



## Original Article

# Predicting prey recovery from scats of California sea lions (*Zalophus californianus*) for novel prey species and sizes

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Diet studies of marine top predators increasingly inform assessments of prey stocks and ecosystems, as well as predator ecology. Prey hard parts provide quantitative information on diet composition. However, species and size variation in digestion of hard parts, and thus in recovery rates, introduces bias in diet reconstruction. Captive feeding studies estimate species- and size-specific recovery rates of prey hard parts in pinnipeds, but such studies can only include a small subset of prey species and sizes consumed by these commonly generalist predators. We developed a generalized linear mixed effects model that estimates recovery rates of otoliths in California sea lion (*Zalophus californianus*) scats from otolith morphometrics, based on previously published captive feeding studies. The resulting model explains 85% of the variance in recovery rates among common teleost prey species of California sea lions. We also reestimated cephalopod beak recovery rate in California sea lion scats using an intercept-only mixed effects model. The resulting models can estimate recovery rates—and numerical correction factors—for novel teleost and cephalopod prey species and sizes in California sea lion scats, supporting more accurate reconstruction of diet composition in the wild and suggesting a way forward for other pinniped species.

**Keywords:** California sea lion, *Zalophus californianus*, pinniped, diet composition, feces, scat, prey hard parts, captive feeding, correction factor, recovery rate.

## Introduction

Time series of top marine predator diets are increasingly recognized for their value in informing not only predator ecology and ecosystem models, but also ecosystem assessment and stock assessment of data-poor prey species (Field *et al.*, 2007; Einoder 2009; Hazen *et al.*, 2019; Ng *et al.*, 2021). Due to the relative expense and logistical difficulty of collecting information on marine predator diets, species composition of marine predators may be well charac-

terized in many cases, but relative contributions of prey items and dynamics of diet composition with time remain unknown (Young *et al.*, 2015). Pinnipeds present an exception, with many species using a central place foraging strategy that affords relatively easy access to scat (fecal) samples at the rookeries or haulouts that they return to between foraging trips. Scats provide a comparatively inexpensive and non-invasive means of obtaining robust sample sizes and both qualitative and quantitative diet information (Prime and Hammond, 1990; Tollitt *et al.*, 2010). These properties facilitate the

establishment of time series with the duration and resolution needed to study trophodynamics and their relationship to variability and trends in predator and prey populations and in the marine environment (e.g. García-Rodríguez and Aurióles-Gamboa, 2004; Bowen and Harrison, 2006; Davis *et al.*, 2006; Mecenero *et al.*, 2006; Melin *et al.*, 2012; Smout *et al.*, 2014).

Scats may provide data on number and sizes of prey consumed, but reconstructing reliable diet composition from this information is not straightforward (Jobling and Breiby, 1986; Laake *et al.*, 2002). Large, often unquantified biases accrue due to several processes during prey intake and digestion. Hard parts from partially consumed prey may not be ingested (e.g. Fallows *et al.*, 2015). Large, digestion-resistant structures may be regurgitated (e.g. Bigg and Fawcett, 1985; Goodman-Lowe, 1998). Digestion obscures consumption of prey lacking hard parts, and alternately leads to differential recovery rates for hard parts from different taxa, including otoliths from different species and sizes of teleost prey (da Silva and Neilson, 1985; Tollitt *et al.*, 1997; Bowen, 2000; Phillips and Harvey, 2009; Sweeney and Harvey, 2011). Large-scale spatial heterogeneity in the prey field of pinnipeds that make multi-day foraging trips may result in biased data from scats at rookeries or haulouts, because far-field prey may be eliminated before the predator returns (e.g. Grellier and Hammond, 2006; Sweeney and Harvey, 2011; Wilson *et al.*, 2017). Lastly, otoliths that are recovered are still most often eroded, such that direct conversion would underestimate prey size (e.g. Tollitt *et al.*, 1997; Phillips and Harvey, 2009; Sweeney and Harvey, 2011; Wilson *et al.*, 2017).

Captive feeding studies are designed to quantify recovery rates and estimate numerical and length correction factors for specific prey species and sizes, reducing bias due to digestion in prey reconstruction from scats (e.g. Prime and Hammond, 1987; Tollitt *et al.*, 1997; Grellier and Hammond, 2006; Phillips and Harvey, 2009; Sweeney and Harvey, 2011). However, the inability to generalize these estimates to other prey species and sizes adds considerable cost, time, and logistical challenges to diet studies of pinnipeds (Tollitt *et al.*, 2010; Wilson *et al.*, 2017). This problem is exacerbated by the fact that most pinnipeds are generalist predators with a diverse prey base, with some pinniped species ranging across multiple biogeographic provinces or even ocean basins (e.g. Fiscus and Baines, 1966; Everitt *et al.*, 1981; Lowry *et al.*, 1990; Tollitt and Thompson, 1996; García-Rodríguez and Aurióles-Gamboa, 2004; Brasseur-Pérez *et al.*, 2019).

Harvey (1989) proposed a “robustness index” for otoliths, obtained by dividing otolith mass by otolith length, to help account for differential recovery of otoliths. Sweeney (2008) took this a step further and found that robustness explained substantial variability among recovery rates of species and sizes consumed. Tollitt *et al.* (1997) also found strong correlation between otolith length, width, and robustness and recovery rates. Yet no dedicated effort has been made to find the strongest relationship between otolith morphometrics and recovery rates, nor to develop a general model to correct for bias in prey species and sizes for which no captive feeding studies were performed.

In this study, we reanalysed data from previously published captive feeding studies on California sea lions (*Zalophus californianus*), in conjunction with predicted otolith morphometrics from an extensive study of prey hard parts of forage species in the California Current Large Marine Ecosystem (Lowry *et al.*, 2020a, b), to develop a model that can predict otolith recovery rates (and numerical correction factors) for novel species and sizes of prey. The mixed effects model framework we used also allowed us to account for individ-

ual effects of captive feeding subjects. We additionally reestimated mean recovery rate (and a numerical correction factor) for cephalopod beaks based on the same published captive feeding study, accounting for individual effects of captive feeding subjects.

## Methods

We developed two separate models to predict proportions of consumed prey recoverable in California sea lion scats: one for teleost prey as a function of otolith morphometric covariates to explain variation in survival of the digestive process, and an intercept-only model for the mean recovery rate of cephalopod prey. These models were fitted to otolith and beak recovery data from previously published captive feeding studies. Otolith morphometrics for prey species and sizes fed were predicted from published regressions.

### Captive feeding study data

We used data from two feeding studies on captive California sea lions: Orr and Harvey (2001) and Sweeney and Harvey (2011). Data from these studies included in this analysis are summarized in Table 1. In both studies, sea lion subjects had a pool to swim in and haul out of, which affects digestion and increases prey part recovery, more closely simulating conditions in the wild than “dry” experiments (Harvey, 1989; Bowen, 2000; Sweeney and Harvey, 2011). We use the term “meal” to refer to all prey of one species fed at the same time. Prey sizes were relatively homogeneous within a given meal. We reserve the term “trial” for discussion of binomial trials (i.e. individual prey items). Meals of known numbers and sizes (lengths and weights) of experimental teleost or squid prey species were rotated into the regular feeding schedule of individual sea lions. Some feedings included more than one prey item, and thus more than one “meal.” Scats and spews (regurgitations) were collected and processed to identify and enumerate corresponding teleost otoliths or squid beaks. Otoliths were classified as lefts or rights, beaks as uppers or lowers.

Data from the two captive feeding studies were filtered for quality and suitability for analytical objectives. Orr and Harvey (2001) observed only scats. Sweeney and Harvey (2011) observed both scats and spews. Primarily scats are collected for long-term monitoring of California sea lion diets (Antonelis *et al.*, 1984; Weise and Harvey, 2008; Orr *et al.*, 2011; Melin *et al.*, 2012), so we treated spews as a generic contributor to prey hard part loss along with digestion. Our objective for the otolith recovery model was to estimate the probability of surviving the digestive process based on otolith morphometrics, so for the teleost model, we eliminated meals for which more than 10% of fed otoliths were recovered in spews. Meals eliminated accordingly constituted at most 7% of all individual fish fed across both experiments for all but two experimental teleost prey species (18% for Pacific hake, *Merluccius productus*, and 11% for steelhead smolts, *Oncorhynchus mykiss*). Observations of spews in the wild are also less frequent than scats, and, in a 35-year time series of quarterly collections from the southern Channel Islands off California, most hard parts identified in spews of California sea lions were cephalopod beaks (unpublished data). In Sweeney and Harvey (2011), of 668 scat and spew samples containing prey hard parts, fewer than 5% were spew or mixed spew and scat samples.

For Orr and Harvey (2001), only the reported maxima of left and right otolith (upper and lower beak) counts for each meal were available. But proportions based on maxima vary with sample size, and therefore cannot be used to estimate correction

**Table 1.** Summaries of data from two captive feeding studies (Orr = Orr and Harvey, 2001, Sweeney = Sweeney and Harvey, 2011) included in this analysis, with prey species, mean size fed (standard length for teleosts, mantle length for squid), total meals with this species, total prey fed  $n$ , total prey recovered  $k$  (after rounding mean of left and right otolith counts per meal), and proportion recovered  $p$ . Common prey of California sea lions are noted with a “c” in parentheses (>10% frequency of occurrence in a diet study; Lowry *et al.*, 1990; Lowry *et al.*, 1991; Melin *et al.*, 2008; Weise and Harvey, 2008; Melin *et al.*, 2010; Melin *et al.*, 2012; Robinson *et al.*, 2018).

Prey type	Species	Study	Size (mm)	Meals	n	k	p
Teleostei	<i>Clupea pallasii</i>	Orr	230	4	40	26*	0.65*
	<i>Engraulis mordax</i> (c)	Orr	126	2	20	7*	0.35*
		Sweeney	133	23	957	536	0.56
	<i>Hypomesus pretiosus</i>	Orr	134	2	48	11*	0.23*
	<i>Mallotus villosus</i>	Orr	149	2	40	2*	0.05*
	<i>Merluccius productus</i> (c)	Orr	226	4	52	35*	0.67*
		Sweeney	384	14	49	42	0.86
	<i>Microgadus proximus</i>	Orr	223	3	30	26*	0.87*
	<i>Oncorhynchus mykiss</i>	Sweeney	198	14	199	87	0.44
	<i>Sardinops sagax</i> (c)	Sweeney	200	45	818	183	0.22
	<i>Scomber japonicus</i> (c)	Sweeney	244	49	876	385	0.44
	<i>Sebastes jordani</i> (c)	Sweeney	173	5	79	44	0.56
	<i>Thaleichthys pacificus</i>	Orr	152	4	67	27*	0.40*
	<i>Trachurus symmetricus</i> (c)	Orr	228	2	20	3*	0.15*
		Sweeney	194	23	566	360	0.64
Cephalopoda	<i>Doryteuthis opalescens</i> (c)	Sweeney	141	25	677	537	0.79

\*Based on reconstructed mean of left (upper) and right (lower) hard part counts.

factors for application to field-collected scats, where meal sizes are unknown (“Advantage of using mean of left and right (upper and lower) counts,” below). Unbiased estimates of prey proportions recovered and corresponding correction factors that are independent of meal size require using either mean or total counts of lefts and rights (uppers and lowers), rather than maxima. Using total counts assumes independent fates of paired otolith or beaks after ingestion. We reconstructed the expected mean of left and right (upper and lower) counts of prey hard parts recovered for each meal in Orr and Harvey (2001) through simulation, given the reported maximum of left and right otoliths and the number of prey fed (Supplementary Material Section 1).

Further details on the two captive feeding studies, reconstruction of expected mean counts for Orr and Harvey (2001), and data filtering are provided in Supplementary Material Section 1. Prey species, numbers, and sizes fed in each study and used in this analysis are summarized in Table 1 (data provided in Supplementary Material Section 5).

Individual otoliths could not be traced back to individual fish fed unless meal size was one, so data from captive feeding experiments were aggregated to a binomial format of numbers of prey fed  $n_i$  (“trials”) and recovered  $k_i$  (“successes”) per meal  $i$ . Successes equalled the mean of left and right otoliths (or upper and lower beaks) recovered, rounded to an integer. In all, the resulting data set from the two captive feeding studies included 3861 individual teleost prey representing twelve species, fed to 14 sea lions in 198 meals; and 677 individual cephalopod prey from one species, fed to 9 sea lions in 25 meals. Recovery rates of otoliths were far more variable among teleost species than among captive feeding subjects (Figure 1).

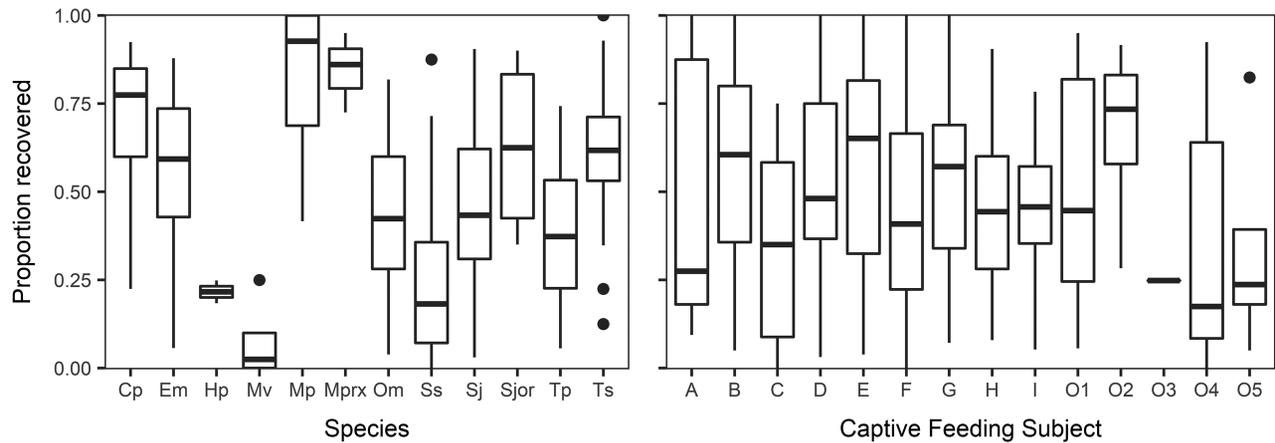
### Advantage of using mean of left and right (upper and lower) counts

Captive feeding studies for pinnipeds often characterize proportions of hard parts recovered in terms of the “minimum number

of individuals” (MNI), which in this case would be the maximum of left and right recovered otolith counts (or upper and lower squid beak counts) for each meal. However, due to the discrete nature of binomial draws, estimated proportions recovered based on MNI increase with decreasing meal size even as the true probability of recovery is held constant. In order to estimate an unbiased recovery rate that is independent of meal size, we used the mean of the two counts instead, which does not vary with sample size. If paired hard parts within individual prey have independent fates, one could argue for using the total hard parts fed and recovered (e.g. sum of left and right otoliths) for model fitting, rather than the mean. While we did not find consistent evidence in the data for non-independence of left and right otolith counts, we used the mean rather than total counts to reduce overconfidence in model estimates and to enhance the relative weighting of prey species with small numbers of trials (i.e. individual prey items fed). Note that means could also be calculated from total counts by dividing by two if lefts and rights (upper and lowers) were not enumerated separately.

### Otolith morphometric data

Otolith morphometrics for prey species and sizes fed were predicted from published regressions as follows. Species-specific linear regressions of prey standard length to otolith length (provided in Supplementary Material Section 2) were inverted to predict mean otolith length (mm) from mean measured prey length for each meal. Mean otolith length was then used to predict otolith width (mm), perimeter length (mm), projected area (i.e. the scaled area of the otolith in a digital image; mm<sup>2</sup>), and weight (g) per species per meal based on published species-specific regressions of otolith morphometrics (Lowry *et al.*, 2020a and b). The necessary statistics to estimate prediction error and propagate it starting from standard length to otolith length prediction were not available for half the species, so we used point estimates throughout the rest of the analysis. Otolith morphometrics based on mean prey length were a reasonable approximation of reality since each meal consisted of



**Figure 1.** Boxplots of proportion of fish fed that were recovered per meal by species (left panel) and across species by captive feeding subject (right panel). Scientific name abbreviations are Cp = *Clupea pallasii*, Em = *Engraulis mordax*, Hp = *Hypomesus pretiosus*, Mv = *Mallotus villosus*, Mp = *Merluccius productus*, Mprx = *Microgadus proximus*, Om = *Oncorhynchus mykiss*, Ss = *Sardinops sagax*, Sj = *Scomber japonicus*, Sjr = *Sebastes jordani*, Tp = *Thaleichthys pacificus*, Ts = *Trachurus symmetricus*. Subjects A through I correspond to Sweeney and Harvey (2011), Subjects O1 through O5 correspond to Orr and Harvey (2001). Boxes extend from the first to the third quartile, with a horizontal line for the median. Whiskers extend to the most extreme value no further than 1.5 times the interquartile range. Data beyond the whiskers are plotted as individual points.

similar-sized prey of a single species (mean coefficient of variation of length within meal was 3.4%).

For the teleost recovery rate model, we calculated a suite of quantitative indices to characterize otolith morphometry as it might relate to the digestion of otoliths by sea lions (Table 2). Many of these indices were drawn from other studies that have considered otolith dissolution (Harvey, 1989; Jones, 2016) or, more generally, particle abrasion (Hunt, 1993). Some indices require differentiating between the major and minor axis of an otolith. For this study, otolith length, as defined above, was always greater than otolith width, but in other prey species this is not always true, so we use “major axis” and “minor axis” in Table 2, rather than otolith length and width.

### Model framework

For both the beak recovery model and the otolith recovery model, we fit a binomial generalized linear mixed-effects model (GLMM) with a cauchit link to the binomial response variable—numbers of trials (prey fed)  $n_i$  and successes (prey recovered)  $k_i$  per meal  $i$ —with random intercepts for captive feeding subjects. Squid beak recovery rate was estimated as an intercept-only model. The otolith recovery model included otolith morphometric covariates, calculated as described above. The fat-tailed Cauchy distribution avoids the potential problem of predicting minuscule recovery rates (and thus astronomical numerical correction factors) for otoliths whose morphometrics considerably exceed the range of our experimental data (see Discussion), an artefact observed when preliminary results from a logit-link model were applied to field-collected samples. The model structure for otolith recovery is thus

$$Y_{ij} \sim \text{Bin}(n_{ij}, p_{ij})$$

$$\text{cauchit}(p_{ij}) = \tan\left(\pi\left(p_{ij} - \frac{1}{2}\right)\right) = \alpha + \beta\mathbf{x}_{ij} + u_j$$

$$u_j = N(0, \sigma_u^2)$$

where  $Y_{ij}$  is the observed number of successes for meal  $i$  and sea lion  $j$ ,  $n_{ij}$  is the number of trials (prey fed),  $p_{ij}$  is the probability of success

(recovery),  $\alpha$  is a common intercept,  $\beta$  is a vector of coefficients for covariate vector  $\mathbf{x}$  of otolith morphometrics for that meal, and  $u_j$  is the random intercept for sea lion  $j$ , where  $u_j$  is drawn from a random distribution with mean zero and standard deviation  $\sigma_u$ . The squid model took the same form but without the term for morphometric covariates. Covariates were not considered for squid, because they are subject to breakage rather than dissolution, no captive feeding studies are available with large sample sizes of different sizes and species of cephalopods, and experimental recovery rates for a range of cephalopod taxa fall within a relatively narrow range compared to teleosts (see Discussion).

### Model selection for otolith recovery

We considered all covariates that were potentially relevant to the digestive process, including otolith length, projected area, and weight, and the calculated indices described in Table 2. We used cross-validation to compare the performance of all possible models with zero, one, or two covariates in addition to an intercept and random effects. Higher degrees of freedom, including interactions among variables, were initially considered, but preliminary cross-validation results indicated that models with more than two covariates tended to overfit the data and had frequent convergence issues. For model selection, covariates were scaled to a mean of zero and standard deviation of one. To avoid collinearity issues, a given candidate model included a maximum of one of each of the following groups of highly linearly correlated variables (i.e. scatter plots showed little scatter and an approximately linear relationship): (i) RobustIndex, DepthIndex, and otolith weight; (ii) InvRobustIndex, InvDepthIndex, and Perim2PA; and (iii) otolith length, projected area, and PA2Perim. In total, 12 covariates were considered in 70 candidate models (full list provided in Supplementary Material Section 4).

We used a blocked, “leave-one-species-out” cross-validation approach (Roberts et al., 2017) for model selection, designed to evaluate the model’s ability to predict mean otolith recovery rates for novel species. Observed recovery rates for each species were

**Table 2.** Otolith morphometric indices used as candidate covariates in models of otolith recovery. We use “perimeter” as shorthand for perimeter length, “weight” for otolith weight, and “area” for projected area. Units of dimensions used in these indices are mm for lengths, mm<sup>2</sup> for projected area, and g for weights.

Index	Abbreviation	Definition	Reference
Aspect ratio	AspectRatio	$\frac{\text{major axis}}{\text{minor axis}}$	Hunt 1993
Circularity	Circularity	$\frac{2 \sqrt{\pi * \text{area}}}{\text{perimeter}}$	Hunt, 1993
Depth index	DepthIndex	$\frac{\text{weight}}{\text{area}}$	
Inverse depth index	InvDepthIndex	$\frac{\text{area}}{\text{weight}}$	
Robustness index	RobustIndex	$\frac{\text{weight}}{\text{major axis}}$	Harvey, 1989
Inverse robustness index	InvRobustIndex	$\frac{\text{major axis}}{\text{weight}}$	
Perimeter-to-length ratio	Perim2Len	$\frac{\text{perimeter}}{\text{major axis}}$	
Projected-area-to-perimeter ratio	PA2Perim	$\frac{\text{area}}{\text{perimeter}}$	Hunt, 1993; Jones, 2016
Perimeter-to-projected-area ratio	Perim2PA	$\frac{\text{perimeter}}{\text{area}}$	Hunt 1993

calculated from a mixed effects model with species as fixed effects and captive feeding subjects as random intercepts, fitted to the complete data set (i.e. data from both studies for all teleost species). For cross-validation, all captive feeding data for one species at a time were held out, and the model was refitted to the data for the remaining eleven species. Otolith recovery rates were predicted for the meals of the omitted species from this new model, assuming an average captive feeding subject (i.e. random effect of zero). Prediction error  $e_s$  was then calculated as the difference between the observed recovery rate  $p_s$  for the omitted species  $s$  and the aggregate of predicted recovery rates  $p_{ij}$  for the corresponding omitted meal data, weighted by number of trials in each meal  $n_{ij}$ :

$$e_s = p_s - \frac{\sum \hat{p}_{ij} n_{ij}}{\sum n_{ij}}$$

This procedure was repeated for each of the 12 species. Root mean square error (RMSE), mean absolute error (MAE), and bias were calculated from the resulting species-level errors. The model with the lowest RMSE was chosen.

The final otolith recovery model was refitted using unscaled otolith morphometric covariates to estimate the correct intercept for application to estimating recovery rates for wild diet data.

We evaluated the final model by comparing species-level cross-validation statistics to prediction error from the corresponding null models with captive feeding subjects as random effects (i.e. models fitted to the corresponding leave-one-species-out data sets).

All analytical work was conducted in R v. 3.6.2 (R Core Team, 2019). We used the *tidyverse* suite of packages and the *magrittr* and *readxl* packages for data importation, wrangling, and editing (Bache and Wickham, 2014; Wickham and Bryan, 2019; Wickham et al., 2019), the *lme4* and *optimx* packages to fit generalized linear mixed models (Nash and Varadhan, 2011; Nash, 2014; Bates et al., 2015), and *dredge()* in the *MuMIn* package to obtain all possible models within the specified limitations (Barton, 2020).

## Results

Parameter estimates for the squid beak recovery model and the selected otolith recovery model are provided in Table 3. MAE and RMSE results for all models considered are provided in Supplementary Material Section 4. Candidate models for which at least one

**Table 3.** Coefficients and standard errors for cauchit-link binomial GLMMs of otolith and beak recovery rates. Parameters are intercept  $\alpha$ , AspectRatio coefficient  $\beta_{AR}$ , InvRobustIndex coefficient  $\beta_{IRI}$ , and standard deviation of random effects  $\sigma_a$ , in cauchit-link space. See Table 2 for description of otolith morphometric variables and units of measurement.

Prey type	Parameter	Estimate	Standard Error
Teleostei	$\alpha$	− 0.64	0.31
	$\beta_{AR}$	0.75	0.14
	$\beta_{IRI}$	− 1.14	0.08
	$\sigma_a$	0.37	–
Cephalopoda	$\alpha$	1.96	0.56
	$\sigma_a$	1.40	–

cross-validation fold continued to return a convergence warning after trying three different optimisation approaches were dropped. For the squid model, the parameter estimates translate to a constant estimated recovery rate of 0.85 (bootstrapped 95% profile CI 0.74–0.90; bootstrapped S.E. 0.043). The standard deviation of mean recovery rates for individual sea lions (back-transformed sum of intercept and random effects) is 0.13. For the teleost model, the predictors that explained the greatest amount of variation among recovery rates for different species were AspectRatio (major axis divided by minor axis) and InvRobustIndex (major axis divided by weight) (Table 3). An example of a meal with a medium expected recovery rate is Pacific mackerel (*Scomber japonicus*) with a mean standard length of 254 mm, whose otoliths have a mean expected recovery rate of 0.46 (bootstrapped 95% profile CI 0.39–0.52; bootstrapped S.E. 0.035). The uncertainty in the intercept is similar in magnitude to the random effects of individual captive feeding subjects.

Compared with estimating otolith recovery rates from the mean (i.e. from a null model with random effects for captive feeding subjects), predicted species-wise recovery rates from cross-validation of the final model have approximately half the root mean square error, half the mean absolute error, and lower absolute bias (Table 4). When limited to otolith recovery rates for common prey species of California sea lions in the Channel Islands, which also had much larger numbers of trials than most other experimental species

**Table 4.** Overall cross-validation results for selected model of otolith recovery rate: species-wise overall root mean square error (RMSE<sub>x</sub> and RMSE<sub>xv</sub>), mean absolute error (MAE<sub>x</sub> and MAE<sub>xv</sub>), and bias (bias<sub>x</sub> and bias<sub>xv</sub>) from mean prediction (i.e. intercept-only; “x”) and leave-one-species-out cross-validation prediction from the final model (“xv”). Cross-validation statistics are provided for all teleost species in the data set and for common teleost prey species of California sea lions (see Table 1).

Cross-validation scope	RMSE <sub>x</sub>	RMSE <sub>xv</sub>	MAE <sub>x</sub>	MAE <sub>xv</sub>	bias <sub>x</sub>	bias <sub>xv</sub>
All teleost species	0.264	0.138	0.223	0.095	0.046	−0.009
Common teleost prey	0.221	0.033	0.193	0.025	0.073	−0.019

(Table 1), the model explained approximately 85% of the variance among species (RMSE of cross-validation prediction divided by RMSE of mean prediction; Table 4). Predicted versus observed recovery rates by species from species-wise cross-validation approximate a one-to-one relationship (Figure 2).

Residuals at the level of individual meals show consistently good model behaviour across all species (Supplementary Material Section 3). All residuals combined (Figure 3) show no consistent trend or heteroscedasticity with fitted values, and there is a clear positive relationship between observed and fitted values. Residual plots for the selected model against all candidate covariates (not shown), selected or not, showed no clear trend.

## Discussion

The otolith recovery rate model we developed for California sea lion scats enables us to predict recovery rates and thus numerical correction factors for novel species not included in captive feeding studies, as well as for different prey sizes than were fed experimentally. The cephalopod beak recovery model was based only on feeding trials of market squid (*Doryteuthis opalescens*), but the estimated recovery rate of 0.85 is similar to recovery rates from feeding trials of other squid and octopus species in both otariids and phocids (Tollitt et al., 1997; Orr and Harvey, 2001). The recovery rates that our models predict can be used to at least partially account for relative differences among prey recovery rates and thus reduce biases in estimating relative prey composition from enumerated hard parts in sea lion scats.

The cross-validation results indicate that the otolith model provides robust prediction of recovery rates for a wide variety of teleost species, a substantial improvement over mean prediction (i.e. from an intercept-only model). The strongest results were for common teleost prey species, which also had large sample sizes in the captive feeding experiments (Tables 1 and 4). Even though a diversity of otolith morphometric covariates were included in this analysis, the variables selected, inverse robustness index (otolith length divided by weight) and aspect ratio (otolith length divided by otolith width), reinforce previous results relating otolith length, width, and robustness to recovery rate in scats from captive feeding trials (Tollitt et al., 1997; Sweeney, 2008).

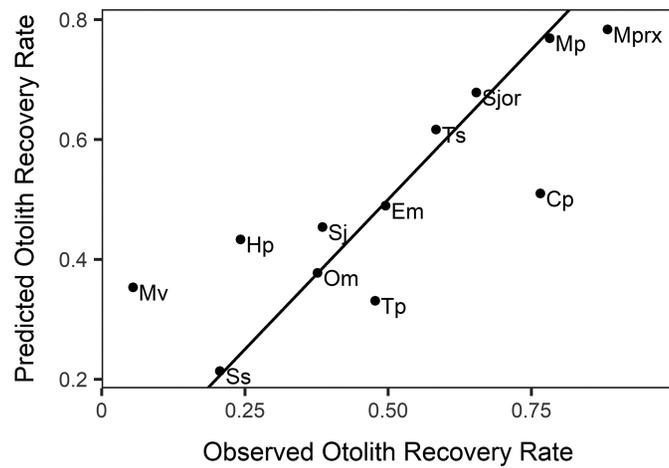
## Sources of uncertainty and bias

The standard errors of the otolith model coefficients are underestimates of true uncertainty, because error in the prediction of otolith morphometrics from fish length was not propagated. Error propagation in our cross-validation approach to model selection would have been computationally prohibitive, but the final model could be bootstrapped with propagated errors if the necessary information on uncertainty were available for the otolith morphometric re-

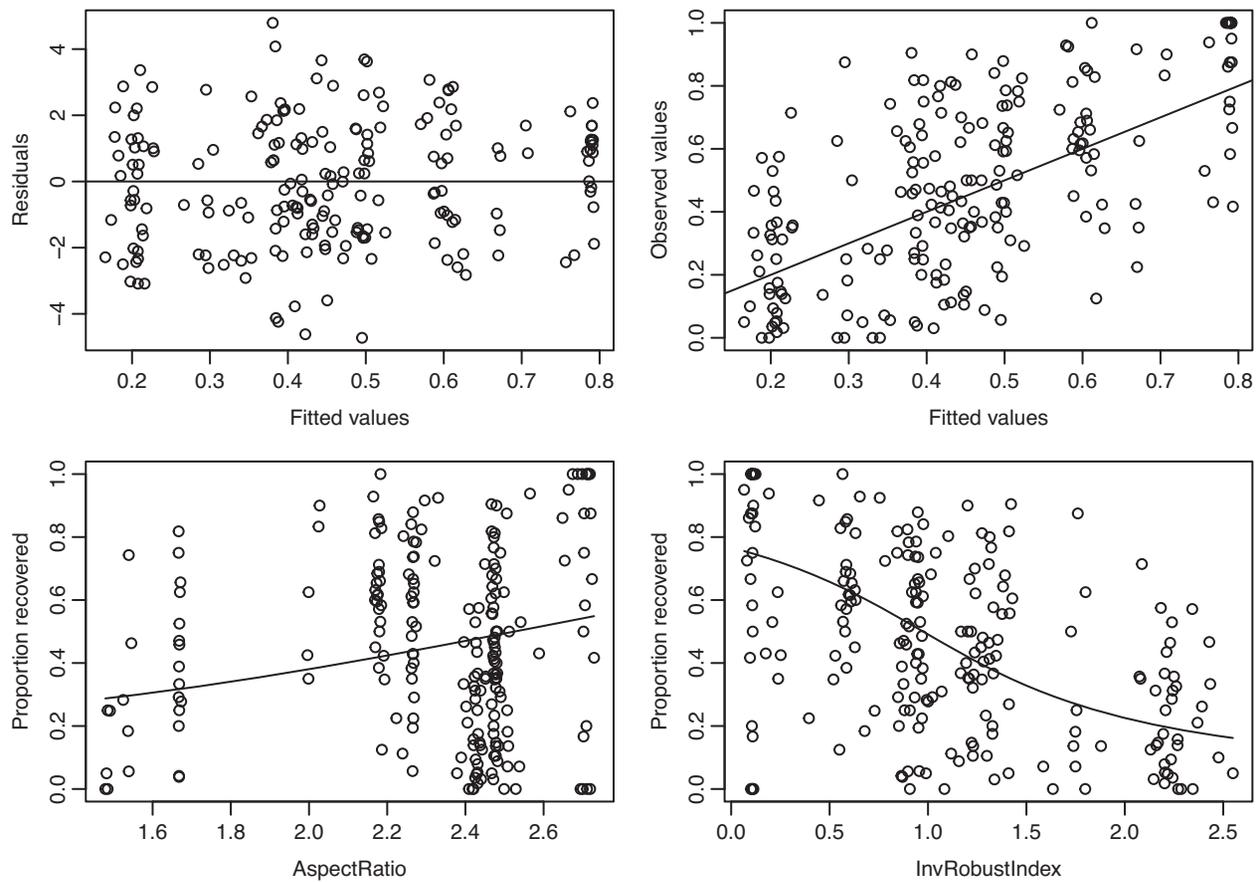
gressions of all species. That said, uncertainty and bias due to field sampling error for California sea lions are likely larger in magnitude than the unaccounted-for uncertainty in model covariates and thus coefficients, at least in cases where foraging ranges extend more than a day’s travel from the rookery or haulout (see further discussion below). Application of the model to parameter space that was not included in its estimation is also likely a greater source of uncertainty and potential bias in diet reconstruction than unpropagated error (see Figure 4 and related discussion). Nonetheless, the lower panel of Figure 4 does provide a sense of the true variation in otolith morphometrics within species for similar-sized fish as well as across sizes.

The captive feeding study data on which the models are based are subject to a range of potential biases. The majority of the captive feeding subjects were animals that were being rehabilitated. The feeding schedules, activity levels, and energetic requirements of captive animals may not be representative of the digestive process in wild sea lions that complete multi-day foraging trips. Nor were additional known complicating factors, such as mixed versus single species meals and large versus small meals accounted for here (Marcus et al., 1998; Phillips and Harvey, 2009). On a positive note, captive feeding subjects included subadults and adults of both sexes (Sweeney and Harvey, 2011), yet variance of otolith recovery rates among prey species far exceeded the variance of individual captive feeding subject random effects (Figure 1, Table 3), suggesting that the model is robust to sex and age class differences between captive feeding subjects and wild populations.

Recovery rates predicted from the otolith model can only account for differences in survival rates of otoliths that pass through the digestive tract. Both otariids and phocids have been observed to regurgitate non-negligible fractions of some prey species and sizes (e.g. Everitt et al., 1981; Goodman-Lowe, 1998). Other cases were observed where heads, and thus otoliths, of large fish were not ingested in the first place (Sweeney and Harvey, 2011). Relative importance of spews as a source of bias likely varies with prey field in different geographic locations. For California sea lions, large size classes of hake and salmonids that were sometimes regurgitated in Sweeney and Harvey (2011) are more important in the diet of the subadult and adult males that forage in waters off the Pacific Northwest between breeding seasons than in the diet of animals based at the southern Channel Islands rookeries (e.g. Everitt et al., 1981; unpublished data). Still, even in the southern Channel Islands, there is likely at least some bias towards underestimating the consumption of larger teleost prey and of certain teleost prey taxa from scat samples. Similar underrepresentation of larger beaks from cephalopod prey, such as from adult octopuses, might also be expected, but field-collected spews from Channel Islands rookeries have a smaller proportion of large cephalopod beaks (defined as upper or lower rostrum or hood length greater than 5 mm) than scat samples do (unpublished data).



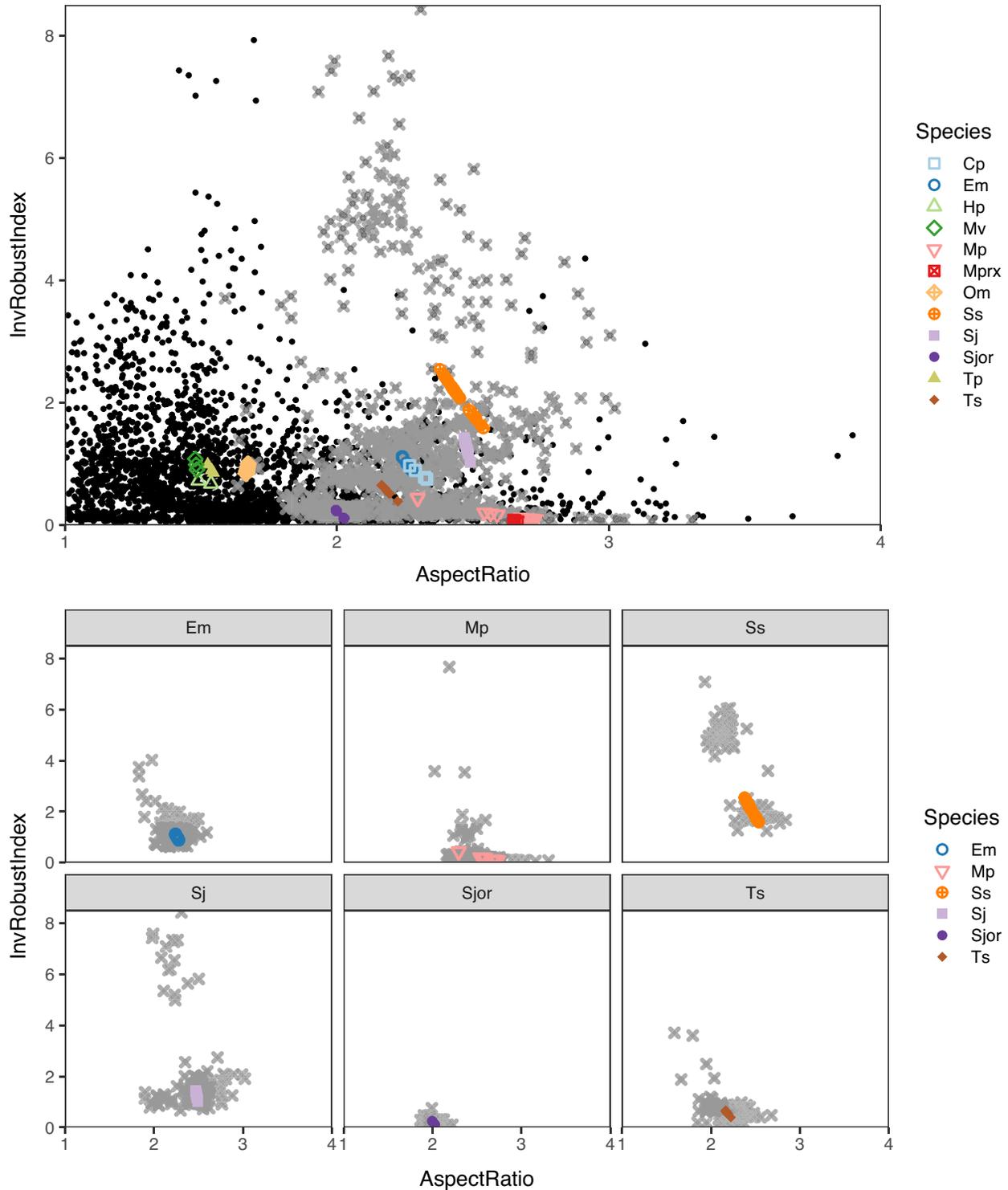
**Figure 2.** Predicted otolith recovery rates from species-wise cross-validation versus observed otolith recovery rates, overlaid on 1:1 line. Predicted recovery rates were aggregated by species and weighted by meal size. Observed recovery rates were calculated as species-wise fixed effects in an intercept-only model with captive feeding subjects as random effects. Scientific name abbreviations as for Figure 1.



**Figure 3.** Pearson scaled residuals (top left) and observed values (top right) plotted against fitted values, and observed (points) and fitted (lines) values plotted against covariates (lower panel) for selected model of otolith recovery rate. Top right panel includes 1:1 line for reference. Residuals are at the level of the response variable, i.e. the meal level.

Field-collected samples are subject to additional potential biases that may not be accounted for through captive feeding studies or hard part recovery models. Temporal and spatial patchiness of prey

and varying distance of different prey species and sizes from island rookeries or other terrestrial haulouts may lead to scat samples not reflecting prey composition of pinniped diet at the indi-



**Figure 4.** Values of InvRobustIndex and AspectRatio for teleost prey from captive feeding studies included in this analysis (multicolour points), and for all otoliths in a data set that was collected to provide a near-exhaustive reference for otolith morphometrics of prey of California sea lions at Channel Islands rookeries in Southern California (black points; Lowry *et al.*, 2020a). Common teleost prey species, whether included in captive feeding data (see Table 1) or not (blacksmith, saury, and smoothtongue; see Table 1 for citations), are overplotted in gray. Upper panel shows all species; lower panel breaks out individual common prey species included in the captive feeding data. For the lower panel, prey size decreases towards the top left of the parameter space (lower AspectRatio, higher InvRobustIndex). Scientific name abbreviations as for Figure 1.

vidual or population level. This problem may be partially mitigated by identifying fish prey via skeletal remains as well as otoliths, as bones remain in the digestive tract longer (Sharon Melin, Alaska Fisheries Science Center, pers. comm.; Sweeney and Harvey, 2011). Some skeletal remains can be enumerated; others may only be used to adjust taxonomic composition and frequency of occurrence metrics. Lack or relative fragility of digestion-resistant prey hard parts may also lead to prey rarely or never being represented in scat samples, regardless of prey distance from the point of scat sampling. The latter issue may be addressed by complementing identification and enumeration of prey hard parts with DNA-based prey identification (e.g. Tollitt *et al.*, 2009; Bowen and Iverson, 2013), which may further inform taxonomic composition and frequency of occurrence metrics. Comparing diet composition based on taxonomic composition and frequency of occurrence metrics from enumerated hard parts versus bones or DNA provides a measure of the potential bias in numeric diet composition data from hard parts.

### Application of numeric correction factors

The otolith measurements used to inform otolith morphometrics and fit recovery models were estimated from the measured dimensions of whole prey fed in the experimental captive feeding studies. In real world applications, of course, original whole prey length is not known. Hard parts that survive are still subject to partial erosion, so their measurements first require length (or width) correction (e.g. Tollitt *et al.*, 1997; Phillips and Harvey, 2009; Sweeney and Harvey, 2011; Wilson *et al.*, 2017). Once original hard part dimensions have been estimated through length or width correction, numerical correction factors (the inverse of recovery rates) can be predicted from the model using estimated covariate values from otolith morphometric regressions. Taxonomically extensive otolith morphometric regressions for California Current prey species support estimation of otolith morphometrics and thus application of the recovery rate model to a wide diversity of teleost species and sizes (Harvey *et al.*, 2000; Sinclair *et al.*, 2015; Lowry *et al.*, 2020a, b). For cephalopod beaks, only a single numerical correction factor is available from this study. For teleosts, individual-level numerical correction factors may be calculated for each otolith measured.

A mean correction factor for a given species in a sample can then be calculated as the arithmetic mean of individual-level correction factors, assuming a representative sample of otolith lengths was measured. Individual- and sample-level numerical correction factors can be applied to reconstruct total number and length distributions of prey consumed per sample, which can in turn be averaged across samples to represent a collection of samples in reconstructing relative biomass.

The recovery models published here provide a basis for numerical correction of positive samples, but they do not correct for reduced frequency of occurrence of prey in a collection of multiple scats, because any multiple of a zero count remains zero. Therefore, they do not mitigate biases in frequency of occurrence or split sample frequency of occurrence metrics (Olesiuk *et al.*, 1990) for diet composition resulting from recovery rate variation. Frequency-based metrics are also influenced by variation in dispersion indices of prey numbers consumed and gut residence times. Where geographic bias is not expected, as in pinniped species that forage primarily within a day's distance of their haulouts, recovery rate models such as those presented here should help reconcile frequency-based metrics with diet composition based on enumerated hard parts (e.g. Laake *et al.*, 2002), with the latter preferred as it is not

subject to bias from small-scale prey patchiness and gut residence times. For pinnipeds ranging far from their haulouts during foraging trips, geographic bias in prey availability necessitates consideration of both relative biomass reconstruction and frequency-based metrics, ideally in light of complementary information on prey frequency as discussed earlier, to avoid overconfidence in conclusions about diet composition.

### Coverage of otolith morphometric parameter space

An extensive data set on otolith morphometrics, covering most California sea lion prey species and sizes in the Channel Islands, was amassed to estimate the otolith morphometric regressions that were cited above and used in this study for prediction of other otolith morphometrics from otolith length (Lowry *et al.*, 2020a). The prey fed in the captive feeding studies included in this analysis occupy much of the sample space of the otolith morphometric data set (Figure 4) and most common prey species of California sea lions at the Channel Islands and in Central California, which include northern anchovy (*Engraulis mordax*), Pacific hake, Pacific sardine (*Sardinops sagax*), Pacific mackerel, shortbelly rockfish (*Sebastes jordanii*), jack mackerel (*Trachurus symmetricus*), blacksmith (*Chromis punctipinnis*), Pacific saury (*Cololabis saira*), and California smoothtongue (*Leuroglossus stilbius*) (Lowry *et al.*, 1990; Lowry *et al.*, 1991; Melin *et al.*, 2008; Weise and Harvey, 2008; Melin *et al.*, 2010; Melin *et al.*, 2012; Robinson *et al.*, 2018). However, the smallest size classes of sardine, anchovy, shortbelly rockfish, and hake often are common prey items but are not represented in the captive feeding studies. Of those, small sardine and anchovy occupy the sample space of low AspectRatio and high InvRobustIndex that represents the largest gap in the data included in the model (Figure 4). Additional captive feeding studies with the smallest size classes of sardine, anchovy, shortbelly rockfish, and hake would help ensure that the model performs well for these prey items, which are also important species for fisheries management and thus for many applications of sea lion diet data. Numerical correction factors derived from this model for these size classes of these species should be used with commensurate appreciation for the associated uncertainty and potential bias. Lastly, data on recovery rates for juvenile and adult Eastern Pacific red octopus (*Octopus rubescens*) would address another important prey species and help understand recovery rates for large cephalopod beaks.

### Conclusions

The otolith recovery model presented here represents a novel approach to dealing with the problem of estimating numeric correction factors for a prey base too diverse to be addressed through captive feeding studies alone. Similar models for other pinniped predators might also help interpolate correction factors for intermediate prey sizes not included in captive feeding studies. Such recovery rate models have the potential to add considerably to the tremendous value of existing time series of pinniped diet, in this case of California sea lion (Lowry *et al.*, 1990; DeLong *et al.*, 1991; Lowry *et al.*, 1991; Weise and Harvey, 2008; Melin *et al.*, 2012; Robinson *et al.*, 2018), enabling their application to a wide variety of questions that require quantitative reconstruction of prey consumed, such as stock assessments, prey selectivity studies, and ecosystem modelling to support ecosystem-based management.

## Supplementary Data

Supplementary material is available at the ICESJMS online version of the manuscript.

## Animal Ethics

Any applicable permits and other animal ethics information pertinent to the original captive feeding studies were reported in the respective original publications.

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## Author Contributions

MSL conceived of the reanalysis study. JTH conceived of the captive feeding studies. JMS, AJO, and JTH designed and executed captive feeding studies. MSL and KAC edited the data for reanalysis. KAC designed and implemented the data analysis, drafted the manuscript text, and revised the manuscript. MSL, JMS, AJO, and JTH assisted in reviewing and editing the manuscript. All authors approved the final submission, and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

## Data Availability

Data for this study have either already been published (Lowry *et al.*, 2020, a, b; Orr and Harvey, 2001) or are made available here in Supplementary Material.

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