AN EXPERIMENTAL TEST OF RESPONSE BY COMMON RAVENS TO NEST EXCLOSURES

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ABSTRACT

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Common ravens (*Corvus corax*) are intelligent generalists and a principal predator affecting population recovery of several threatened and endangered species, including the threatened western snowy plover (*Charadrius nivosus nivosus*). In Humboldt County, raven predation is a primary cause of low nest survival. Nest exclosures, cages around eggs that preclude entry by predators but allow plovers access to incubate, are known to increase nest success. However, speculation exists that exclosures may attract predators. The aims of this study were to summarize corvid distribution on Clam Beach County Park and Little River State Beach, evaluate habitat features associated with corvid activity on the ground, assess how ravens respond to exclosures around artificial plover nests, and to determine if this response changed over time. I used raven tracks as an index to quantify raven activity. Using Generalized Linear Mixed Models (GLMMs), I evaluated overall raven response and response within each of five 28-day trials. There was no evidence that ravens were attracted to exclosures, nor that their responses changed over time. These results suggest that the use of exclosures may be a viable option for managing raven nest predation in Humboldt County in the future.

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INTRODUCTION

The common raven (*Corvus corax*; hereafter, raven) is an intelligent, synanthropic generalist, recognized as both a scavenger and predator (Boarman and Heinrich 1999; Boarman 2003; Wilmers et al. 2003). Studies have shown that corvids have the capacity for insight (Heinrich 1995), tool use (Weir et al. 2002), cooperative problem-solving (Fritz and Kotrschal 1999; Seed et al. 2008), planning for the future (Raby et al. 2007), and recall of past specific events (Clayton & Dickinson 1998). For example, ravens may learn how to distinguish and avoid non-lethal management techniques (Brinkman 2015), and work cooperatively to depredate the nests of endangered ground nesting birds (Coates et al. 2008).

Ravens occur in much of the northern hemisphere and can be found in most habitats including mountains, forests, ice floes, and beaches (Boarman and Heinrich 1999). Ravens have been able to adapt to human use and development of their habitat by including urban and agricultural environments in their range, in addition to exploiting anthropogenic food and water sources, and structures for nesting (Boarman and Heinrich 1999; Kristan and Boarman 2003; Marzlufff and Neatherlin 2006; Kristan and Boarman 2007; Bui et al. 2010).

The ability to exploit anthropogenic resources is thought to be the primary cause of increased raven populations in western North America (Boarman and Heinrich 1999; Demers and Robinson-Nilson 2012). Increased raven numbers due to anthropogenic subsidies have proven to be problematic for some threatened and endangered species,

including greater sage grouse (*Centrocercus urophasianus*; Coates et al. 2008), desert tortoises (*Gopherus agassizii*; Boarman 1993; 2003), and least terns (*Sternula antillarum browni*; Marschalek 2011). Additionally, predation of western snowy plover (*Charadrius nivosus nivosus*) nests by ravens has been well-documented (Burrell and Colwell 2012; Demers and Robinson-Nilson 2012).

In 1993, the United States Fish and Wildlife Service (USFWS) listed the Pacific Coast population of the western snowy plover (hereafter, plover) as threatened (USFWS 1993). In 2001, the USFWS drafted a recovery plan for this population and designated Humboldt, Mendocino, and Del Norte counties as Recovery Unit 2 (RU2), one of six recovery units within the population range (USFWS 2007). Since 2001, monitoring of the plover population has been coupled with management to affect recovery, which is focused on increasing reproductive success. Three factors are thought to negatively impact plovers and limit the Pacific coast population: 1) predation of eggs and chicks by introduced and native vertebrates; 2) development and human recreational use of beach habitats; and 3) habitat degradation by non-native plant species (USFWS 2007).

In northern California, raven predation is suspected to be a primary cause of low nest survival of plovers. Specifically, on Clam Beach County Park (hereafter, Clam Beach) and Little River State Beach (hereafter, LRSB) in Humboldt County, overall proportionate nest success between 2002 and 2015 was low (19.7%, n = 259; Appendix A). Plover nest survival has been especially low in the only area of restored habitat on LRSB at just 2.4% since its completion in 2009 (Appendix B). Exclosures used between 2002 and 2006 were responsible for 60.8% of the total successful nests. Various studies

exploring the relationship between ravens and plovers in Humboldt County have offered support for the hypothesis that ravens are primarily responsible for nest predation. When compared to other beaches in Humboldt county, ravens are most abundant on Clam Beach and LRSB (Colwell et al. 2014, 2015; Lau 2015) and raven activity correlated positively with predation of plover nests (Burrell and Colwell 2012). Moreover, video and photographic evidence supports the hypothesis that ravens are the primary predator of plover eggs (Burrell and Colwell 2012).

Nest exclosures are structures used to protect eggs during the incubation period. They allow adults to move freely in and out of the exclosure to incubate, but keep out larger nest predators. Nest exclosures were used from 2001 – 2006 (nest survival data not available for 2001) in an attempt to protect plover nests from raven predation. The use of exclosures ended when predation shifted from nest predation by ravens to adult predation by a different predator, suspected to be a great horned owl (*Bubo virginianus*) or peregrine falcon (*Falco peregrinus*; Hardy and Colwell 2008; Burrell and Colwell 2012). In 2014, nest predation by ravens within and around a restored area on LRSB was likely the cause of failure of all 27 nests initiated in that area (Colwell et al. 2014). After the 100% failure rate on LRSB in 2014, the use of exclosures was considered again. Studies involving other shorebird species have shown that the use of nest exclosures may result in increased adult mortality (Murphy et al. 2003; Neuman et al. 2004; Niehause et al. 2004). Considering the potential increased risk to adults, my goal was to explore the use of exclosures as a management option on Clam Beach and LRSB by using an experimental approach to assess raven response to exclosures.

Given the low productivity of plovers on Clam Beach, where ravens occur in comparatively high numbers and negatively impact plover reproductive success (Burrell and Colwell 2012; Colwell et al. 2014; Lau 2015), I aimed to 1) summarize raven distribution, 2) evaluate habitat features that are associated with variation in raven activity on the ground, and 3) evaluate the response of ravens to exclosures in an experiment using mini-exclosures around artificial plover nests. For my third objective, I hypothesized that if exclosures attract ravens (and thus increase predation risk for plovers), then I would find more tracks around exclosures than other areas). I also hypothesized that raven attraction to exclosures would vary across time due to both initial neophobia (Kijne and Kotrschal 2002; Richardson et al. 2009; Peterson and Colwell 2014) and then eventual loss of interest (due to a lack of an association of the exclosure and a reward [obtaining plover eggs]). Thus, I specifically predicted that I would find fewer raven tracks around exclosures at the beginning on my trials (neophobia), more in the later days (attraction), and then a decrease at the end of the trials (loss of interest).

MATERIALS AND METHODS

Study Area

I evaluated raven activity at Clam Beach and LRSB near McKinleyville, California. I focused my exclosure experiment on a small (17 ha), restored piece of land on LRSB. LRSB is bordered to the north by the mouth of the Little River and is adjacent to Clam Beach. LRSB is an ocean-fronting beach approximately 2.4 km long including sandy dunes dominated by invasive European beach grass (*Ammophila arenaria*) and iceplant (*Carpobrotus* spp.) in unrestored areas. Native plant species found in the habitat restoration area include pink and yellow sand verbena, (*Abronia* spp.), beach strawberry (*Fragaria chiloensis*), beach bur (*Ambrosia chamissonis*), American and European searocket (*Cackile* spp.), and American dunegrass (*Leymus mollis*).

I conducted this experiment in the restoration area of LRSB (Figure 1). The restoration area covers between the fore- and backdune and is located at the southern end of LRSB. Restoration was initiated in 2005 with the primary goals of restoring ecological function to the dunes and providing breeding and sheltering habitat for plovers (Forys 2011). In 2009, personnel of the North Coast Redwoods District treated an additional 13.8 ha using mitigation funds from the Stuyvesant oil spill resulting in 17 ha of treated land (Forys 2011; California State Parks 2011, 2014). Symbolic fencing delineates the restoration area during the plovers’ breeding season to provide extra protection (California State Parks 2011, 2014). I chose to conduct my study in the restoration area

for two reasons: 1) protection from beachgoers provided by the seasonal symbolic fencing; 2) this area is consistently used by both plovers and common ravens (Colwell et al. 2014).

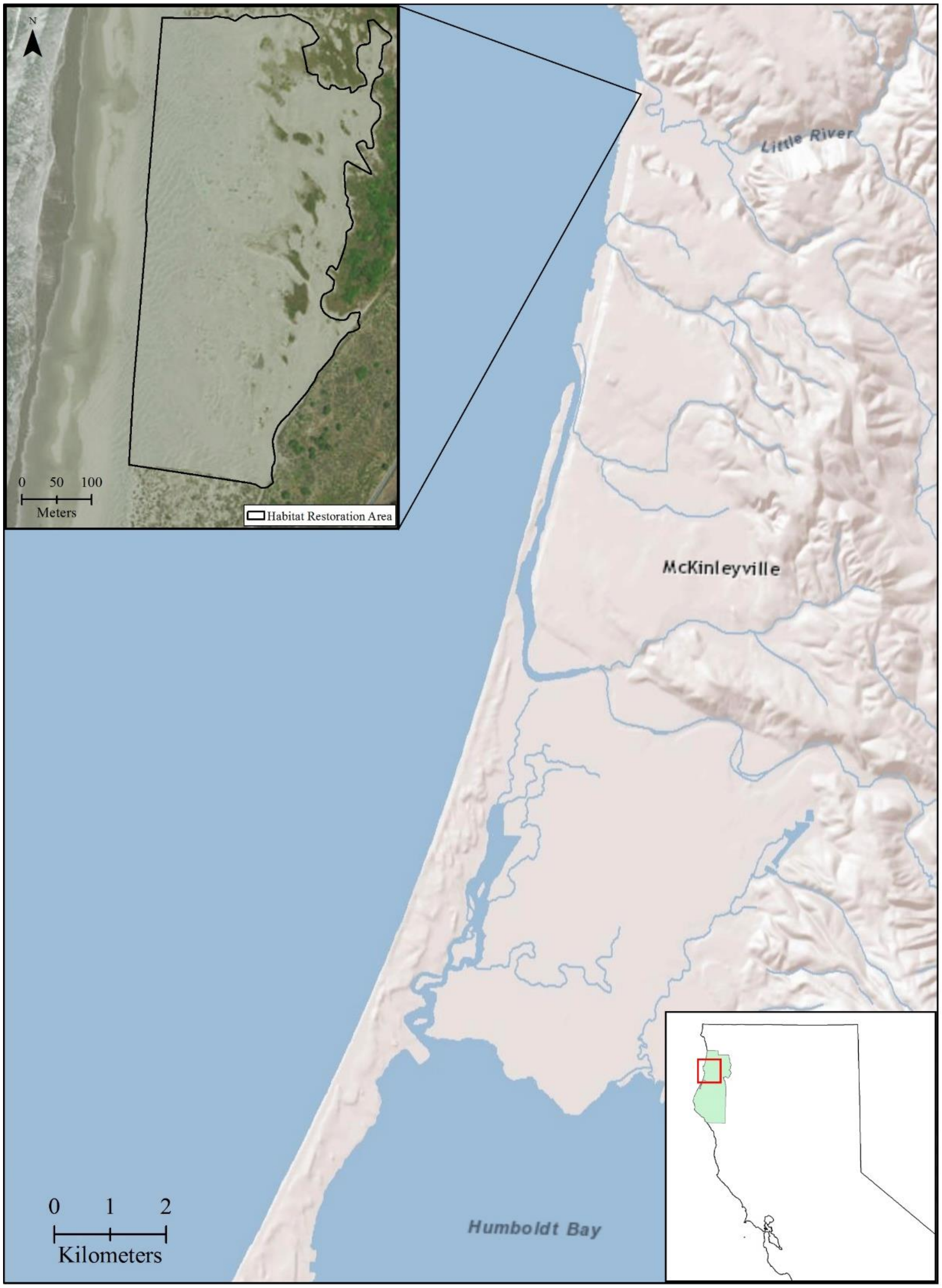

Figure 1. Study area showing habitat restoration area (inset) on Little River State Beach in Humboldt County, California.

Field Methods

To evaluate habitat variables that influence raven activity, and map raven distribution on Clam Beach and LRSB, I used ground plot data collected from 2009-2015. Observers collected data using protocol established in 2007, which quantified raven activity using tracks in the sand (Colwell et al. 2007). During each survey, observers stopped every 20 mins, prompted by a preset alarm to record the presence of common raven tracks in a 3 m radius circular plot centered on their location. Observers also recorded habitat features on a $\log_{10}$ ordinal scale (i.e., 1 = 1-10 plants, 2 = 11-100 plants, etc.) including: woody debris, stones, vegetation, shells, and anthropogenic debris.

I followed this established protocol to select random control plots in the restoration area during surveys, and to record both raven track presence and habitat features at plots with (treated) and without (control) exclosures. After recording track data, I swept clean all tracks within the 3 m radius of the exclosure but not random (control) plots. I collected data from 16 March through 6 August 2015. During this time period, I performed 5 separate 28-day trials. Every 48 hours, I collected data within a 3 m radius of each treatment and control location, following established protocols (Colwell et al. 2007). I conducted the exclosure experiment under federal (USFWS permit TE-73361A-0), state (California Department of Fish and Wildlife collecting permit #SC0496; Department of Parks and Recreation permit #08-635-011), and university (Humboldt State University IACUC #14/15.W.07.A) permits and protocols.

I built exclosures based on the Oregon Biodiversity Information Center's "mini-exclosure" design (Appendix C). Exclosures covered an area of approximately 1.5 m^2 and were approximately 80 cm tall. The sides were made of 5 cm by 10 cm wire fencing and held together with copper pig rings (traditionally inserted into pigs' snouts by farmers to prevent digging). Each exclosures had two separate tops: a soft top made of 2.54 cm^2 netting attached tautly to the top, and a hard top made of 5 cm^2 wire fencing "bubbled" over the netting. This double-top system is designed to protect plovers from avian predators as well as provide a soft barrier in the event that a plover flushes inside the exclosure. I buried the exclosures approximately 20 cm into the sand and secured them with 46 cm long, 0.95 cm diameter rebar stakes. I placed a clutch of 3 wooden quail eggs painted to resemble plover eggs, inside each exclosure (Appendix D).

At the start of each trial, I placed 24 exclosures at random locations (selected using a random point generator in ArcGIS; ESRI 2011) throughout the restoration area. I set the minimum allowed distance between exclosures to 20 m based on nearest neighbor minimum distance of real plover nests as calculated by Patrick (2013). Exclosures remained in these random locations for 28 days, equivalent to the average incubation period of plovers (Page et al. 2009), after which I moved them to new random locations at the start of the next trial. I collected data at each of these treated plots and random control plots for 21 weeks resulting in a total of 666 plots and 2,235 observations.

Statistical Analyses

Spatial analysis of raven activity

I used raven tracks (i.e., the presence of at least one set of raven tracks in a 3 m circular plot) as an index of activity, limiting analysis to conditions that favored detection of tracks ("good" tracking conditions characterized by the ability to clearly see and identify tracks). I collated ground plot data from 2009-2015 and removed observations (*n* = 352) labeled as "poor" because observers could not determine what kind of track, or how many, were within the 3 m ground plot they were surveying. Poor conditions were typically due to wind or wet sand caused by rain or high tide. These conditions accounted for approximately 12% of the total ground plots (*n* = 2,909) surveyed.

I used observations of common raven tracks recorded on a $\log_{10}$ ordinal scale (i.e., 0 = 0 tracks, 1 = 1-10 tracks, etc.) to summarize the spatial pattern of raven activity, I applied a fishnet polygon consisting of 50 m^2 grids over Clam Beach and LRSB. Next, I used the Spatial Join tool to calculate the average raven track value (derived from the $\log_{10}$ ordinal scale), for each cell (Appendix E). I used this layer as the input layer in the Optimized Hot Spot Analysis tool.

I used the Optimized Hot Spot Analysis tool in ArcGIS v.10.4.1 (ESRI 2011) to characterize the spatial distribution of raven activity on Clam Beach and LRSB. The analysis calculates a Getis-Ord Gi* spatial statistic using parameters derived from the input data

$$G_i^* = \frac{\sum_{j=1}^{n} w_{i,j}x_j - \bar{x}\sum_{j=1}^{n} w_{i,j}}{S\sqrt{\frac{\left(n\sum_{j=1}^{n} w_{i,j}^2 x_j - \left(\sum_{j=1}^{n} w_{i,j}\right)^2\right)}{n-1}}}$$

Where x_j is the attribute value for feature j, $w_{i,j}$ is the spatial weight between feature i and j, n is equal to the total number of features and $\bar{x} = \frac{\sum_{j=1}^{n} x_j}{n}$ and $S = \sqrt{\frac{\sum_{j=1}^{n} x_j^2}{n} - (\bar{x})^2}$ (ESRI 2011). If necessary, the Optimized Hot Spot Analysis tool automatically adjusts the results using the False Discovery Rate (FDR) Correction to account for multiple testing and spatial dependency (ESRI 2011). This tool calculates statistical significance using a z-score and p-value, whose threshold is reduced, if necessary, using the FDR procedure, for each point or aggregation polygon. Very high and very low (negative) z-scores are associated with very small p-values. These values are returned in the Optimized Hot Spot Analysis output as hot spots (positive z-scores) and cold spots (negative z-scores). For this study, positive (red) z-scores indicate high counts of raven tracks, whereas negative (blue) scores indicate low counts of raven tracks.

Analysis of habitat variables influencing common raven presence

To evaluate correlates of raven activity on the ground on Clam Beach and LRSB, I used Generalized Linear Mixed Models (GLMMs) with a binomial response and logit link:

$$logit(p_{ij}|\gamma_i) = \alpha + X_i\beta + Z_i\gamma_i + \varepsilon_i$$

where α is the intercept; X_i is a matrix of the predictor variables; β is a column vector of the fixed-effects regression coefficients; Z_i is the design matrix for the random effects; γ_i

is a vector of the random effects; and ε_i are the residuals where $\varepsilon_i \sim N(0, \sigma_a^2)$ (Zuur et al. 2009). I related the presence of raven tracks within each ground plot to habitat-related predictor variables. I used ground plot data collated from 2009-2015 and removed observations (*n* = 352) with poor tracking conditions. I utilized ground plot data beginning in 2009 because it is the first year the restoration area was at its current size of 17 ha.

I modeled raven presence using one random and five fixed predictors (Table 1). Based on anecdotal observations of raven foraging behavior on Clam Beach (e.g. digging in vegetation, turning over woody debris, etc.), I hypothesized that five of these predictors (shells, woody debris, vegetation, stones, and garbage) would influence raven presence on the ground. The sixth factor, year, served as the random effect in my models.

Table 1. Predictor variables, their definitions, and effect type used in modeling common raven presence relative to habitat features within a 3m radius on Clam Beach County Park and Little River State Beach in Humboldt County, California using data from 2009-2015.

Predictor Variable	Abbreviation	Definition	Effect Type
Shell/Carapace	shell	Count of shell or carapace debris[1].	Fixed
Woody debris	woody	Count of individual pieces of woody debris[1].	Fixed
Live vegetation	veg	Count of individual sprouts or plants[1].	Fixed
Stones	stone	Count of stones[1].	Fixed
Anthropogenic debris	garbage	Count of anthropogenic debris[1].	Fixed
Year	year	Each year from 2009 through 2015 which data was collected.	Random

[1] Categorized as either a 1, 2, or 3 based on a $\log_{10}$ ordinal scale defined as the following: 0 = 0; 1 = 1 – 10; 2 = 11 – 100; 3 = 100 – 1,000, following established protocol from Colwell et al. (2007).

I constructed a candidate set of 15 models using all possible permutations of my five fixed effects (Appendix E) and used an information theoretic approach to model selection (Burnham and Anderson 2002). I used Akaike's Information Criterion corrected for small sample size (AIC_c) and Akaike weights (w_i) to evaluate the strength of support for each model in my candidate set. Akaike weights represent the relative frequency that a model would have the most support relative to other models in the candidate set if the test was repeated (Burnham and Anderson 2002). Therefore, I selected a model with the largest Akaike weight as the "top model", or best supported model, in my candidate set.

I verified the fit and accuracy of my top model by calculating R^2 generalized to GLMMs and evaluating binned residual plots. I obtained marginal and conditional R^2 ($R^2_{GLMM(m)}$ and $R^2_{GLMM(c)}$, respectively) using Nakagawa and Schielzeth's (2013) method. $R^2_{GLMM(m)}$ describes the proportion of variance explained by fixed effects, and $R^2_{GLMM(c)}$ describes the proportion of variance explained by both fixed and random effects (Nakagawa and Schielzeth 2013). The difference between $R^2_{GLMM(c)}$ and $R^2_{GLMM(m)}$ reflect the proportion of variance explained by the random effects. I obtained these values using the *r.squaredGLMM* function in the MuMIn package for the *R* statistical software (Barton 2014; *R* Develoment Core Team 2016).

Nakagawa and Schielzeth (2013) cautioned against using R^2 as the sole or primary criterion of evaluating model fit, specifically when fitting GLMMs. GLMMs are subject to decreased, or even negative R^2 values with introduction of additional predictor variables (Nakagawa and Schielzeth 2013). Furthermore, R^2 does not give information regarding the practicality of the model, which is important when modeling difficult-to-

predict biological systems (Motulsky and Christopoulos 2004). Finally, although R^2 has been generalized to GLMMs, this method still does not provide the explained variance at each level (Nakagawa and Schielzeth 2013). I remedied this problem by obtaining the proportional change in variance (PCV) for the random effect (Nakagawa and Schielzeth 2013). The PCV explains how additional predictors either reduce (negative value) or increase (positive value) variance at different levels (Nakagawa and Schielzeth 2013).

Finally, I measured dispersion (φ) using a scale parameter for binomial GLMMs using the blmeco package for the *R* statistical software (Korner-Nievergelt et al. 2015; *R* Development Core Team 2016). I also evaluated the residual plot for the top model. I used binned residual plots to evaluate the fit of my model (i.e., how well my predictor variables predict raven presence) because of the inherent difficulty associated with interpreting traditional residual plots of discrete data (Gelman et al. 2000). I used RStudio v.0.99 (RStudio 2016) and Program *R* v. 3.3.1 (*R* Development Core Team 2016) to conduct these analyses.

<u>Analysis of raven activity at exclosures</u>

I evaluated overall raven response to exclosures, as well as the response within each trial. I removed data recorded under poor tracking conditions (n = 153). These conditions accounted for approximately 7% of the total observations (n = 2,235). For each day of a trial, I calculated the proportion of ground plots containing at least one raven track for both exclosures and control plots. I calculated these proportions for each trial within my study period to assess the overall effect of the exclosures on raven activity. I also calculated these proportions for each day (0-26) within each trial to

examine whether or not raven response to exclosures varied from the start to end of each 28-day trial. I used two-sample, two-tailed t-tests with unequal variances and a significance level of 0.05 to examine difference in raven activity between exclosures and control plots both by month and by day.

I evaluated factors influencing raven activity around exclosures and control ground plots using Generalized Linear Mixed Models (GLMMs) with a logit link and the binary response of track presence. I used the optimx package optimizer specifying the "nlminb" method in RStudio v.0.99 (RStudio 2016) and Program *R* v. 3.3.1 (*R* Develoment Core Team 2016) to resolve convergence problems. The "nlminb" method is a bounds-constrained quasi-Newton method used to optimize functions with multiple arguments (Nash 2014).

I related the presence of raven tracks to four predictor variables (Table 2). I investigated how trial and day within trial influenced raven presence using two different models. First, to ascertain the relationship between ground plot type (i.e., treatment [exclosure] or control) and trial, and their effect on presence, I set them as interaction terms. Then, I set "day", "type", and "trial" as a three-way interaction term to evaluate the relationship among day, ground plot type, and trial. Finally, I assessed the fit and quality of my models by plotting the binned residuals, and by calculating $R^2_{GLMM(c)}$, $R^2_{GLMM(m)}$, the PCV for the residuals, and the dispersion (φ).

Table 2. Predictor variables, their definitions, and effect type used to model common raven presence relative to treated (exclosure) and controlled ground plots on Little River State Beach in Humboldt County, California.

Predictor Variable	Abbreviation	Definition	Effect Type
Ground plot type	type	Either control (0) or treated (1). A treated ground plot is one with an exclosure.	Fixed
28-day trial	trial	One of five 28-day trials given an identifying number 1 – 5.	Fixed
Day within trial	day	One of 14 data collection days within a 28-day trial. Represented by even numbers 0 – 26.	Fixed
Unique ground plot	ex_level	A unique identifying number (1 – 666) representing each ground plot.	Random

RESULTS

Spatial Analysis

Observers collected data for a total of 2,557 ground plots over seven years (2009-2015). Raven tracks occurred in 431 (16.9%) ground plots. Ravens were abundant both on Clam Beach and LRSB; they were especially active inside the restoration area on LRSB with an average of 11 ravens recorded in the restoration area every day (+/- 6). The restoration area was the only area on Clam Beach and LRSB identified as a hot spot (Figure 2), with an area of high raven activity compared to other areas on this beach ($z > 5.71$; $\sigma = 2.71$; $P < 0.01$). This area of high raven activity is approximately two standard deviations above the mean. Two areas were identified as cold spots ($z < -1.97$; $\sigma = 2.71$; $P < 0.01$). The first was located immediately north of the restoration area; the second was approximately 800 m south of the restoration area.

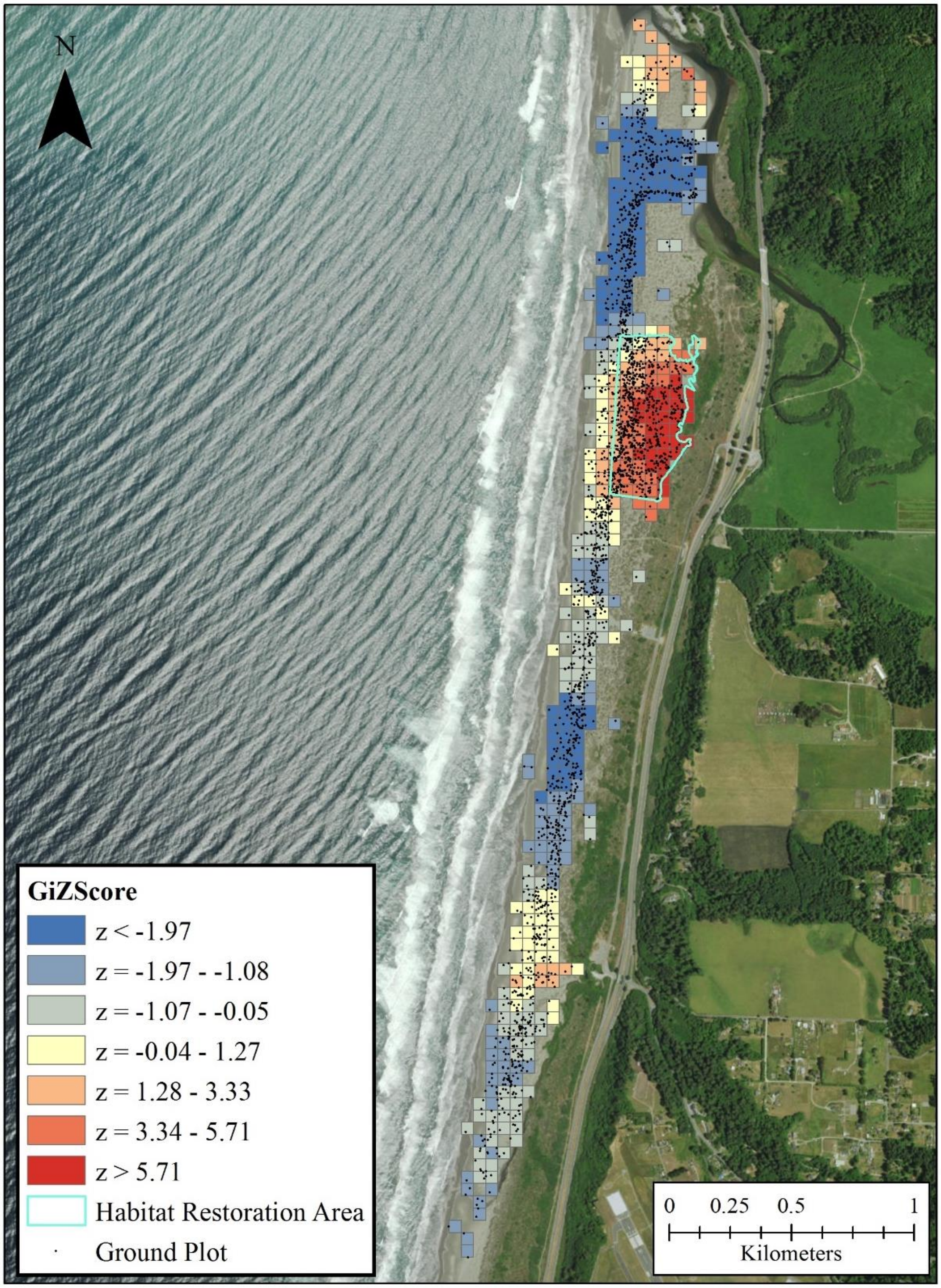

Figure 2. Hot spot map of common raven activity on Little River State Beach and Clam Beach County Park in Humboldt County, California resulting from the Optimized Hotspot Analysis (Getis-Ord Gi*) Tool in ArcGIS v.10.4.1 using ground plot data (n = 2,557) from 2009 – 2015. Dark red areas indicate statistically significant high counts of raven tracks in comparison to other grids. Dark blue areas indicate statistically significant low counts of raven tracks.

Habitat Variables Influencing Common Raven Activity

Within the restoration area, raven activity (based on tracks) was greatest in association with intermediate levels of various types of debris containing a combination of shells, wood, and vegetation (Table 3). This model had the most support with 78% of the weight (w_i = 0.78). R^2_{GLMM} values suggest a weak relationship between raven presence and these three habitat variables included in the model ($R^2_{GLMM(c)} = 0.15$; $R^2_{GLMM(m)} = 0.10$); however, a Type II Wald chi-square test revealed that all three predictors (shell, woody, and vegetation) had statistically significant effects on raven presence ($\chi^2 = 22.29$; df = 3; P < 0.001; $\chi^2 = 19.03$; df = 3; P < 0.001; $\chi^2 = 33.00$; df = 3; P <0.001, respectively). Additionally, the proportional change in variance indicated that the addition of the three predictors reduced variance explained by the random effect by 58.11%. Model performance assessments revealed high prediction accuracy of these variables relative to raven presence (Appendix F), and variance that was not greater than expected for a binomial model ($\varphi = 0.88$). In summary, shells, wood, and vegetation are all significant predictors of raven presence, and model assessments reflect good model fit; therefore, reliable inferences can be made about how these habitat variables are associated with raven presence using this model.

Table 3. Model predictors, AICc, Δ AICc, Akaike weights (w_i), and log-likelihood for 15 candidate models evaluating the relationship between raven presence and habitat features on Clam Beach County Park and Little River State Beach in Humboldt County, California in 2015 using Generalized Linear Mixed Models (GLMM) in Program *R* v. 3.1.1.

Model predictors	AIC_c	Δ AIC_c	w_i	logL
shell + woody + veg + (1|year)	2040.23	0	0.78	-1009.06
shell + woody + veg + stone + (1|year)	2043.81	3.59	0.13	-1007.82
shell + woody + veg + stone + garbage + (1|year)	2044.68	4.46	0.08	-1005.22
woody + veg + stone + (1|year)	2055.72	15.5	0	-1016.81
woody + veg + stone + garbage + (1|year)	2056.09	15.86	0	-1013.96
woody + veg + (1|year)	2056.2	15.98	0	-1020.07
veg + stone + garbage + (1|year)	2061.51	21.29	0	-1019.7
veg + stone + (1|year)	2062.08	21.86	0	-1023.01
veg + (1|year)	2062.43	22.21	0	-1026.2
shell + woody + (1|year)	2067.13	26.9	0	-1025.54
shell + (1|year)	2091.52	51.29	0	-1040.75
woody + (1|year)	2096.87	56.64	0	-1043.42
stone + garbage + (1|year)	2100.13	59.9	0	-1042.03
stone + (1|year)	2103.14	62.91	0	-1046.56
garbage + (1|year)	2106.15	65.92	0	-1048.06

Both woody debris and vegetation had a positive effect on raven presence (Figure 3). Shell debris was the only predictor to have a negative effect on raven presence. Ground plots with dense (i.e., "3+") woody debris and intermediate (i.e., "1" and "2") vegetation were more likely to have raven tracks (i.e., the probability of a raven being present was more likely when there were more woody debris and vegetation); however, ground plots with intermediate (i.e., "1" and "2") shell debris were the least likely to have raven tracks.

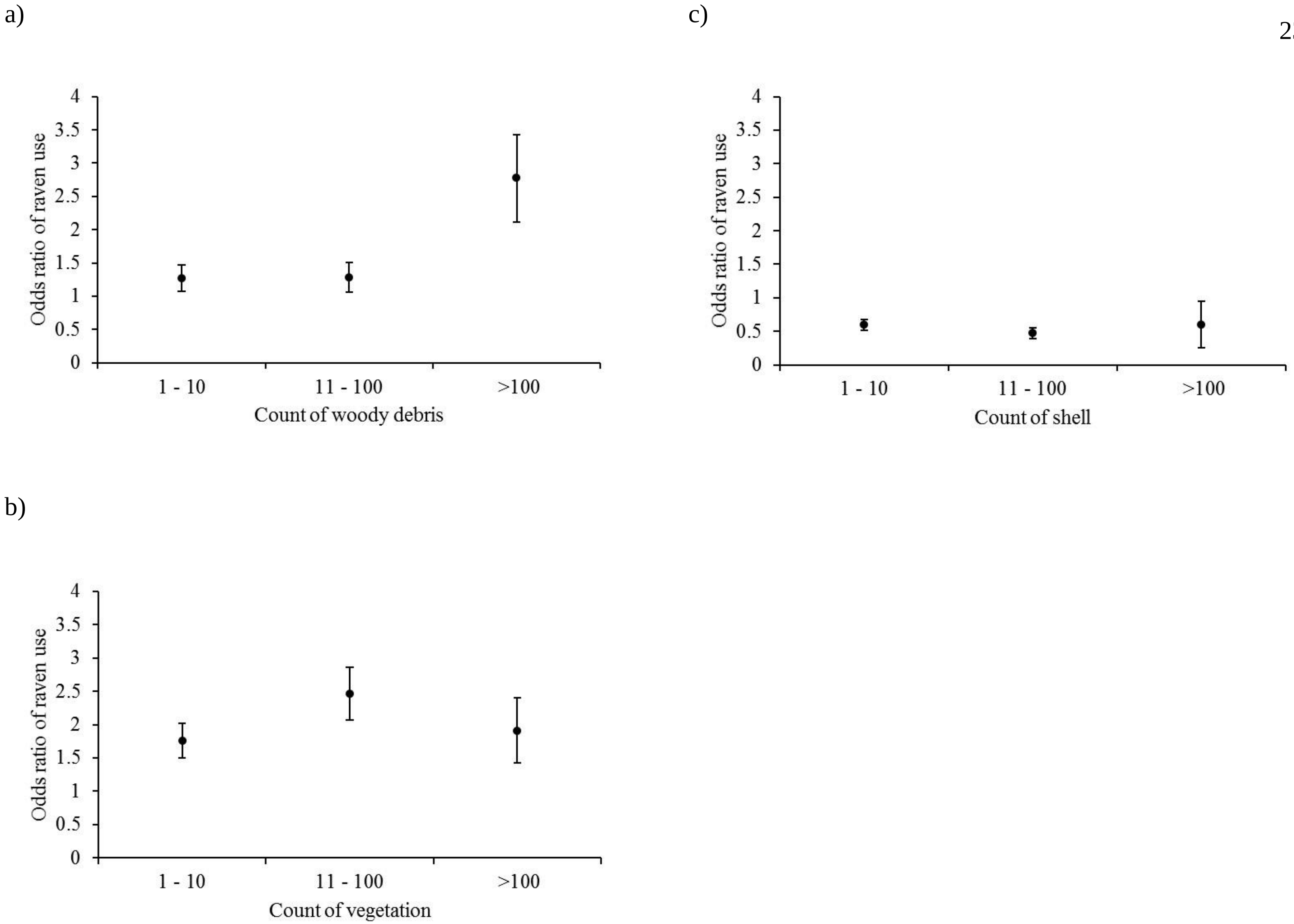

Figure 3. Odds ratios (±SE) of common raven use for woody debris (a), vegetation (b), and shells (c), variables included in the best fitting Generalized Linear Mixed Model (GLMM) of raven track presence in 3 m radius ground plots (n = 2,557) on Clam Beach County Park and Little River State Beach in Humboldt County, California from 2009 – 2015. The x-axes represent three density categories on a $\log_{10}$ ordinal scale following established protocol from Colwell et al. (2007).

Common Raven Response to Exclosures

I collected data for a total of 70 days over 5 months (March – August 2015), resulting in 546 random plots and 1,536 treated plots (i.e., around exclosures). There was seasonal variation in raven activity over the five 28-day trials (Figure 4), but no evidence that the proportion of raven activity was greater at exclosures (43.2%) than control plots (42.1%; $t_{2.31} = 0.55$; P = 0.60). This result was consistent across all five trials.

There was a weak relationship between raven presence and the interaction between trial and ground plot type ($R^2_{GLMM(c)} = 0.15$; $R^2_{GLMM(m)} = 0.10$), indicating that trial and presence of exclosures alone may not be the best predictors of raven presence. A Type II Wald chi-square test revealed that the interaction between trial and presence of exclosures did not have statistically significant effects on raven presence ($\chi^2 = 6.05$; df = 4; P = 0.19). Model performance assessments revealed substandard prediction accuracy (Appendix G), and variance that was not greater than expected for a binomial model (φ = 1.10). The proportional change in variance indicated that the addition of predictors reduced variance explained by the random effect by 87.10%. In summary, trial and presence of exclosures were not good predictors of raven presence, and model assessments indicate the fit of the model may be problematic.

The model detected seasonal variability. Raven activity was significantly greater during trial 4 ($\beta = 2.01$; SE = 0.44; P < 0.001; Figure 4). Although raven activity was greater during trial 4 than it was during the remaining trials, a Pearson's chi-square test

revealed no difference between exclosures and control ground plots ($\chi^2 = 1.4$; df = 3; P = 0.90).

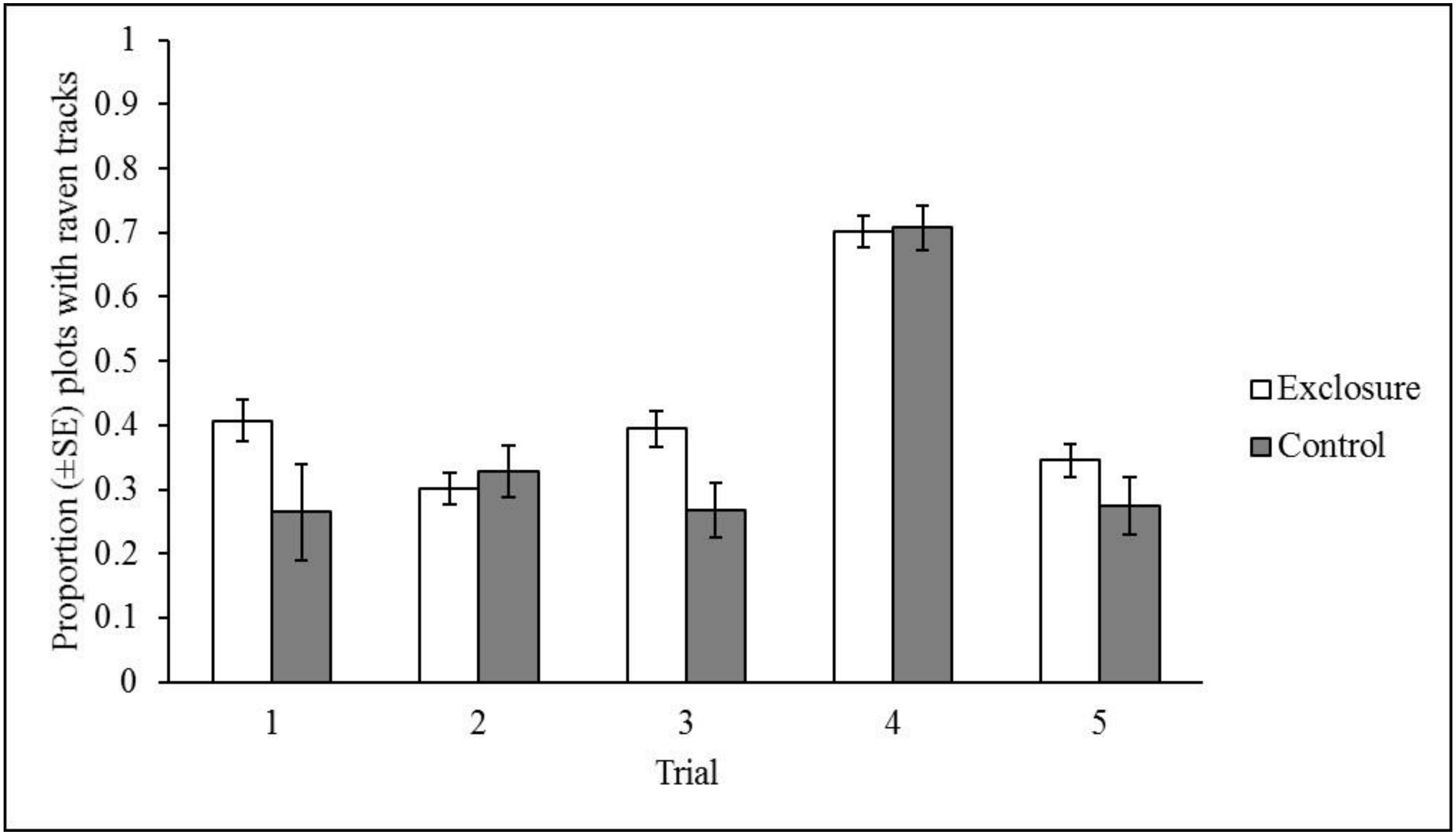

Figure 4. Proportion (± SE) of treated (exclosure) and control 3 m ground plots (n = 2,082) on Little River State Beach in Humboldt County, California with at least one set of corvid tracks calculated for each 28-day trial, represented by trial during the study period. Generalized Linear Mixed Model (GLMM) fit using Program *R* v. 3.3.

Model results revealed no day-to-day change in raven response to exclosures. Raven response appeared to be random, with no obvious or consistent pattern of activity. There was no significant difference between raven presence at exclosures and control ground plots within each 28-day trial ($t_{2.06}$ = 0.33; P = 0.74; Figure 5). This result was consistent across all five trials. Day, trial, and presence of exclosures, may not be the best predictors of raven activity as indicated by their weak relationship with raven presence ($R^2_{GLMM(c)}$ = 0.19; $R^2_{GLMM(m)}$ = 0.14). A Type II Wald chi-square test revealed that the interaction between day, trial, and presence of exclosures did not have statistically significant effects on raven presence (χ^2 = 1.10; df = 4; P = 0.89). Model performance assessments revealed reasonable prediction accuracy (Appendix H), and variance that was not greater than expected for a binomial model (φ = 1.08). The proportional change in variance indicated that the addition of the three predictors reduced variance explained by the random effect by 85.90%. In summary, day, trial, and presence of exclosures are not significant predictors of raven presence, and model assessment results indicate adequate model fit.

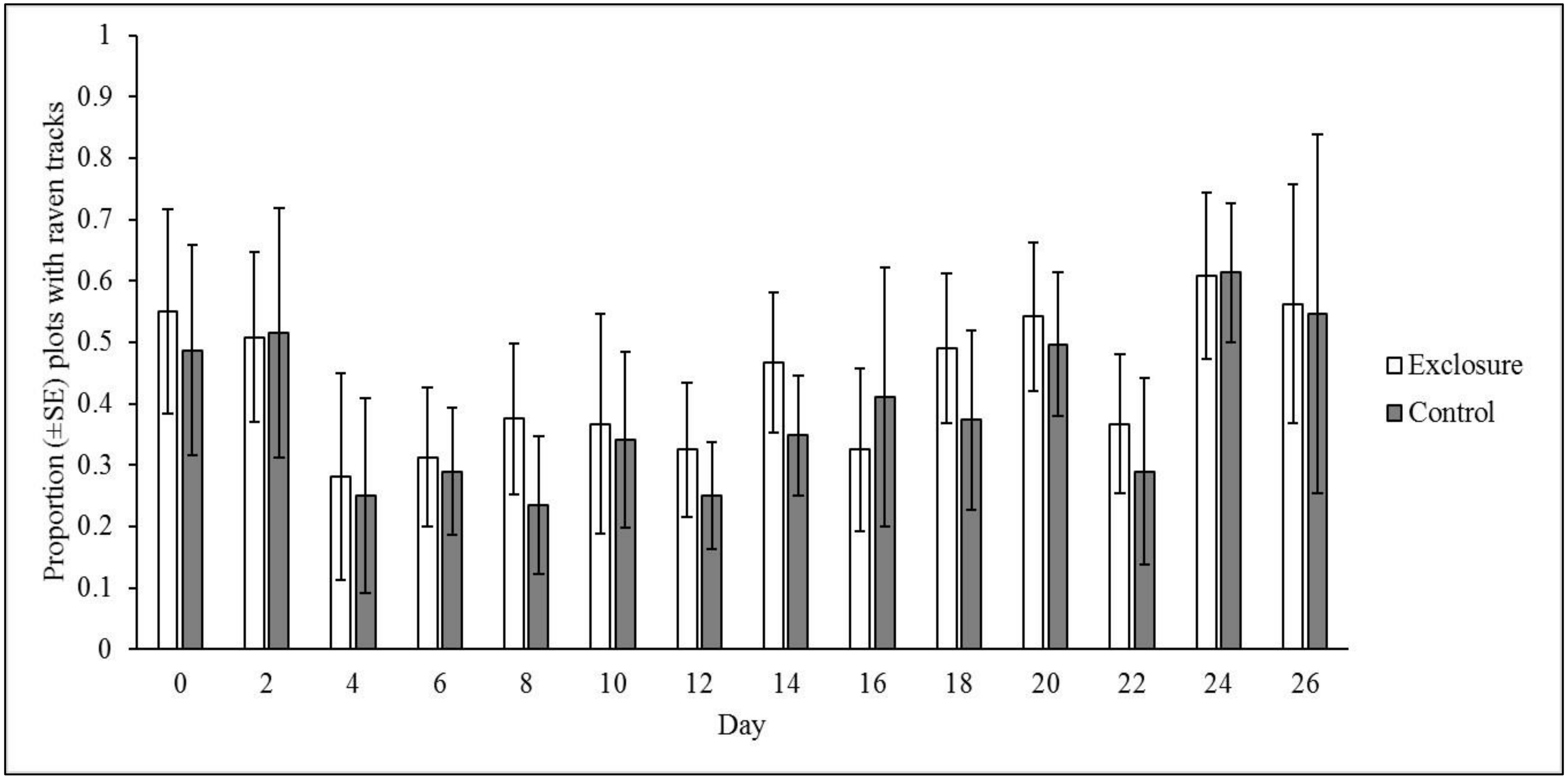

Figure 5. Average (± SE) proportion of treated (exclosure) and control 3 m ground plots (n = 2,082) on Little River State Beach in Humboldt County, California with at least one set of corvid tracks calculated for each observation day within each 28-day trial. Generalized Linear Mixed Model (GLMM) fit using Program *R* v. 3.3.

DISCUSSION

Exclosures are a widely-used method of non-lethal predator management for increasing hatching success of ground-nesting birds (Rimmer and Deblinger 1990; Melvin et al. 1992; Johnson and Oring 2002; Isaksson et al. 2007). However, this management technique may result in adult mortality events and should be used with caution (Murphy et al. 2003; Neuman et al. 2004; Niehause et al. 2004; Hardy and Colwell 2008; Watts et al. 2012). In this study, I found that: 1) ravens were more active on the ground inside the restoration area than they are elsewhere on Clam Beach or LRSB; 2) raven activity is positively influenced by vegetation and woody debris, and negatively influenced by shell debris; 3) exclosures do not increase the likelihood of encountering raven tracks; and, 4) the lack of difference in raven activity between exclosure and random plots did not change over time.

Raven Activity

When compared to other study sites in Humboldt County, Clam Beach and LRSB were hot spots of raven activity (Colwell et al 2014; Lau 2015). Expanding on this information, I evaluated raven presence on a finer scale by evaluating activity on the ground on Clam Beach and LRSB. I found that the only significant hot spot of raven activity occurred within the restoration area. This area is the only restored piece of land on Clam Beach and LRSB. These restoration efforts provide a landscape of native

vegetation and woody debris that, based on my results, may positively influence raven presence.

Habitat Variables Influencing Raven Activity

A primary reason ravens are so successful is because they are omnivorous generalists (Boarman and Heinrich 1999; Boarman 2003; Wilmers et al. 2003). Diet analysis studies of raven pellets conducted in Oregon, Idaho, and California reveal an extremely varied diet, depending on season and habitat type, including: roadkill, livestock carrion, plant material, arthropods, avian egg shells, reptiles, amphibians, small mammals, fish, and trash (Engel and Young 1989; Stiehl and Trautwein 1991; Camp et al. 1993; Kristan et al. 2004). A concurrent study conducted on LRSB revealed that raven diet consisted of predominately marine crustaceans, vegetation, seeds, and coleopterans (Lau et al., Humboldt State University, unpublished data). Anecdotal observations of ravens foraging in the restoration area on invertebrates among native vegetation and woody debris during this study support the findings of Lau et al. (unpublished data). I routinely observed ravens meandering through the restoration area on foot and foraging by using their bills to dig among the native vegetation and flip over woody debris (Appendix I, J).

Habitat analysis results evaluating raven presence relative to different habitat variables support this anecdotal evidence. Results indicated that vegetation and woody debris have a positive effect on raven presence. These results were significant when vegetation density was described as being low-to-moderate. Results were also significant

when the density of woody debris was described as being high. Additionally, results show that shell debris have a negative effect on raven presence at all densities. This is a particularly important finding because shell debris is associated with plover nesting success and is commonly applied to human restored areas to improve plover success (Lauten et al 2006; Hardy and Colwell 2012).

Raven Response To Exclosures

Exclosures did not increase the likelihood of encountering raven tracks. Raven presence increased significantly during trial 4; however, this increase was the same at both treated and control ground plots. This increase took place between late May and early July when anecdotal field observations of pairs of adult ravens changed to observations of family groups including fledglings, confirming that ravens are not attracted to exclosures. While these results are promising for the potentially successful use of exclosures, it is important to keep in mind this study evaluated raven response to dummy exclosures. These exclosures were simply a novel stimulus on the landscape, and were not protecting active nests with a live adult plover to attract the attention of the ravens. Departure of an incubating adult may be the cue that prompts raven predation (Burrell and Colwell 2012).

Raven response to exclosures did not differ compared to random control plots and this lack of difference did not change over time. My results suggest that while ravens did explore around exclosures, they were not more attracted to them than other locations in the study area. In addition, activity around exclosures did not increase or decrease

significantly throughout each 28-day trial. In contrast to my study, ravens have previously been reported as being neophobic (Kijne and Kotrschal 2002; Richardson et al. 2009; Peterson and Colwell 2014). I would have expected significantly low activity around exclosures during the beginning of my study or the beginning of each trial if the population of ravens I studied had a neophobic response.

The lack of a change in response to exclosures over time might be explained by a number of reasons. First, was the absence of a consequence from approaching an exclosure. My study did not include hazing inside the restoration area or near any exclosures, which likely would have resulted in a decrease of activity (Werner and Clark 2006; Peterson and Colwell 2014). Although, this decrease of activity likely would not have lasted very long as ravens habituate to certain hazing (Peterson and Colwell 2014). Secondly, seasonal variation in raven numbers could have attributed to the lack of change in response over time. Trial 4 marked a significant increase in raven activity on the ground due to the increased number of individuals. This increase of individuals corresponded with the seasonal arrival of raven fledglings. The lack of a change in response could be explained by new individuals in the population that had not yet learned that the exclosures do not result in any kind of reward. Finally, it is possible that this study was simply not long enough. More time may have been needed for the ravens to form the association between exclosures and the lack of a reward.

Limitations

In conducting the exclosure experiment, I sought to mimic conditions (i.e., fake eggs painted to imitate a plover clutch) in which managers use this non-lethal technique to boost hatching success. However, three main constraints limit the inferences that can be drawn from my study. One concerns the study population of ravens and the ability of individuals to learn about a novel stimulus in their environment; the other two were methodological challenges. Since I did not study a marked population of ravens, I was unable to evaluate the response of individuals to exclosures. Instead, I evaluated response at the population level. On average, 11 ravens were observed at any single time every day in the restoration area. Given the known territoriality of ravens, I assumed that these birds were mostly the same individuals from day-to-day (Webb et al. 2012). Because of this, I was able to make inferences regarding the change in response that was, or was not, taking place within each 28-day trial.

Two methodological issues affect my conclusions. I gauged raven activity using tracks on the ground, which is an untested index. Indirect indices based on signs of presence or activity, such as tracks, is a widely used and accepted technique; this technique is most useful, and used most often, in terrestrial species (Braun 2005). Video evidence recorded by Burrell and Colwell (2012) suggests that ravens find plover nests via aerial searches. This is significant because this type of activity would not be detected doing ground plot surveys. Using tracks as the sole index of raven activity provides only partial insight into how they are utilizing the beach.

Finally, exclosures were not used to protect active plover nests. This is important because there were no incubating adults to attract the attention of ravens. It is suggested that it is not so much the eggs that attract ravens to a plover nest, but the movement of an incubating adult leaving the nest (Burrell and Colwell 2012). The next step would be to use exclosures to protect active nests and evaluate raven response and activity. However, this type of experiment should be approached with caution. Results of other studies suggest that the use of exclosures to protect shorebird nests may increase adult mortality (Murphy et al. 2003; Neuman et al. 2004; Niehause et al. 2004; Watts et al. 2012). Additionally, if it is found that ravens are, in fact, not attracted to exclosures protecting active nests, that only solves the issue of hatching success. Exclosures are known to increase hatching success, but not fledging success (Neuman et al. 2004; Niehause et al 2004). So, the quandary of predator management to ensure plover fledging success would remain.

In conclusion, I found no evidence that ravens are attracted to dummy exclosures protecting artificial plover nests more so than control plots. Furthermore, this response did not change over time as raven activity did not increase or decrease within each 28-day trial. My work revealed that raven activity is positively influenced by low-to-moderate densities of vegetation, and high densities of woody debris; while shell debris negatively influences raven presence. I illustrated these results using a hot spot analysis which revealed significantly high raven activity inside the restoration area when compared to the rest of Clam Beach and LRSB.

MANAGEMENT IMPLICATIONS

Predator control is an important and necessary aspect of wildlife conservation and management, especially for threatened and endangered species. Reproductive success of western snowy plovers on Clam Beach and Little River State Beach is variable across years but routinely low and raven predation is likely the principal cause. In fact, restoration of native dune ecosystems may have created habitats that are especially attractive to ravens, which poses a conservation dilemma. Consequently, additional predator control methods may be necessary to reduce raven activity in restored areas, although surrounding landscape effects may be the most important cause of variation in raven activity (Lau 2015).

Although restoration has created habitat that is attractive to plovers (Leja 2015), the quality of restored areas on LRSB requires additional management to address predation. Oyster shell hash is routinely added to restored areas in high densities; however, results of this experiment suggest that shell dispersed at medium densities negatively influences raven presence. Furthermore, the LRSB restoration area has not been treated with oyster shell; therefore, ground plots sampled in the experiment contained naturally occurring shell much of which was broken up into small pieces. Given these results, I would recommend treating the LRSB restoration area with low to medium densities of crushed shell.

Ravens do not appear to be attracted to exclosures, thus reducing the threat of raven predation of plover nests. Using exclosures in a way that mimics this experiment

could be an effective tool for increasing plover nest success on Clam Beach. For example, this experiment provides evidence that a landscape saturated with dummy exclosures does not attract the attention of ravens. The novelty of a single exclosure may stimulate interest; therefore, I would recommend deploying dummy exclosures protecting artificial eggs in the vicinity of an exclosed real nest. Additionally, I would recommend employing the same simple 48-hour monitoring technique utilized in this experiment.

Without predator control on LRSB, snowy plover nests will continue to experience low reproductive success. Continuous management efforts in the form of predator control, habitat restoration, and management of these restored habitats is imperative. Therefore, active and multifaceted predator and landscape management, like the aforementioned strategies, is necessary for the recovery of the snowy plover.

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APPENDIX A

Appendix A: Total nests initiated, hatched, and exclosed, on Clam Beach County Park and Little River State Beach (2002-2015).

Year	Initiated	Hatched	Exclosed	Exclosed and hatched	Percent exclosed and hatched (%)	Percent total hatched (%)
2002	18	5	7	5	71.4	27.8
2003	17	5	8	5	62.5	29.4
2004	12	6	7	6	85.7	50.0
2005	21	9	11	9	81.8	42.9
2006	26	7	11	6	54.5	26.9
2007	20	1	0	NA	NA	5.0
2008	12	1	0	NA	NA	8.3
2009	12	1	0	NA	NA	8.3
2010	12	1	0	NA	NA	8.3
2011	9	3	0	NA	NA	33.3
2012	13	3	0	NA	NA	23.1
2013	25	6	0	NA	NA	24.0
2014	40	0	0	NA	NA	0.0
2015	22	3	0	NA	NA	13.6
Total	259	51	44	31	70.5	19.7

APPENDIX B

Appendix B: Total nests initiated, hatched, and exclosed in the habitat restoration area pre-restoration (2002-2008) and post-restoration (2009-2015).

Western Snowy Plover Nests	Pre-restoration	Post-restoration
Initiated	11	42
Hatched	4	1
Exclosed	4	0
Exclosed and hatched	4	NA
Percent total hatched (%)	36.4	2.4

APPENDIX C

Appendix C: Example of an exclosure used in this study based on the Oregon Biodiversity Information Center's "mini-exclosure" design.

APPENDIX D

Appendix D: Example of an artificial egg used inside exclosures. Eggs were wooden and hand-painted to mimic western snowy plover eggs.

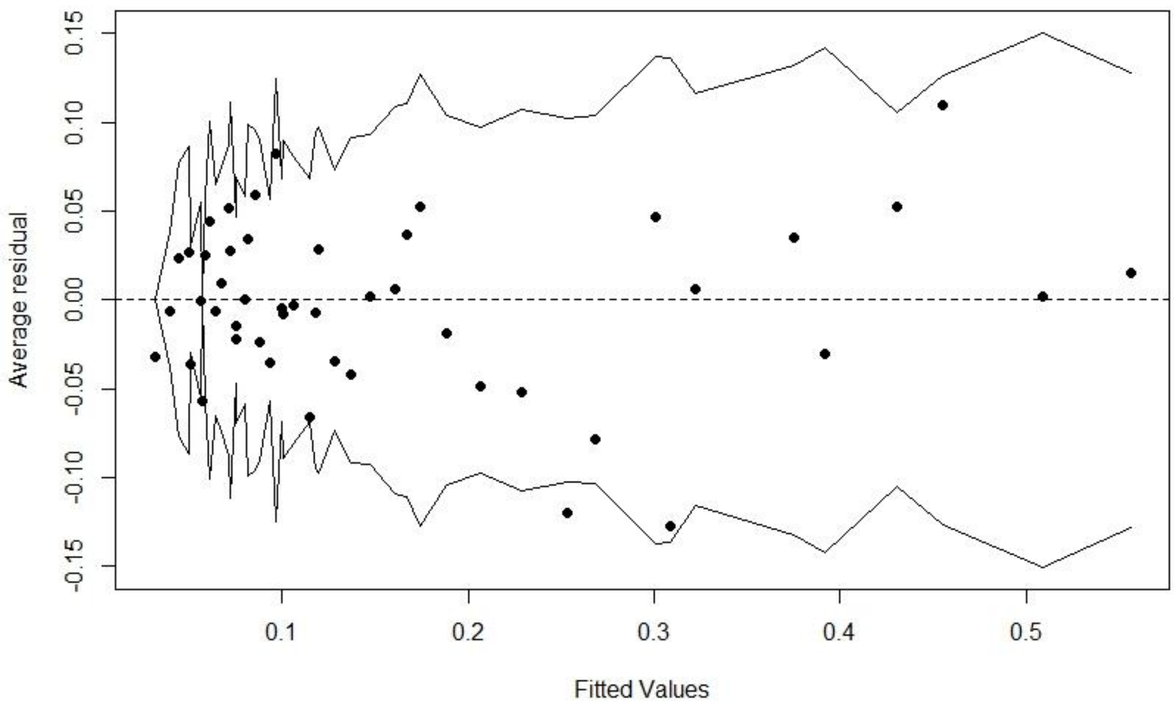
APPENDIX E

Appendix E: Fifteen candidate models based on five predictor variables, used to model common raven presence on the ground.

1. shell + woody + veg + stone + garbage
2. shell + woody + veg + stone
3. shell + woody + veg
4. shell + woody
5. shell
6. woody + veg + stone + garbage
7. woody + veg + stone
8. woody + veg
9. woody
10. veg + stone + garbage
11. veg + stone
12. veg
13. stone + garbage
14. stone
15. garbage

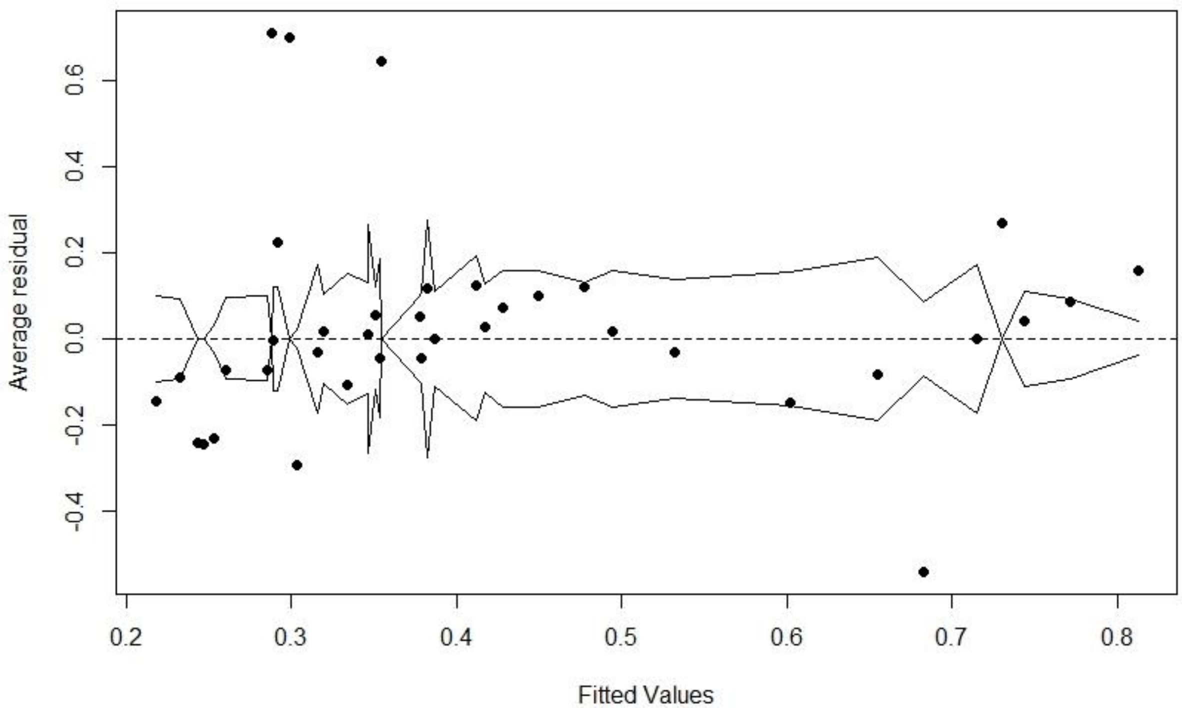
APPENDIX F

Appendix F: Binned residual plot showing averaged residuals versus fitted values for the GLMM relating raven presence to habitat predictors (*presence ~ shell + woody + veg + (1 | year)*) on Little River State Beach in Humboldt County, California. A small number of residuals fall outside the 95% error bounds indicating good model fit.



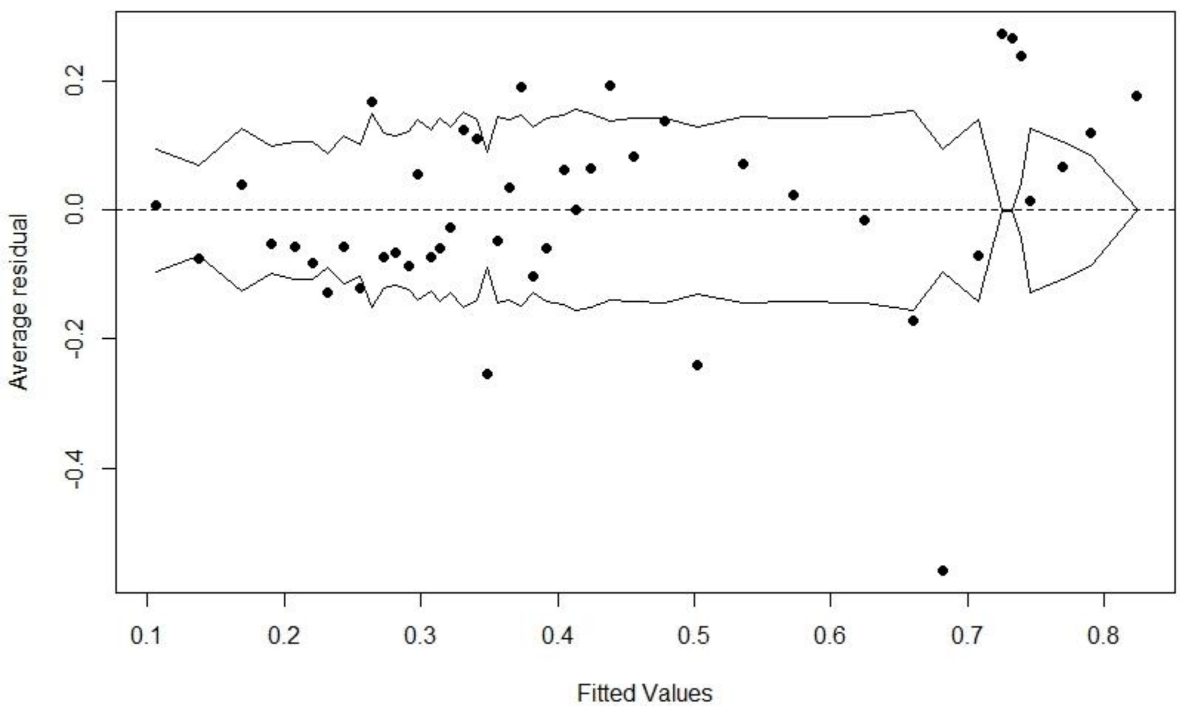
APPENDIX G

Appendix G: Binned residual plot showing averaged residuals versus fitted values for the GLMM relating raven presence to ground plot type (treated or control) and trial (*presence ~ type*trial + (1 | ex_level)*) on Little River State Beach in Humboldt County, California. A number of residuals fall outside the 95% error bounds indicating poor model fit.



APPENDIX H

Appendix H: Binned residual plot showing averaged residuals versus fitted values for the GLMM relating raven presence to day within trial, ground plot type (treated or control) and trial (*presence ~ day*type*trial + (1 | ex_level)*) on Little River State Beach in Humboldt County, California. Few residuals fall outside the 95% error bounds indicating adequate model fit.



APPENDIX I

Appendix I: Evidence of ravens foraging in native vegetation.

APPENDIX J

Appendix J: Evidence of ravens foraging by flipping over woody debris.