Information, Fig. S2[1]), with the maximum bias occurring when p_{mark} was ~0.3. This pattern had the strongest pattern for high p_{det}. When p_{det} = 0.6, the negative bias in $\hat{N}$ decreased by 14% when p_{mark} increased from 0.2 (Fig. 1*b*) to 0.5 (Fig. 2*b*).

Correctly modeling the PIA detection data using PrevCapIC (approach 3) nearly eliminates the bias in all scenarios (Figs. 1–2, right panels), leaving only a small positive bias of 3%–4% in estimates of *N*, which is similar to the bias when PIA detections are

Fig. 2. Similar information as for Fig. 1, except that $p_{mark} = 0.5$ and $p_{act} = 0.1$ for (*a*) $p_{det} = 0.2$ and (*b*) $p_{det} = 0.6$. [Colour online.]

not included (approach 1). When $p_{phy} \geq 0.2$, this bias is almost 0 (i.e., ≤1%; Supplemental Information[1]). While bias is eliminated with PIA data correctly included (approach 3), relatively modest reductions in precision resulted when p_{det} was close to p_{phy}. The CV(N) is reduced by 8%–15% compared with when PIA detections were not used (Figs. 1*a* and 2*a*), with less reduction in CV when p_{mark} is low (Fig. 1*a*). However, when p_{mark} and p_{det} are relatively high, correctly including the PIA detections reduces the CV ($\hat{N}$) by ~20% (Fig. 2*b*). In general, the larger the gap between p_{phy} and p_{det}, the greater the reduction in CV ($\hat{N}$) (Figs. 1 and 2).

Increasing p_{mark} also increases precision, with larger gains as p_{det} increased relative to p_{phy} (Fig. 3). For $p_{det} = 0.2$, CV ($\hat{N}$) was reduced by 6%, 10%, and 20% for $p_{mark} = 0.2$, 0.3, and 0.6, respectively (Fig. 3*a*). We also included the case where p_{phy} is doubled ($p_{phy} = 0.2$; Fig. 3*b*) to highlight the large improvement in precision that comes with increasing p_{phy}. When p_{phy} was doubled from 0.1 to 0.2 and no PIA detections were included, the CV decreased from 16% to 7%, a reduction of 56%. In contrast, when p_{det} was doubled from 0.1 to 0.2 (and $p_{phy} = 0.1$) the CV was only reduced by 1%–9%, depending on p_{mark} (Supplemental Information[1]).

We observed some important consistencies in our two case studies of real data. For adfluvial June sucker in the Provo River, Utah, USA, correctly including the PIA data resulted in great increases in precision (Fig. 4*a*). The CV ($\hat{N}$) was reduced 39%–82% and the width of the 95% CI was reduced by 42%–82%. In this case, the estimated probability of first capture (*p*) was very low without PIA detections (mean ≤ 0.01 over four sampling occasions) and relatively high when PIA detections were included (mean ≥ 0.16 over four sampling occasions). For fluvial bull trout in Hells Canyon of the Snake River, Idaho, USA, the benefit of adding the PIA detections was not as dramatic but was still important (Fig. 4*b*). When PIA detections were included, the CV ($\hat{N}$) was reduced 4%–18% and the width of the 95% CI was reduced by 8%–34%. In this case, the estimated *p* was low without PIA detections (mean 0.04–0.06 over four sampling occasions) and only slightly higher when PIA detections were included (mean 0.06–0.09 over four sampling occasions). A more subtle improvement to the estimates of *N* when including PIA data was the improved stability in model parameter estimates from year to year (Fig. 4). Although we only had 3 years

of data where a complete comparison is possible for both case studies, the interyear variability decreased with inclusion of PIA detections.
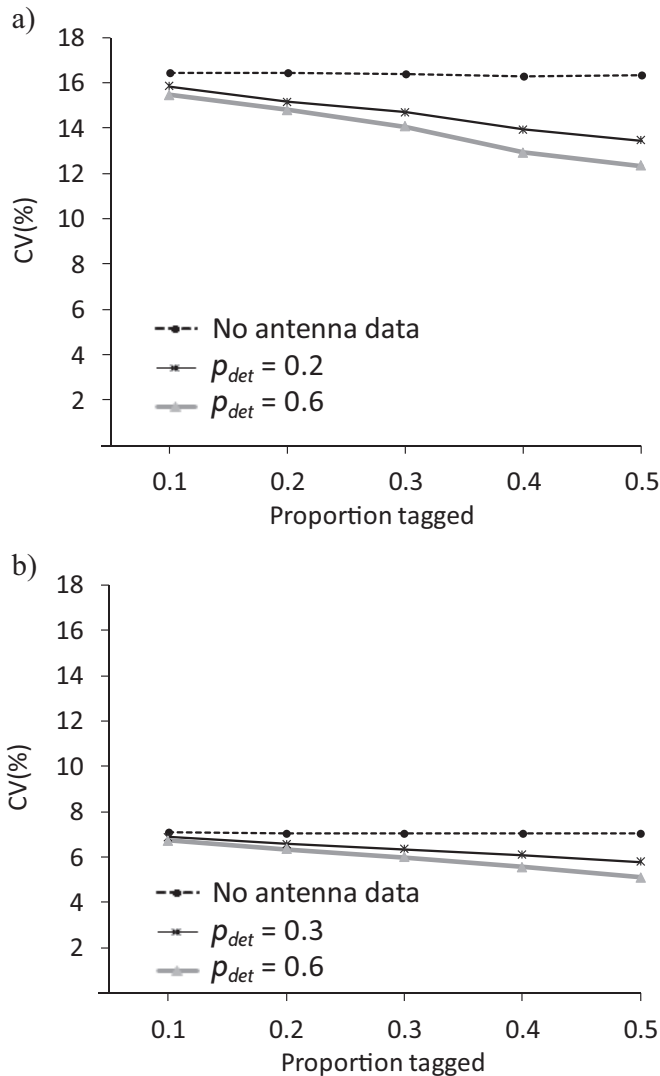
Discussion

Over the last decade, there have been numerous technical advances in mark–recapture techniques and passive PIT tag detection, in particular PIAs. There has been a proliferation of PIAs for monitoring PIT-tagged fish, resulting in data sets containing diverse combinations of physical captures and PIA detections of fishes. PIA detections can be treated as captures (*p*) or recaptures (*c*) in capture–mark–recapture models. Consequently, PIA detection data have great potential in the estimation of vital rates and abundance, as well as increasing precision of the estimates. However, including PIA detections comes with some unique challenges that should not be overlooked. The most important challenge addressed herein is the inherent model bias (underestimation of $\hat{N}$) associated with mixing data with different capture probabilities, such as from physical captures with PIA detections. Our goal was to propose solutions to remove biases from the estimates of *N* that are different from the multistate approach of Pearson et al. (2016) but rely on a similar decomposition of empirical detection probability. Our study results are predicated on the assumption physical capture and PIA locations were located (i.e., generally close enough in space) such that they sampled the same population. We discuss other spatial arrangements below.

Simulations — benefit of PIA data on precision

Using simulations, we demonstrated that, relative to not using PIA data, precision in estimates of *N* increased (i.e., CV ($\hat{N}$) decreases) from slightly to substantially when PIA data are included and capture heterogeneity is appropriately modeled. There were greater reductions in CV ($\hat{N}$) as p_{det} increased and when p_{mark} increased. These decreases in CV ($\hat{N}$) increased our ability to detect actual declines or increases in *N*, a critical component of monitoring small or imperiled populations. Our simulations also demonstrated that the larger the difference between p_{phy} and p_{det}, the greater the reduction in CV ($\hat{N}$) as p_{mark} increased. That is, there was a synergy among the differences among p_{phy} and p_{det} and
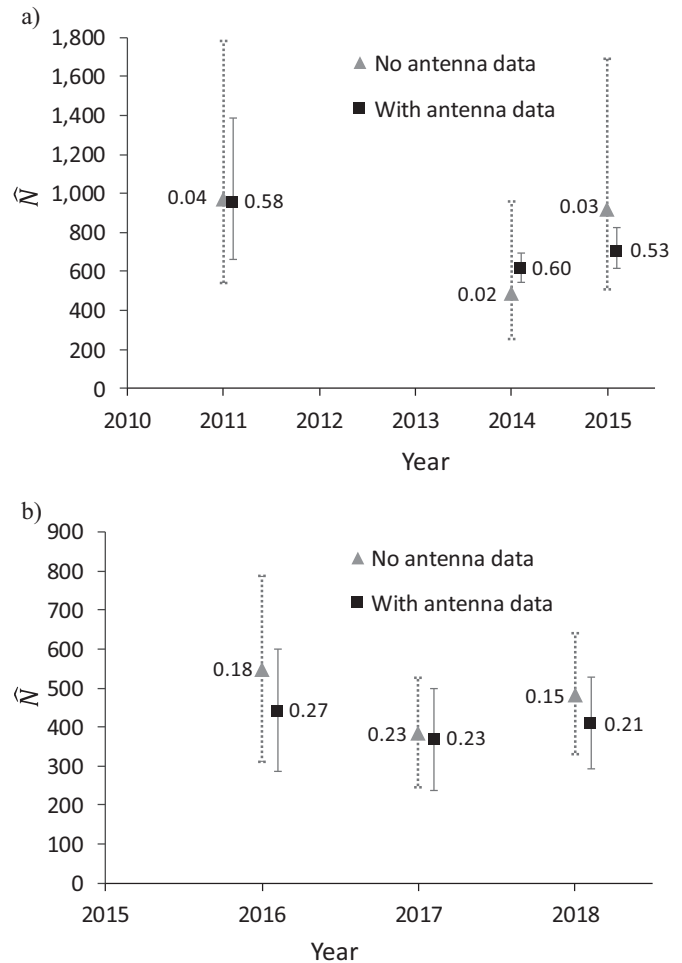
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Fig. 3. Simulation results showing coefficient of variation (CV) of population abundance versus proportion of PIT-tagged fish in the population at the start of the closed capture sampling period for different methods of incorporating passive PIA detections with physical capture data for closed capture models when only physical captures are used (no antenna data; approach 1) versus when passive PIA detection data are incorporated using an individual covariate to model heterogeneity in probability of initial capture (approach 3). Results are shown for a population abundance = 1000 and sampling occasions = 3. Results are shown for (*a*) probability of physical capture (p_{phy}) = 0.1 and (*b*) p_{phy} = 0.2 with relatively low and high levels of probability of passive antenna detection (p_{det}).

Fig. 4. Estimates of population abundance ($\hat{N}$) and 95% confidence intervals based on top closed capture models, with and without the inclusion of PIA detections for (*a*) female June suckers in the Provo River, Utah, and (*b*) bull trout in Hells Canyon, Snake River, Idaho. The numbers next to the estimates of $\hat{N}$ are estimates of p^* (probability of being captured at least once during the four sampling occasions).

p_{mark}. We note that only three sampling occasions were used in our simulations, which we considered a practical number for many field sampling scenarios. However, if there were additional sampling occasions, reductions in variance should be even greater when PIA detections are included in closed capture models.

While the bull trout case study demonstrated reductions in precision within the simulated range, the June sucker case study exhibited much larger reductions. The differences are due to two factors. First, for June suckers, mean p_{phy} = 0.007 (i.e., $p_{phy} \ll 0.1$) and mean p_{det} = 0.178, such that p_{det} was 25 times larger than p_{phy}. This difference is a larger relative difference than any of our simulation scenarios because it was not practical to simulate scenarios where $p_{phy} < 0.1$. When $p < 0.1$, a substantial proportion of

simulations fail due to random binomial variation, and $\hat{N}$ becomes unreasonably large (e.g., >20 000 when truth = 1000). Second, there were likely a higher proportion of June suckers PIT-tagged in the sampling population compared with bull trout. Similar to increases in precision of abundance estimates, Pearson et al. (2016) demonstrated a significant increase in precision of survival probability estimates for endangered humpback chub (*Gila cypha*) in the Little Colorado River when PIA detections were added to physical capture (hoop netting) data. In their study, adding the PIA detections nearly doubled the recapture probability but with no concordant handling of fish. Thus, we believe our simulated increases in capture information provided by PIAs represent a conservative view of what is feasible in the field.

Simulations — issue with PIA data on accuracy (bias) if not corrected

Despite the growing list of benefits of PIAs in aquatic ecology and management, failure to properly account for heterogeneity in mixed capture probabilities of physical capture and PIA detections can lead to negative bias in N and its variance. In simulations, treating the capture types as the same resulted in a significant simulated underestimate of N and CV ($\hat{N}$), such that coverage of the 95% CI ($\hat{N}$) would be poor. For a range of inputs likely to represent field studies (p_{det} = 0.1–0.6 and p_{mark} = 0.2–0.5),

the negative relative bias ranged from 8% to 46%. However, when either the IC or group approach was used in the model, the relative bias dropped to a positive 3%–4% and even less as physical capture probabilities increased. Additionally, when $p_{phy} > 0.2$, the bias was essentially 0% (Supplemental Information[1]). This small positive bias was the same for the approach where no PIA detections were used and is common when p (p_{phy} in simulations) is low. The positive bias occurs because sometimes the estimate of p is very low (close to 0), which results in estimates of N that are extremely high (Otis et al. 1978; Rosenberg et al. 1995; Kery and Royle 2016). Although it is typically more conservative to underestimate population abundance, underestimating the population abundance by 8%–46% could result in misguided management decisions. For example, this bias could lead to a conclusion that an expensive or time-sensitive management or conservation action had failed to have the desired effect. Similarly, harvest opportunities could be missed and interesting ecological phenomenon could be masked (e.g., density dependent regulation; Rose et al. 2001).

Both the individual and group "corrections" implemented herein make sense biologically and are heuristically similar to modeling approaches to correct the bias resulting from trap-happy animals (Otis et al. 1978; White et al. 1982). However, the IC is also relatively simple to incorporate and offers more modeling flexibility, particularly for robust-design modeling of multiple years of closed capture data (see case studies in Supplemental Information[1]). As mentioned previously, one method to account for heterogeneity in capture probability for a robust-design model is to use the multistate robust-design model (Pearson et al. 2016) where state is analogous to group in our single year closed capture model. However, the multistate model is complex, and the IC approach may be easier to implement for biologists who are primarily interested in estimates of N and survival for a study population. In addition, an IC can be used in a multistate model to simplify modeling when there are other states of interest. However, while the IC and group approach improved model fit for our case studies, neither approach improved model parsimony because additional parameters need to be included (i.e., IC for previously captured fish or an additional initial capture probability (p) for the PIT-tagged group). We note that the increase in model parameters is why the increases in precision are modest when p_{phy} is similar to p_{det}. This issue of heterogeneity in p also can result in biased estimates of survival, as the same recapture probability (p in survival models) among individuals is an assumption of the Cormack–Jolly–Seber model (Pollock et al. 1990; Lebreton et al. 1992).

Case studies — benefit of PIA data on precision, detection of trend, and estimate stability

Our two case studies using real data demonstrate two ends of a range of scenarios we can expect to encounter in fish studies incorporating PIA detections for estimating N. Scenarios with a low probability of being captured physically and a high probability of detection at PIAs mimic the common life history expression of an adfluvial fish like June suckers. These fish make discrete spawning migrations through a medium-sized stream bottleneck, thus forcing them to pass over one or multiple PIAs with a high probability of detection. In the June sucker case, the PIAs span the entire stream, and almost all adult spawning fish make a discrete migration. Further, in this case, many suckers are only captured once physically (or never, as some are stocked already tagged), and the greatest proportion of the captures are passive detections during the targeted spawning run into tributaries. Over four closed capture sampling occasions, p averaged <0.01 without PIA detections, yet averaged 0.18 with PIA detections included. The incorporation of PIA detections reduced the CV ($\hat{N}$), on average, from 33% (no detections) to 11% (with detections). Based on the change in the average CV ($\hat{N}$), a decline ≥ 30% in N can be detected in

~6 years when including PIA detections, compared with >32 years without PIA detections (based on $\alpha = 0.10$, $\beta = 0.80$, one-tailed linear decline; Gerrodette 1987, 1993). Thus, in the case of a fish having very low physical capture and moderately high detection probability due to targeted spawning movements across PIA, the improvement gained from incorporating PIA detections into abundance estimates is profound.

For the second case study on bull trout in Hells Canyon of the Snake River, Idaho, USA, the effect of the addition of the PIA detections to the abundance estimate was more subtle, but still significant. In this case, initial capture probability (p) with PIA detections (mean was 0.08) was closer to p without PIA detections (mean was 0.05), because bull trout are detected less frequently on smaller circular PIAs in a larger river, with a much lower chance of being encountered. In this case, the incorporation of PIA detections at most reduced the CV ($\hat{N}$) from 19% to 15%. This scenario generally reflects capture and detection probabilities of fluvial bull trout in the Pacific Northwest, where some portion of the population migrate to tributaries to spawn and overwinter and are detected at a PIA, and another portion of the population is resident, resulting in a lower p (Al-Chokhachy et al. 2009; Budy et al. 2017). However, even in the low p_{phy} and p_{det} scenarios, the precision of the estimate is still improved with no additional handling of the fish. This reduction in the handling of fish is a vital consideration for an ESA-listed fish, where numbers are naturally low and physical capture is restricted (MacKenzie et al. 2005).

In addition, for both case studies the incorporation of the PIA data stabilized model selection in Program MARK and reduced the year-to-year variability in estimates of N relative to models estimated with only the physical capture data. Although we lacked sufficient years to fully quantify the reduction, this is an understated but important improvement, and it occurred even when capture probabilities that included PIA detections remained relatively low (i.e., the bull trout scenario).

PIA data applications

Finally, for both populations, the reduction in CV ($\hat{N}$) results in a reduction in the time to detect declines in N when PIA detections were used compared with when they were excluded. Even for the modest reduction of CV ($\hat{N}$) of bull trout, a decline ≥ 30% in N can be detected in 9 years when including PIA detections, compared with 14 years without PIA detections (based on $\alpha = 0.10$, $\beta = 0.80$, one-tailed linear decline; Gerrodette 1987, 1993). Thus, without PIA data the population can undergo an undetected decline to such low numbers that the risk of extirpation increases. Detecting population declines is particularly important in small or endangered populations more susceptible to extinction vortex forces including the effects of variable environmental conditions, demographic stochasticity, and Allee effects (Gilpin and Soulé 1986; Stephens and Sutherland 1999; Fagan and Holmes 2006). In general, the addition of PIA data will facilitate early detection of declines (or increases), which allows more time to implement appropriate management actions.

Notably, in their seminal work on estimating fish survival with mark–recapture data, Burnham et al. (1987) suggested additional research be pursued using "high technology" PIT equipment, as they "would not be surprised to achieve a doubling or tripling of recapture rates with PIT tags". Their prediction has come to fruition, and now the issue is how to best utilize a mixture of capture information to optimize estimates of vital rates and abundance. The issue is particularly relevant for fish, since literally millions of fish are currently (or will be) PIT-tagged, and PIAs are deployed at dams, passages, culverts, and tributary mouths, as well as fully spanning some large rivers such as the Columbia River (e.g., high-profile endangered salmon; National Marine Fisheries Service (NMFS) 2014; Conner et al 2015), the Colorado River (e.g., highly imperiled pikeminnow (*Ptychocheilus lucius*); Osmundson and White 2017; Dzul et al. 2018), and very recently the Rio Grande River (endan-

gered Rio Grande silvery minnow (*Hybognathus amarus*; P. Budy, personal communication). While there are other analytical and logistical hurdles to using PIA detection data (e.g., antenna efficiency, dead versus live tags), there are feasible solutions (Pearson et al. 2016; Stout et al. 2019; Stout et al., in press) and well-tuned and designed PIAs that can produce detection efficiencies approaching 100% (Aymes and Rives 2009). Accordingly, PIT technology has been implemented in countless small streams and rivers worldwide, and its use for estimating population parameters is not limited to fish.

Thus, results of this study also have implications for non-fish animals, as the use of internal PIT tags and passive antennas includes the study of mammals, amphibians, reptiles, birds, and invertebrates (reviewed in Gibbons and Andrews 2004). For example, handheld PIAs have recently been shown to be much more effective than physical capture of Queensnakes (*Regina septemvittata*), offering additional data to bolster demographic analyses (Oldham et al. 2015). PIA detections have also been used to estimate population parameters for penguins (P.D. MacKinnon, personal communication), voles (*Microtus ochrogaster* and *Microtus pennsylvanicus*) (Harper and Batzli 1996), bats (Kunz 2001), and desert tortoises (*Gopherus agassizii*) (Boarman et al. 1998). Mark–recapture study designs using DNA to estimate abundance, wherein systematic hair or fecal samples are collected, along with alternative sampling methods (Boulanger et al. 2008; Kendall and McKelvey 2008; Pfeiler 2019) that have different capture probabilities, are analogous to the fish scenarios we model herein. That is, this method is generalizable to any situation where data are collected with multiple methods having different capture–detection probabilities. However, all these examples assume the different methods are sampling the same population of animals. We speculate our method can be extended to estimate population size when some animals are not vulnerable to all sampling methods. For example, if the antenna is separated by enough distance, resident animals may be vulnerable to only physical capture, while migrant animals may be vulnerable to physical capture and PIA detection. The development of methods to estimate population size when sampling vulnerability varies for different sampling methods would be a logical and potentially useful extension of current models.

In summary, we present a relatively simple method whereby population abundance can be estimated more precisely and robustly using appropriately modeled combinations of physical capture and passive detection information. Moreover, improvements from including PIA data do not pose any additional handling stress to fish populations and can improve the ability to detect population trends over shorter time periods. These attributes make including PIA data an attractive option for many situations but particularly for sensitive and imperiled fish sampling regimes. The results of this study have implications for estimating abundance for any situation where data are collected with methods having different capture–detection probabilities.

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