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AN APPROACH FOR LONG-TERM MONITORING OF RECOVERING POPULATIONS OF NEARCTIC RIVER OTTERS (*LONTRA CANADENSIS*) IN THE SAN FRANCISCO BAY AREA, CALIFORNIA

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ABSTRACT—We present results from the first 5 y of a long-term monitoring study of recovering populations of the North American River Otter, *Lontra canadensis,* in Marin County, California. Historically present, but extirpated due to trapping and habitat loss, this apex aquatic predator is recolonizing coastal, lentic, and riverine habitat areas around San Francisco Bay. Using camera traps and a community science effort, we estimated an annual minimum population size at each of 14 focal study sites (FSS). Based on those estimates over 5 y, we developed a new Bayesian-statistics model to estimate population parameters for each FSS, including initial population abundance, annual rate of change in abundance, and probability that abundance is in decline. Our results show significantly different changes in abundance among the various FSS, with annual rates ranging from a high of 0.86 to a low of –0.44. Using a Random Forest framework, we then investigated the relative value of select spatial, environmental, and anthropogenic variables as predictors for each FSS population parameter. In our analysis spatial factors, and specifically latitude, were the best predictor of differences in FSS population parameters. Higher latitudes correlated with higher initial population abundance, greater annual increase in abundance, and lower probability that abundance is in decline. Our results provide new information about the rate and pattern of natural River Otter recolonization of areas from which they have been absent for decades. The results also serve as a demonstration of an approach to long-term monitoring, with the goal of increased understanding of the ecological function of River Otters in the San Francisco Bay Area.

Key words: California, long-term monitoring, *Lontra canadensis,* Marin County, North American River Otter, recovering population, San Francisco Bay Area

Research on North American River Otters (*Lontra canadensis*) has tended to focus on reintroduced, rather than remnant or recovering populations, and coastal areas have received comparatively little attention (Serfass and others 2018). River Otters were historically present in Northern California (Grinnell and others 1937), but were extirpated from substantial parts of their range largely as a result of fur trapping (Schempf and White 1977). In addition to trapping, habitat loss and poor water quality have been established as contributing factors for River Otter extirpation (Melquist and others 2003; Larivière and Walton 1998). The gradual recovery and range expansion of the species in the San Francisco Bay area (SFBA) has only recently been documented (Bouley and others 2015), creating a valuable opportunity for long-term study of the population dynamics of that recovery and expansion (Serfass and others 2018).

Grinnell and others (1937) described the coastal California distribution of River Otters as "...north from San Francisco Bay," and a contemporary occurrence "...from the Oregon line south to Marin County, or nearly that far." He did not document River Otters in Marin County, as they were likely extirpated prior to the time of his surveys. Trapping records from 1938 to 1961 show no otters were taken in Marin County or in Napa County immediately to the northeast (Kirk 1975). In Sonoma County north of Marin, River Otters persisted in a limited area, and a population in Contra Costa County across San Francisco Bay to the east was likewise never extirpated (Zeiner and others 1988; CWHR 1995). After California banned trapping in 1961, River Otter populations began to recover in some areas of Northern California, particularly the far northern central and coastal areas, and the Sacramento River delta (Schempf and White 1977; Kirk 1975). Kirk noted "[r]ecent public concern over the status of this attractive mammal...," perhaps a sign of increased awareness as a consequence of an increase in abundance. In Marin County, the reappearance of River Otters was first noted in isolated reports during the late 1980s (Bouley and others 2015).

Grinnell and others also noted in 1937 that "[f]resh-water habitats of a sort to provide proper food and shelter for otters are becoming more and more restricted." From the mid-1800s in the San Francisco Bay area, habitat destruction and pollution were widespread. For example, as documented by the San Francisco Bay Conservation and Development Commission (BCDC), from 1849 to 2001, tidal marsh habitat in San Francisco Bay declined from 190,000 acres to 40,000 acres (76,890–16,187 ha; BCDC 2002); in 1964, pathogen levels were 3 to 10 times the safe level for human contact (BCDC 1987). During 1968, the California State Water Board adopted its 1st plan to manage water quality in the SFBA. That original plan was superseded by the Basin Plan for the Region in 1975, which in revised form remains in effect today (CA Water Boards 2017). Complementary to the Basin Plan, the Comprehensive Conservation and Management Plan (CCMP) was first developed in 1993 by the San Francisco Estuary Partnership (SFEP). The CCMP contains a compendium of management actions aimed at improving water quality, restoring habitat, and recovering species (SFEP Blueprint 2016). Over time these efforts to improve water and habitat quality have had some positive effect. According to SFEP's 2015 State of the Estuary Report, the Bay is generally safe for direct human contact, and tidal marsh has increased by $>$10,000 acres (4047 ha; SFEP 2015).

As apex predators using a variety of terrestrial and aquatic habitats, River Otters are sentinel indicators of watershed function and health (Larivière and Walton 1998). They prey upon a wide variety of native and non-native species in freshwater and marine environments (Penland and Black 2009; Garwood and others 2013). They also are susceptible to potential pathogens such as *Cryptosporidium* and *Giardia* spp. (Gaydos and others 2007), and *Vibrio* spp. (Bouley and others 2015), and bioaccumulate environmental contaminants such as mercury, metals, organochlorines, and hydrocarbons (Francis and Bennett 1994; Halbrook and others 1996; Bowyer and others 2003). Furthermore, understanding River Otter ecology and population status is an important element of ecosystem management (Bowen 1997; Kruuk 2006; Ben-David and Golden 2009). River Otters transport aquatic nutrients to land (Ben-David and others 2004); transmit trophic effects (Crait and Ben-David 2007); and affect the composition and abundance of prey species via trophic subsidy and removal (Garwood and others 2013).

Long-term monitoring of River Otter populations can provide information on the ecological health of wetlands, water quality, pollutant levels, and human impacts on habitat (Melquist and others 2003), all of which remain critical issues in the San Francisco Bay area. The design and implementation of estuarine and riverine restoration projects also may benefit from understanding River Otter population trends. In Marin County, in north-central California, for example, the National Park Service has recently undertaken 3 large restoration efforts: at Rodeo Lagoon; Redwood Creek and Muir Beach; and Giacomini Wetlands. Gauging the progress of those efforts may be assisted by understanding the interactive effects of River Otter populations and the restoration-management actions, and their mutual outcomes. As an example, interactive effects may include predation on special-status species such as the federally listed Coho Salmon (*Oncorhynchus kisutch*). Hatchery-reared fish released to supplement Coho Salmon populations, for instance, provide prey for River Otters, and the timing and location of releases might be adjusted according to their presence.

Lastly, study of changes in population abundance of River Otters as they recolonize areas from which they were extirpated may help elucidate the spatial, environmental, and anthropogenic factors that influence their habitat choices and ecological success (Barbosa and others 2001; Weinberger and others 2016). Although sensitive to habitat disturbance, River Otters also are highly adaptable to human presence on the landscape (Weinberger and others 2016). Information about the relative influence of spatial, environmental, and human factors on presence and population trends may increase understanding of the potential for range expansion, and the likely areas for expansion.

Beginning in 2012, using camera traps and "Otter Spotter," (a community science initiative to collect River Otter sightings), River Otter Ecology Project (ROEP) launched the 1st study to document current recovering populations of River Otters in the 9 counties (Alameda, Contra Costa, Marin, Napa, San Francisco, San Mateo, Santa Clara, Solano, Sonoma) of the SFBA (Bouley and others 2015). At the same time, ROEP commenced a long-term monitoring project to study the status and ecology of River Otter populations at 14 focal study sites in Marin County, 1 of the 9 aforementioned counties. This long-term monitoring project is the 1st in north-central California to quantify changes in River Otter population abundance using a consistent camera-trapping and community-based science method.

The objective of this study was to develop a method to quantify changes in River Otter population abundance at 14 focal study sites in north-central California, Marin County, and to investigate differences in FSS abundance changes based on spatial, environmental and anthropogenic influences. Building on the "minimum population" method described by Bouley and others (2015), we introduce in this paper a Bayesian statistical method for estimating changes in population abundance from camera trap and community science data. In addition, we apply a Random Forest Framework to investigate the relative predictive value of select spatial, environmental, and anthropogenic factors on population abundance and its change over time. Results reported here serve as a baseline for assessing future changes in population abundance, and as a demonstration of a useful approach for long-term monitoring in the SFBA, with the goal of increased understanding of the ecological function of River Otters as their populations recover.

METHODS

Study Area

The study area is located along the north central coast of California, in Marin County (Fig. 1). Marin County has a relatively low human population density of 485 people per square mile (US Census Data 2010); only 11% of the county's area has been developed, whereas 84% is parkland, tidelands, open space, or agricultural lands (Marin Countywide Plan 2007). The coastal area is part of the Greater Farallones National Marine Sanctuary, and 3 of the largest wetland areas (such as Bolinas Lagoon, Tomales Bay, and San Francisco Bay (SFB) are designated under the UNESCO Ramsar Convention as Wetlands of International Importance. The 4th-largest wetland area in Marin County, Drakes Estero, is a congressionally designated marine wilderness under the Wilderness Act. The region also includes designated critical habitat for Central California Coast Coho Salmon under the Endangered Species Act (NOAA 2012).

In 2012, ROEP identified a study area consisting of approximately 225 linear km of coastline, stream, and reservoir spanning an area from San Francisco Bay north to the mouth of Tomales Bay, including Lagunitas Creek and its tributaries and reservoirs, and parts of the shoreline of San Pablo Bay (Bouley and others 2015).

Focal Study Sites

Beginning in February 2012, Bouley and others (2015) surveyed for active River Otter latrines, characterized by fresh scat deposits and identifiable paths leading to or from the scat, which indicated recent presence of otters (Bowyer and others 1995, 2003), and identified 35 latrines at 23 sites. During 2012 and 2013, Bouley and others (2015) selected 11 focal study sites (FSS). During 2014, we expanded the number sites, adding 3 additional sites for a total of 14 sites. Using the same methods as Bouley and others (2015), we selected geographically separated sites with active latrines, and acquired landowner permission for access, to encompass multiple landowners and a variety of aquatic habitats (Fig. 1). Distances between any FSS and the next-closest site ranged from 3 km to 11 km, with a median of 7 km, consistent with earlier studies of River Otters in coastal California (Brzeski and others 2013; Bouley and others

FIGURE 1. Locations and assigned regions of focal study sites in Marin County, California.

2015). Of the 14 FFS, 9 are on National Parks land, 2 are on undeveloped, protected watershed land owned and administered by Marin Municipal Water District, 1 is on private land adjacent to a ferry terminal and retail-commercial complex, 1 is at reclamation ponds operated by a municipal sewer district, and 1 on private property in the vicinity of Bolinas Lagoon.

Camera Trapping

At the FSS, using the methods from Bouley and others (2015), we deployed 1 to 3 motion-activated trail cameras (Bushnell HD Trophy Cams, Bushnell Products, Overland Park, KS) at or adjacent to FSS latrine sites in order to estimate population size. For this study, the cameras were active 24 h each day from June through November, and were set to record videos 30–60 s long. Trained volunteers maintained the cameras and retrieved data every 1 to 3 wk. Data from each camera consisted of location, videos detecting otters, date and time of otter detections, number of adults and pups (based on observable size difference) per detection, and behavior (such as scent-marking, interactions with conspecifics and other species, and vocalizations).

"*Otter Spotter*" *Community Science Program*

Concurrent with the deployment of the camera array in 2012, we launched a community science program called "Otter Spotter" to solicit from the public structured data on River Otter sightings in the 9 counties of the SFBA. Using outreach to interest groups and the general public, and solicitations of sightings in various media, and we encouraged use of a web portal to submit sightings of River Otters (https://riverotterecology.org/otter-spotter-community-based-science). Data were structured to include information on date and time of sighting, location, total number of otters observed, and other relevant data, including photographs or videos. To assist observers in making accurate reports, the web portal included a "How To Identify A River Otter" guide, which included descriptive information about River Otter size and movement on land and in water. The guide also included photos of species commonly mistaken for River Otters, including Beaver (*Castor canadensis),* Muskrat (*Ondatra zibethicus),* and Harbor Seal (*Phoca vitulina*). From 2012 through 2016, we received 1938 submissions.

We validated each submitted sighting, determining whether it was credible based on the weight of evidence contained in the report, especially photographs. In the absence of photographs, which were included in 30% of the reports, we substantiated the sightings based on the self-reported experience level of the observer, whether the observer was sure or unsure of the sighting, the location, habitat type (such as bay, lake, pond, river, etc.), and any description of otter signs or behavior. If we required additional information to validate the sighting, we interviewed the observer by phone or email. We discarded sightings not deemed credible. Of the 1938 sightings reported, we mapped 1723 that were deemed credible, using ArcMap 10.5 (ESRI, Redlands, CA).

Estimates of Minimum Populations at Focal Study Sites

Based on the methods of Bouley and others (2015), we estimated the minimum population size at each FSS as the largest grouping of River Otters observed together at any one time at that location from June through November of each year (see also Brzeski and others 2013). From the camera data for each FSS, we extracted the maximum group size appearing on a single video during those months each year. From ArcMap, we extracted all validated "Otter Spotter" reports, corresponding to the location of the FSS, from June through November in the same year. We considered a report to correspond to the FSS if it was from the same water body or discrete section of water body as the camera site (Bouley and others 2015; Black 2009; Brzeski and others 2013). We based the minimum population estimate on camera data unless a validated Otter Spotter submission reported a larger group size, in which case we based the minimum population at that site on the validated report. We used a total of 5,698 camera trap videos and 366 "Otter Spotter" sightings to estimate the minimum population sizes at the FSSs (Table 1).

TABLE 1. Yearly aggregate number of camera videos and Otter Spotter reports used to estimate the minimum populations of River Otters at focal study sites (FSS) in Marin County, California from 2012 through 2016.

Year	Videos at FSS	Otter Spotter Reports at FSS
2012	893	37
2013	1917	57
2014	882	124
2015	1132	88
2016	874	60
Total	5698	366

Each annual minimum population estimate was based on a single observation of the largest group size for the FSS. Multiple observations of the same otter group, whether by camera trap or "Otter Spotter" report, did not confound the estimates, as the observations were not aggregated. This method results in minimum population estimates that are directly comparable across sites and across years, which is the basis for determining changes in population abundance at each FSS over time as well as a comparison of those changes among the FSS.

Statistical Analysis

Statistical analysis consisted of 2 parts: an analysis of FSS population change using a Bayesian mixed effects linear model, followed by a Random Forest analysis of factors influencing FSS population change model parameters. All parts of the statistical analyses were conducted in R, and all regression-based models

TABLE 2. Focal study site (FSS) population parameters and predictor variables used in the Random Forest analysis of influences on population trends of River Otters in Marin County, California from 2012 through 2016.

Variable	Type	Description	Source
Initial abundance	FSS population parameter	Minimum otter population at site in the first year	model-derived
Change in abundance	FSS population parameter	Average change in size of the site population per year	model-derived
Likelihood of decline	FSS population parameter	Likelihood that a population has a negative growth rate	model-derived
Main habitat type	categorical predictor variable	Main habitat feature at the FSS	ROEP assigned
Latitude	numeric predictor variable	Latitude of the FSS	ArcGIS
Longitude	numeric predictor variable	Longitude of the FSS	ArcGIS
Population density	numeric predictor variable	Density of the human population in the census tract containing the FSS	US Census Bureau
Log of population density	numeric predictor variable	Logarithm of the density of the human population in the census tract containing the FSS	calculated
Distance to San Francisco	numeric predictor variable	Shortest driving distance from San Francisco to the FSS	Google Maps
Primary access method	categorical predictor variable	Primary method the public can use to access the immediate area containing the FSS (e.g. car, boat, hiking trail)	ROEP assigned
Region	categorical predictor variable	Spatial grouping of the FSS (Pt Reyes, Inland, Coastal, SF Bay)	ROEP assigned
Annual visitors	numeric predictor variable	Average number of public visits per year to the immediate area containing the FSS	landowner statistics

were constructed with the ’rstan’ package (Stan Development Team 2018). Data for the population change analysis consisted of the yearly estimates of the minimum population at each FSS. For the analysis of influence factors, we defined predictor variables as spatial, environmental, and anthropogenic. To represent spatial factors, we used the latitude and longitude of each FSS as separate variables. We also divided the study area into 4 regions representing broad geographical areas: the Point Reyes Peninsula; Coastal; Inland; and SFB shore (Fig. 1). Each of the 14 FSS was assigned to 1 of the 4 regions. To explore environmental factors, each site was assigned a main habitat type of bay/estuary ($n = 5$), lagoon ($n = 4$), reservoir/lake ($n = 3$), or stream ($n = 2$), following Bouley and others (2015). To explore anthropogenic factors, we obtained statistics on annual visitor use at each site from the associated land manager. We also defined the ease of access to each site, with road access as the easiest, followed by hiking-only and boating-only as the most difficult. To represent human impacts separately from visitor use, we included the population in the US Census tract containing the site. Additionally, to represent potential visitor use as a purely spatial influence, we included the distance from San Francisco to the sites as a variable (Table 2).

Analysis of FSS Population Change

The goal of the population change analysis was to model otter population abundance along with the change in abundance over time at each FSS. We fit a Bayesian mixed effects linear model to the FSS minimum population estimate data time-series, using year (y_i) as the predictor variable and otter population abundance (P_i) as the response variable (Carpenter and others 2016; Equation 1):

$$P_i = \alpha + \alpha_{[FSS]} + y_i(\beta + \beta_{[FSS]}) \qquad (1)$$

where α represents the initial population abundance at a given FSS and β represents the change in abundance. FSS was included as a varying effect to mitigate the effects of spatial autocorrelation. This was necessary because linear models assume observations are independent. Estimates of minimum population numbers at different FSSs, however, are not independent, because FSSs that are closer together are more likely to experience similar conditions with regard to resource availability and human activity, and the possibility of exchange of individuals. We added FSS as a varying effect to the model to address this problem.

Using this model, we next estimated 3 population parameters for each FSS: initial population abundance, annual change in abundance, and likelihood that abundance is declining. The output of a Bayesian model for a given parameter is not a single value, but rather a distribution of values (Betancourt 2017). To estimate initial population abundance, we calculated the mean of α and $\alpha_{[FSS]}$ for each site and added them together. We repeated this with β and $\beta_{[FSS]}$ to estimate the change in abundance. To determine the likelihood that abundance was in decline, we used Markov Chain Monte Carlo to generate the posterior distribution of the change in abundance (Betancourt 2017). We then calculated the proportion of parameter values where $\beta + \beta_{[FSS]}$ was less than zero, since a value of $\beta + \beta_{[FSS]} = 0$ would indicate that the FSS maintained a constant population abundance over time. Thus $\beta + \beta_{[FSS]} < 0$ would imply the FSS was experiencing declining abundance.

Random Forest Analysis of Influences on FSS Population Change

The Random Forest analysis focused on investigating relationships among differences in the 3 FSS-specific population parameters (initial population abundance, annual change in abundance, and likelihood that abundance is declining), and the variables we defined as influencing those parameters (Table 2). Owing to the use of both numeric and categorical predictor variables, the large number of predictor variables relative to the number of observations, and the strong correlations among predictor variables, we used a Random Forest Analysis to identify the most useful variables for predicting differences among each of the population parameter values (Genuer and others 2010). Using the 'randomForest' R package (Liaw and Wiener 2002), 1 Random Forest model was fit for each of the 3 FSS population parameters using all available variables as predictors. Then the average decrease in the accuracy of the model was calculated to identify the most important of these variables for predicting differences between FSS population parameters.

We tested the data for spatial independence using Moran's I statistic before fitting regression models for the 3 FSS population parameters. Moran's I was calculated using the 'spdep' R package (Bivand and others 2013). When calculating Moran's I, it is necessary to specify which sites are adjacent (next to each other). Adjacency can be defined in a number of ways, depending on the situation (O'Sullivan and Unwin 2014). In order to ensure that our results were not contingent on a particular arrangement of these adjacencies, we calculated the statistic with 2 different adjacency structures (Fig. 2). For the 1st, we defined 2 sites to be adjacent if their locations were <10 km apart (10-km threshold). For the 2nd, the 3 closest sites to the focal site were considered adjacent (3-nearest-neighbors).

Based on the results of the Random Forest analysis, we next fit fixed-effects Bayesian generalized linear models for each of the FSS population parameters using the influence variable with the most value (latitude, L_i) as a predictor. We used Gaussian likelihoods for both initial population abundance (S_i, Equation 2) and change in abundance (R_i, Equation 3). Both the initial population abundance and the change in abundance are parameters from the mixed effects linear model. Consequently, they are both means and can be estimated using a Gaussian (normal) likelihood. The likelihood of decline (D_i, Equation 4) necessitated a beta distributed likelihood because it is a probability, and thus constrained between zero and 1. We then retested the residuals from those models to check for remaining spatial autocorrelation:

$$S_i = \alpha + L_i * \beta \qquad (2)$$

$$R_i = \alpha + L_i * \beta \qquad (3)$$

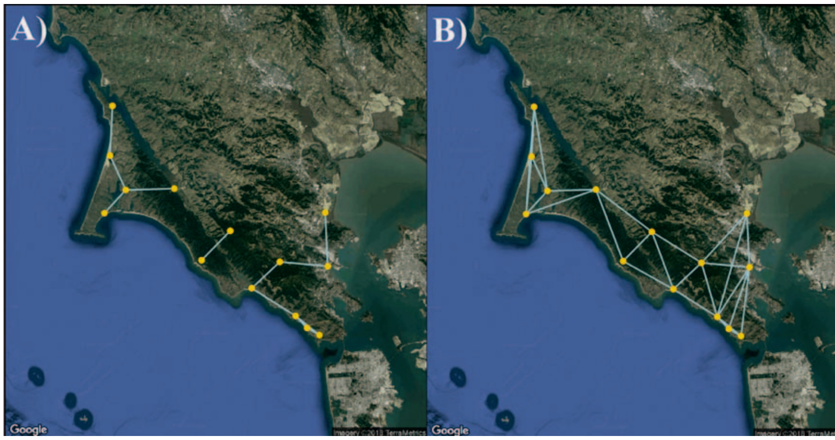

FIGURE 2. Schema of Marin County focal study site adjacencies for the 2 arrangements of site connections: (A) sites are adjacent if their centers are <10 km apart; (B) 3 closest sites are considered adjacent to the focal site.

$$\log\left(\frac{D_i}{1-D_i}\right) = \alpha + L_i{*}\beta \qquad (4)$$

To assess the quality of these models, each model was compared to the corresponding intercept-only model. We used the root mean squared error (RMSE) as the measure of model quality. The RMSEs for all models were calculated using 7-fold cross-validation (James et al. 2013).

Results

Estimates of Minimum Populations at Focal Study Sites

We estimated minimum populations for 8 sites over 5 y (2012–2016), 11 sites for 4 y (2013–2016), and all 14 sites for 3 y (Table 3). Overall, 75% ($n = 46$) of the estimates were based on camera trap data, and 25% ($n = 15$) on Otter Spotter reports. Generally, minimum population estimates for each FSS were relatively stable over the survey period, with only incremental changes, or no change, from year to year (Table 3). Increases in minimum population estimates did occur at Giacomini Wetlands, where the minimum population estimate increased from 4 in 2012 to 8 in 2013, and at Las Gallinas, where the estimate increased from 3 in 2014 to 7 in 2015. At both sites, estimates stabilized around the higher level in subsequent years.

The largest number of River Otters ($n = 9$) was observed during 2016 at each of the following FSS: Northern Tomales Bay, Giacomini Wetlands, and Middle Lagunitas. The smallest number of River Otters ($n = 1$) was observed at Muir Beach and at Tennessee Valley. At Muir Beach, the number of otters observed declined from 3 in 2013 to 1 in 2015 and 2016. In contrast, the number of River Otters observed at Tennessee Valley fluctuated from 1 to 3 to 1.

Analysis of Changes in FSS Population Abundance

Of the 14 FSS, 4 had increasing population abundance (Table 4). Three FSS had decreasing abundance and a greater than 50% likelihood that abundance was in decline, based on the approximated posterior distribution. The re-

TABLE 3. Annual minimum population estimates of River Otters from camera trap data and Otter Spotter reports for each focal study site (FSS) in Marin County, California.

FSS	2012	2013	2014	2015	2016
Abbotts Lagoon	6	6	6	6	6
Northern Tomales Bay	7	6	5	8	9
Giacomini Wetlands	4	8	7	8	9
Rodeo Lagoon	4	6	4	4	4
Muir Beach	NA	3	3	1	1
Greenbrae	3	4	4	4	4
Tennessee Valley	1	2	3	1	1
Bolinas Lagoon	3	3	3	3	2
Drakes Bay	5	4	4	4	7
Bass Lake	NA	4	5	5	4
Reservoirs	NA	4	5	6	7
Middle Lagunitas Creek	NA	NA	6	8	9
Las Gallinas	NA	NA	3	7	6
Drakes Estero	NA	NA	6	4	4

TABLE 4. Model-derived median annual change in River Otter population abundance with credible interval (95 % CRI) for each focal study site (FSS) in Marin County, California, from 2012 through 2016. Asterisks indicate results that are statistically significant.

FSS	Median Change	95% CRI
Giacomini Wetlands*	0.86	(0.33, 1.40)
Middle Lagunitas Creek*	0.83	(0.23, 1.53)
NorthernTomales Bay*	0.65	(0.16, 1.16)
Reservoirs*	0.54	(0.05, 1.17)
Las Gallinas	0.45	(–0.05, 1.16)
Drakes Bay	0.32	(–0.12, 0.80)
Abbotts Lagoon	0.27	(–0.25, 0.72)
Bass Lake	0.13	(–0.40, 0.63)
Greenbrae	0.13	(–0.33, 0.59)
Drakes Estero	0.05	(–0.64, 0.56)
Rodeo Lagoon	0.01	(–0.49, 0.44)
Bolinas Lagoon*	–0.17	(–0.66, 0.32)
Tennessee Valley*	–0.24	(–0.77, 0.29)
Muir Beach*	–0.44	(–1.08, 0.14)

TABLE 5. Values of the Moran's I statistic, a measure of spatial autocorrelation of focal study sites, and their associated pseudo p-values. The low-connectivity adjacency scheme used a 10-km distance threshold and the high-connectivity scheme used the 3 nearest-neighbors method.

Spatial Connectivity	Moran's I	p-value
Initial abundance		
high	0.296	0.029
low	0.460	0.029
Change in abundance		
high	0.051	0.218
low	0.112	0.264
Likelihood of decline		
high	0.149	0.106
low	0.384	0.069

maining 7 FSS had insufficient data to derive a result with statistical significance.

Random Forest Analysis of Factors Influencing Changes in FSS Population Parameters

In the Random Forest analysis, latitude, a spatial factor, was the best predictor for 2 of the FSS population parameters, initial population abundance and the likelihood that abundance was declining. The number of annual visitors and region were the best predictors the 3rd parameter, the change in abundance (Fig. 3). Habitat type and primary access were poor predictors for all 3 population parameters. Overall, spatial factors were the most important predictors for the FSS population parameters.

Moran's I results indicated spatial autocorrelation for both the high- and low-connectivity spatial structures (Table 5). Initial population abundance showed strong evidence of spatial autocorrelation using both adjacency schemes; however, there was little evidence that the change in abundance or likelihood of decline were spatially autocorrelated.

Using the fixed-effects Bayesian generalized linear models, latitude predicted all 3 FSS population parameters better than the corresponding intercept-only model (Table 6). Higher latitudes correlated with: (1) greater initial FSS population abundance; (2) greater positive change in FSS population abundance; and (3) lower likelihoods of the FSS population abundance being in decline. The relationships between latitude and each FSS population parameter are represented by the following linear regression models fitted using a Bayesian framework:

1) Initial FSS Population Abundance: $y = 0.71x + 4.21$
2) Change in FSS Population Abundance: $y = 0.26x + 0.24$
3) Likelihood of FSS Population Abundance Being in Decline: $= \frac{1}{1+e^{0.96(x)+0.92}}$.

The credible intervals and model accuracy, expressed as root mean squared error, for these models are found in Table 6. There was no evidence of spatial autocorrelation in the parameter regression residuals, evidence that spatial autocorrelation in the data is related to latitude itself, or to a variable that is correlated with latitude, such as region (Table 7).

DISCUSSION

Our results show that there are significant differences in the change in abundance, and the likelihood that abundance is declining, among populations of River Otters at our FSS. In our analysis, the differences are predominantly due to spatial, rather than environmental or anthropogenic, factors. The results provide new information about the rate and pattern of natural recolonization by River Otters of areas around the SFB from which they had been absent for decades.

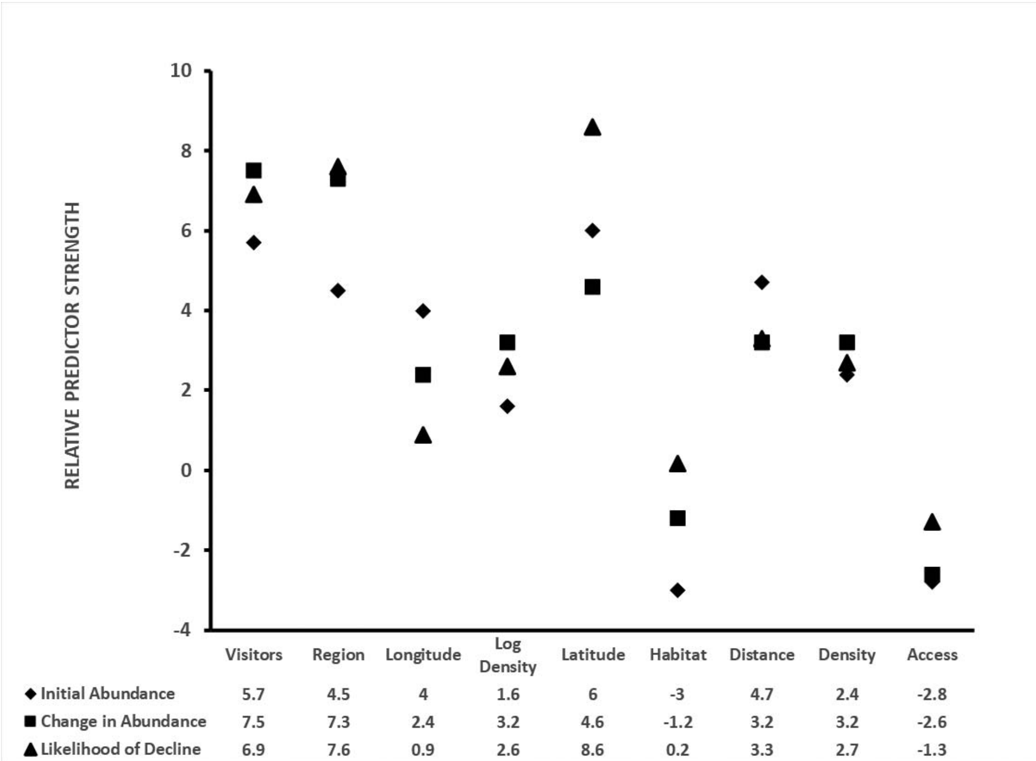

FIGURE 3. Random forest relative predictor importance for the model-derived parameters initial abundance, change in abundance, and likelihood of decline.

FSS Population Change

In other areas of the United States, efforts to monitor River Otter populations have often been connected with reintroduction programs, and have tended to be short-term efforts using radio transmitters or marking of released otters in order to estimate survival rates (Raesly 2001). In some cases, population growth models have been created in an attempt to estimate state-wide abundance of River Otters as a result of reintroduction. The Missouri Department of Conservation, for example, created a deterministic model based on parameter values for annual survival rate, pregnancy rate, average litter size, and the rate of capture by trappers

TABLE 6. Coefficient estimates and Root Mean Squared Error (RMSE) for models using Latitude to predict each of the 3 focal study site population parameters. Credible intervals for the parameter estimates were computed using the highest posterior density interval (HPDI).

		HPDI		RMSE	
Coefficient	Estimate	Lower 95%	Upper 95%	Latitude	Null
Initial abundance					
intercept	4.21	3.80	4.62	0.62	0.81
Latitude	0.71	0.28	1.13		
Change in abundance					
intercept	0.24	0.06	0.44	0.32	0.36
Latitude	0.26	0.06	0.47		
Likelihood of decline					
intercept	−0.92	−1.53	−0.31	0.23	0.41
Latitude	−0.96	−1.65	−0.25		

TABLE 7. Values of the Moran's I statistic for the Marin County focal study site population parameter regression residuals, and their associated pseudo p-values for both positive and negative autocorrelation. The low-connectivity adjacency scheme used a 10-km distance threshold and the high-connectivity scheme used the 3 nearest-neighbors method.

Spatial Connectivity	Autocorrelation	Moran's I	p-value
Initial abundance			
high	positive	–0.200	0.749
high	negative	–0.200	0.247
low	positive	–0.210	0.666
low	negative	–0.210	0.334
Change in abundance			
high	positive	–0.068	0.428
high	negative	–0.068	0.572
low	positive	–0.118	0.535
low	negative	–0.118	0.463
Likelihood of decline			
high	positive	0.617	0.000
high	negative	0.617	1.000
low	positive	0.808	0.000
low	negative	0.808	1.000

(Goedeke and Rikoon 2008). Researchers in Kentucky and Illinois developed similar models (Barding and Lacki 2014; Nielsen 2016). These models are highly sensitive to changes in the parameter values, and while some of those values were directly observed, others were estimated based on prior studies, or assumed, such as future harvest rates, resulting in widely different population estimates as the parameter values change (Goedeke and Rikoon 2008).

Long-term studies in northern California's Humboldt County (Black 2009; Black and others 2016), north of the SFBA, relied solely on opportunistic community-based science observations over larger areas, compared to the FSS in this study. In contrast, the model we developed for this study to estimate changes in abundance is based only on the minimum population estimates for each FSS that we determined from camera trap data and "Otter Spotter" reports. The model is intended to compare change over time for each FSS, and is unsuitable for estimating population abundance over a large area because the FSS minimum population estimates rely on the assumption of a closed population at the FSS. The Bayesian mixed-effects model, however, does incorporate elements of the aggregate population abundance of all the FSS into the estimates of population abundance and change for each FSS. Therefore, the estimated population change for each FSS incorporates and is representative of changes in the aggregate population abundance of all the FSS.

The estimates of minimum populations assume closed populations in the months June through November at each of the FSS (Brzeski and others 2013). Field observations and analysis of camera data show that pups were 1st observable in June to early July. Larger group sizes during June through November were consistent with results reported by Black (2009) using observational data, and Brzeski and others (2013) using fecal-sample DNA analysis. Given the geographic separation of the FSS, and based on an earlier study in Humboldt County, we assumed that individual otters travel infrequently, if at all, between FSS during the months when the minimum population estimate for each FSS was determined (Brzeski and others 2013). We assumed that any such travel was episodic rather than representing recruitment from one FSS to another, minimizing the likelihood of counting the same otter at more than one FSS. However, such recruitment may occur, violating the assumption of closed populations. A study using fecal-sample DNA analysis to identify individuals, similar to Brzeski and others (2013), could validate the assumption that there is no recruitment to the FSS in the months of June through November. Such a study may also provide information on the comparative accuracy of minimum population estimates based on camera trap and community-science observation data. Future studies that include sites in other parts of the SFBA could also be used to validate our approach.

Random Forest Analysis

Location more strongly influences differences in the change in abundance among FSS populations than anthropogenic or habitat factors. Of all factors analyzed, latitude was the strongest. Latitude is generally associated with photoperiod, weather, and severity of winter weather. Given the relatively small scale of the study area (latitude 37.832 to latitude 38.207, approximately 56 km north to south), photoperiod and weather are not likely significant. A study of Eurasian Otters (*Lutra lutra*) in southern Italy related both latitude and high levels of aquatic macrophyte cover area to otter abundance in a study area of similar size to ours (Remonti and others, 2008). That study was in an area at the southern boundary of otter range in Italy, and may reflect the rate and pattern of natural recolonization. Similarly, Barbosa and others (2001) related longitude and spatially varying environmental factors to the distribution of recovering populations of *Lutra lutra* in Spain, and speculated that otters had a biogeographical response to that spatial variation.

The 1st evidence of recovery of River Otters in Marin County were observations in Tomales Bay, in the northernmost part of the study area, and at Rodeo Lagoon, in the southernmost part, beginning in the late 1980s (Bouley and others 2015). Tomales Bay was likely recolonized from a source population in Sonoma County, immediately to the north. The source population for Rodeo Lagoon and other southern areas is more uncertain. The contemporaneous occurrence of otters at both the far northern and southern extents of Marin County at the early stage of recolonization may suggest that latitude is not a proxy variable for the spatial pattern of recolonization. Further study that includes genetic analysis of the relationship of source populations to current populations could help in understanding the importance of latitude as a predictor of changes in abundance in the study area.

Latitude may be a surrogate for some other factor or factors influencing differences in FSS initial population abundance, change in abundance, and likelihood of abundance decline that we did not include in our model. Higher densities of River Otters have been associated with coastal marshes, estuaries, lower river reaches, and coastal waters protected from ocean swell (Melquist and Dronkert 1987). Other habitat elements that have been identified as important include riparian cover (Melquist and Hornocker 1983), shoreline complexity (Dubuc and others 1990), and beaver ponds, which are associated with stable water levels and herbaceous cover (Dubuc and others 1990). Finer-scale topographic differences between northern and southern parts of our study area may exist. Moving from north to south, the coastline becomes cliff-backed, steeper and more rugged. Drainages in the areas of the Muir Beach and Tennessee Valley FSS in the south are more constrained within steeper, narrower valleys relative to the drainages in the areas of the Northern Tomales Bay and Giacomini Wetlands FSS in the northerly parts of the study area. Other fine-scale habitat elements that may be important that we did not include in the models are prey density, the size or complexity of wetlands, and shoreline aspect, which is a proxy for exposure to ocean swell and storm surge.

In coastal areas, otters generally tend to forage in shallow water close to the shore (Blundell and others 2001). A common characteristic of the FSS with increasing population abundance was the availability of relatively large expanses of shallow estuarine water at the confluence of river and bay for foraging with potentially a larger diversity and abundance of prey. The Northern Tomales Bay site combines these features with its relatively low-profile shoreline, extensive shallow-water areas, and the mouth of Walker Creek approximately 1.5 km directly to the east. Similarly, Giacomini Wetlands is situated where Lagunitas Creek flows through an expansive wetland area into the shallow southern end of Tomales Bay. The Middle Lagunitas and Reservoir sites have interconnected perennial streams and large expanses of shallow lentic foraging areas.

In contrast, the Muir Beach and Tennessee Valley sites, where population abundance is decreasing, lacked the aforementioned characteristics. Perennial streams that flow to small lagoons on narrow sandy beaches are the main habitat features at those sites. The coast at these sites lacks shallow foraging areas owing to deep nearshore waters and sheer coastal bluffs on either side of the beach, suggesting that the size of nearshore foraging area may influence population changes.

Bolinas Lagoon, the other site with a negative change in abundance and a high probability that abundance is declining, shared many characteristics with the northern sites. The lagoon was fed by numerous perennial streams, and coastal foraging areas were more expansive than at Muir Beach and Tennessee Valley. We speculate that other factors not captured in our analysis account for the negative change in abundance at this site. One is that the lagoon itself is extremely shallow, especially at low tides, when large expanses of mudflats are exposed in its shoreline areas, limiting foraging opportunities. In addition, minimum population estimates at this FSS were based entirely on Otter Spotter observations, which are opportunistic, and not on the more extensive camera trap data. The Otter Spotter counts may be inaccurate, although repeated field surveys over multiple years have not revealed a larger otter presence than this study produced. Subsequent to 2016, we discontinued this FSS because of a lack of willing landowners for suitable camera trap locations, so it may not be possible to determine what factors we missed in this location.

Anthropogenic variables also may have had a larger role in determining population changes. The variables that we included in the Random Forest model may not have adequately captured human activities. Density of visitor use as an anthropogenic measure, for example, may better represent human activities compared to simply the annual number of visitors. High visitor density may fragment habitat and create a physical barrier affecting access to proximate near-shore marine prey. This putative dynamic may be impeding River Otter foraging at several sites such as Muir Beach, Tennessee Valley, Bass Lake, and Rodeo Lagoon, where visitors tend to crowd into the relatively small available areas of sandy beach. The present study was not designed to measure the relative effects of visitor density (such as people per hectare) at different sites, but it would be a fruitful area for future research.

Conclusion

A long-term effort to monitor River Otters in the SFBA takes advantage of a rare opportunity to gain insight into naturally recovering populations through the use of a consistent method to model minimum population estimates and changes in abundance over time, as River Otters become more established. The results of this study may help in understanding the potential for further southward expansion of River Otters in the SFBA, and in identifying potential areas for that expansion. Understanding the factors influencing the population recovery serves the larger goal of supporting conservation and restoration by linking River Otters to watershed health and function.

Further study will help to determine the status of the FSS populations for which we had insufficient data, and to document whether the populations with declining abundance do in fact disappear from the FSS they presently inhabit. Given the declining abundance in the southern part of Marin County, it becomes more important to understand the role River Otters play in localized ecosystems and food webs.

Finally, results presented here may be of importance to resource managers in planning for wetland restoration projects and for shoreline adaptation to rising sea levels. Such projects may increase and enrich River Otter habitat, with consequent increases in predation on both native and pest species. At the same time, changes in waterflow or vegetative cover may alter the pattern and frequency of River Otters' use of the habitat, affecting the progress of restoration or adaptation projects. Results suggest that these factors should be considered at a localized or site-specific scale.

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