Steller's jay density declines in response to human education and policy enforcement in a protected area

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ABSTRACT

Anthropogenic food subsidies have ecological and evolutionary implications for wildlife on a global scale. In protected areas where habitat for species of conservation concern and extensive human use intersect, abundant food subsidies to generalist predators can create an existential threat to rare species by way of spillover predation. One potential long-term solution is limiting subsidies by educating visitors to protected areas and enforcing policies related to food management. However, the effectiveness of visitor education and policy enforcement in reducing human food subsidies and the effectiveness of subsidy reduction as a management strategy are yet to be determined. We studied a generalist predator, the Steller's jay, both before and after implementation of a management program combining visitor education and enforcement of food policies. We used stable isotope analysis to assess the quantity of human foods in jay diets and a combination of point counts, telemetry, and growth bar analysis to understand how jay density, space use, and body condition changed in response to management. The proportional contribution of human foods to jay diets decreased significantly after management from 0.65 to 0.42, indicating that the program was successful at reducing jay consumption of anthropogenic foods. Jay density also decreased substantially from 4.33 to 0.65 jays/hectare in response to management. While overlap between jay territories decreased, home range size and body condition remained stable after management and fecundity increased for jays remaining in subsidized areas. Human visitation to protected areas is increasing globally, and our results indicate that visitor education can be part of a broader solution to make species protection and human recreation within protected areas more compatible.

INTRODUCTION

Anthropogenic food subsidies have ecological and evolutionary implications for wildlife on a global scale (Shochat et al. 2006, Oro et al. 2013). Spatially and temporally predictable food subsidies can impact basically every aspect of species ecology. For example, food subsidies can shape foraging behaviors (Almaraz and Oro 2011) and modify time budgets and territorial behavior (Strain and Mumme 1988, McLeod and Ritchison 2018). For birds, supplementary food can impact every aspect of their ecology (Robb et al. 2008). Food subsidies can increase adult (Jansson et al. 1981) and juvenile (Gill and Hatch 2002, Oro et al. 2008) survival, fitness (Almarez and Oro 2011), increase fecundity (Verboven et al. 2001, Nagy and Holmes 2005), and modify interspecies interactions like predation and competition (Rodewald et al. 2011, Ciucci et al. 2020). Much work studying the effects of food subsidies on birds has traditionally focused on urban environments, but food subsidies in protected areas may have even more serious consequences for species of conservation concern (West et al. 2019).

Protected areas are a foundation for global biodiversity conservation (Bruner et al. 2001, Naughton-Treves et al. 2005, Watson et al. 2014), and increasingly, they are also relied upon to provide recreation and ecotourism opportunities (Balmford et al. 2009, Watson et al. 2014). Extensive use of protected areas for human recreation can result in abundant anthropogenic food subsidies for wildlife (West et al. 2016) and lead to spillover predation, in which plentiful food resources in one habitat allow predators to move into adjacent areas and prey upon species that are already rare (Holt 1984). Spillover predation can exacerbate declines and, in some cases, present an existential threat to rare species (Kristan and Boarman 2003). Generalist predators, in particular, are adept at taking advantage of human food subsidies (Newsome et al. 2010), and those capitalizing on human food available at campgrounds or picnic areas within protected areas have the potential to spill over into natural areas that provide important habitat for species of conservation concern. Several management strategies have been recommended for limiting spillover predation, including lethal control of populations and selective removal of problematic individuals (Boarman 2003, Peery and Henry 2010). However, these strategies come with their own problems, including high cost, potential for community changes such as meso-predator release when predators are removed, and public opposition to lethal tactics (Goodrich and Buskirk 1995). One strategy that has been proposed as a potential long-term solution is limiting anthropogenic food subsidies to these predators by educating visitors to protected areas (Peery and Henry 2010; West et al. 2019). However, both the effectiveness of visitor education in reducing human food subsidies and the effectiveness of subsidy reduction as a management strategy for generalist predators remain yet to be determined.

The Steller's jay is a generalist predator native to coniferous and mixed forests of the western U.S. whose omnivorous diet includes nuts and seeds, berries, arthropods, and the eggs and nestlings of other birds (Vigallon and Marzluff 2005), but Steller's jays also readily take advantage of human food subsidies (Marzluff and Neatherlin 2006). Frequent and abundant human visitors and their food subsidies in protected areas have been implicated in producing abundant populations of Steller's jays in central California (West et al. 2016, 2019; West and Peery 2017). Steller's jay densities are elevated in campground areas and jay body condition and fecundity is improved by food subsidies provided by park visitors (West and Peery 2017, West et al. 2019). Importantly, these protected areas also harbor the majority of remaining nesting habitat for the central California population of the marbled murrelet, a federally threatened seabird (Halbert and Singer 2017). One of the direst threats to this population of murrelets is low reproductive success, which is largely attributed to high predation rates by corvids such as Steller's jays and common ravens (Peery et al. 2004, Marzluff and Neatherlin 2006, Peery and Henry 2010). In fact, population viability analyses have shown that reducing corvid predation may be the most effective way to recover marbled murrelets in central California (Peery and Henry 2010). Collectively, these findings spurred an intensive visitor education and food management program within California State Parks in an effort to reduce food subsidies to Steller's jays, in particular. The "Crumb Clean Campaign" (hereafter referred to as "management") began in 2013 and combined visitor education, enforcement of food policies, and improved refuse management to reduce access to human food subsidies for park wildlife, particularly corvids. Food management strategies included the installation of secure food lockers at campsites and better dishwashing procedures to reduce the accessibility of human foods to jays. However, the effectiveness of the Crumb Clean Campaign remains unclear, as does the effect of reducing food subsidies on the density and fitness of Steller's jays.

Here, we aimed to evaluate (1) the effectiveness of management efforts in reducing human food subsidies to jays, and (2) the response of jays to the limitation of previously abundant anthropogenic food. We predicted that management efforts would reduce anthropogenic food subsidies available to Steller's jays in campgrounds and that this would result in lower densities of jays in campground areas, while densities of jays in unsubsidized forest areas would remain comparatively stable between pre- and post-management periods. We also predicted that reductions in subsidies associated with enhanced visitor education would increase jay home range size, as birds would need to travel greater distances to meet their nutritional needs, and decrease the amount of overlap between jay territories, as jays may increase territory defense if resources are more scarce or more uniformly distributed rather than concentrated in campgrounds. Finally, with regard to jay body condition we had two alternative predictions: either body condition would decrease in response to lower food abundance, or it would increase as jays switched from anthropogenic food to a forest based diet with higher nutritional content made up of mast and arthropods (e.g., Annett and Pierotti 1999). Given the limited assessments of the effectiveness of public education program on biodiversity conservation in protected areas, understanding these links will help guide ongoing and future conservation initiatives in protected areas that provide important opportunities for outdoor recreation but also serve as crucial habitat for species of conservation concern.

MATERIALS AND METHODS

Study area and time periods

We studied a population of Steller's jays in Big Basin Redwoods State Park (Santa Cruz County, California) to understand the effects of management on their diet, demography, and fitness. Big Basin includes approximately 4,300 acres of old-growth forest, with an overstory largely composed of Coast Redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*). Big Basin includes the largest tract of remaining old-growth forest nesting habitat for marbled murrelets in central California

(Baker et al. 2006). We collected data related to jay diets and fitness during the breeding season in two distinct time periods: The “pre-management period” includes 2011 to 2013 before the education campaign began (West and Peery 2017), and the “post-management period” includes 2017 to 2019, and begins after the campaign had been in effect for three years. We were interested in changes in jay populations in areas where human food subsidies were abundant in pre-management years (West and Peery 2017), so we studied jays that lived primarily in campground areas.

Capture and sampling

We captured Steller’s jays to collect data related to diet, home range, and body condition (see next sections), using a combination of mist nets (Avinet Research Supplies) and live traps (Havahart or homemade) during the breeding season (May – August) in both pre- and post-management periods. Jay capture and sampling mainly took place within seven heavily-used campgrounds in Big Basin (Figure 1). We banded jays with a steel USGS band and a unique combination of colored plastic bands (Avinet Research Supplies) to enable individual recognition. We determined the sexes of jays in the field when possible by noting sex-specific vocalizations, and we confirmed all sexes later using extracted DNA from blood samples that we collected from the brachial vein (Griffiths et al. 1998). We distinguished adult jays from juveniles using a combination of vocal characteristics (e.g., use of begging calls) and differences in gape coloration and plumage pattern (Pyle 1997). We weighed jays, measured their tarsus length, and collected feather samples from some individuals (see human food enrichment and body condition, below). To determine patterns of space-use and territory boundaries, we fit a subset of individuals with radio transmitters (pre-management: model A1050, post-management: model A1070, Advanced Telemetry Systems), which we attached using backpack-style harnesses made of 0.1” natural tubular spectra tape or 2.5 mm Teflon ribbon (Bally Ribbon Mills).

Human food enrichment

We quantified the reduction in human food subsidies to Steller's jays using stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ in feathers by comparing (1) the proportion of the diet composed of human food, and (2) the level of anthropogenic food enrichment, between pre- and post-management periods. Because human foods are often made up of corn (a C_4 plant) and corn-based by-products, they are enriched in the heavy isotope of carbon, making them isotopically distinct from natural prey items in western North America where primary production is driven by native C_3 plants (Newsome et al. 2010, West et al. 2016). We clipped approximately 50mm of a newly grown primary flight feather from each jay at the end of the breeding season (early – mid-August) in post-management years. These samples reflected breeding season diet because feathers incorporate the isotopic signature of the diet during periods of feather growth (Hobson and Clark 1992), and jays begin to molt during the latter part of the fledgling provisioning period in late July (KB and EW personal observations). We rinsed feather samples three times in 2:1 Chloroform:Methanol solution to remove surface contaminants, homogenized them with scissors, and dried them at 55°C for ≥ 72 hours. We then weighed feather samples and sealed them into tin capsules. Analysis of $\delta^{13}C$ and $\delta^{15}N$ was conducted using a Thermo Scientific Delta V mass spectrometer connected to a Costech 4010 elemental analyzer and a high-temperature conversion elemental analyzer. Results are presented as per mil (‰) ratios relative to international standards, Vienna-Pee Dee Belemnite limestone (C) and atmospheric nitrogen (N).

In order to understand how the overall diet of jays changed after management began, we estimated the proportional contribution of distinct diet sources to adult jay diets in pre- and post-management periods using the Stable Isotope Analysis in R mixing model (SIAR 4.2, Parnell et al. 2010). To construct the mixing space, we sampled potential diet sources, including invertebrates, berries, acorns, conifer seeds, and human foods, approximately every two weeks at Big Basin during the pre-management period (2011-2013). Based on K randomization tests, we grouped diet sources into three distinct groups: anthropogenic (human-derived), mast (e.g., berries and acorns), and invertebrate (West et al. 2016). We did not include marbled murrelet eggs or chicks in diet analyses because they likely made up a negligible proportion of the jay diet due to the small number of murrelets and large number of jays in our study area. Additionally, all diet sources included in a mixing model are assigned some level of contribution to the diet, which could lead to overestimation of the importance of murrelets in the diet and underestimation of the importance of more common diet sources (Phillips et al. 2014). To account for tissue-specific isotope discrimination, we adjusted the isotopic values of diet sources using trophic discrimination factors for a wild-caught passerine with an omnivorous diet similar to that of a Steller's jay: +3.3‰ (SD = 0.04) for δ^{15}N and +3.5‰ (SD = 0.1) for δ^{13}C (Pearson et al. 2003). We also corrected for differences in elemental concentrations of diet sources by including the average measured elemental concentrations (weight% C, weight% N) for each diet group in our mixing models. Results are presented as Bayesian 95% credible intervals where the median is considered the most likely level of contribution to the diet (Parnell et al. 2010).

To determine how consumption of human food by jays differed due to management, we compared pre- and post-management mean δ^{13}C enrichment of adult jays. We removed one post-management individual from analysis because it was never seen in the campgrounds after initial capture, and its territory did not coincide with campground areas (based on telemetry data). We compared δ^{13}C enrichment between pre- and post-management periods using a one-way ANOVA with management as a factor. We detected heterogeneous variance in δ^{13}C enrichment in campground birds between pre- and post-management periods (determined through Levene's test). However, sample sizes of campground birds pre- and post-management were almost equal, and F-tests are robust against violation of the homoscedasticity assumption when sample sizes are equal. Additionally, the consequence of violating this assumption is loss of power (increased Type II error), and we were comfortable making a conservative estimate of the difference in human food consumption between pre- and post-management years. We also compared δ^{13}C enrichment within pre-management years and post-management years using a two-way ANOVA to determine if δ^{13}C enrichment was different among the three years in each period.

Density and reproduction

To assess the effect of the education campaign on jay populations, we estimated the density of adult jays in campground and forest areas and in the pre- and post-management periods using point count surveys and distance sampling. We conducted monthly 5-minute point count surveys at seven campground and seven forest points during the breeding season (mid-May – mid-August) in pre- and post-management periods. We conducted point count surveys between 7:00 and 10:00 a.m. when weather conditions were suitable (i.e., low wind and no rain). We noted whether each detected bird was an adult or a juvenile, as determined by vocalization or plumage characteristics. In pre-management years, we used flagging at 10-m intervals marked from the center of the point to estimate distances to visual and auditory detections, and in post-management years, we used rangefinders (Bushnell Laser Rangefinder) to do the same. To correct for imperfect detection in our estimates of jay density, we implemented distance-sampling techniques using the package Distance (version 1.0.0, Miller et al. 2019) in the R statistical environment (R Core Team 2018). We estimated monthly jay densities each year in campground and forest areas in two separate models. To better estimate the detection function and density of juvenile jays in the post-management period, we included both adult and juvenile jays in our campground model, and we used age as a covariate in the model so that detection probabilities and densities were estimated separately for juveniles and adults. We evaluated five potential detection functions using AIC: a half-normal key function with a cosine transformation, a half-normal key function with a hermite-polynomial transformation, a uniform key function with a cosine transformation, a hazard-rate key function with a cosine transformation, and a hazard-rate key function with a simple polynomial transformation. In pre-management years, monthly adult and juvenile jay densities in campground and forest areas each year were estimated in four separate models (see West and Peery 2017 for full methods). We assessed the fit of each top model by plotting detection functions and by using a Cramér-von Mises goodness-of-fit test, in which a p-value <0.05 indicates a poor model fit.

To evaluate whether management affected jay reproduction, we calculated the juvenile to adult ratio for campground areas. The juvenile to adult ratio can be used as a snapshot of productivity of a population because it integrates all the components of productivity, including clutch size, nest success rate, and proportion of breeders (Ricklefs and Bloom 1977, Peery et al. 2007). We used the density of adults in June (to minimize the effects of post-breeding adult movements) and juveniles in August (which is the peak fledging period) to calculate ratios for both pre- and post-management years (West and Peery 2017).

Home range size and overlap

We used telemetry data to evaluate changes in Steller's jays home range size and in the median amount of overlap in home range among individuals between pre- and post-management periods in campgrounds. We collected telemetry data from mid-May to early August, a period that largely coincides with the breeding season of Steller's jays in this area. Each year, we found and recorded the location of each radio-tagged individual between 25 and 35 times by hiking on foot and using a telemetry receiver and handheld GPS unit. We varied the times of day we tracked each individual throughout the season (between 7 a.m. and 7 p.m.) and also collected roost locations (between 10 p.m. and 3 a.m.) for each bird 3-4 times per year.

To assess how home range sizes changed between pre- and post-management periods, we calculated the home range of each jay, which we defined as the 95% utilization distribution, using the adehabitatHR package (Calenge 2006) in the R Statistical Environment (R Core Team 2018). We log-transformed all home range sizes for normality and excluded females from analysis due to a small sample size and differences in home range size between males and females in pre-management years.

We also compared median overlap between Steller's jay territories in pre- and post-management periods by calculating the Utilization Distribution Overlap Index (UDOI), a measure of the degree of overlap, for each pair of jays captured in the same campground. A UDOI value of zero indicates no overlap, whereas a value of one indicates complete overlap; however, this statistic can also be greater than one if two utilization distributions are non-uniformly distributed and have a high degree of overlap (Fieberg and Kochanny 2005). We compared median UDOI values and the distribution of UDOI values between 2011-2012 and 2019 to ensure sample sizes were similar between pre- and post-management periods, as sample size can greatly affect the reliability of comparing UDOI across studies (Fieberg and Kochanny 2005).

Body condition

We assessed the body condition of campground jays in pre- and post-management periods using feather growth bar width as a proxy. Feather growth bars consist of a dark bar, produced during the day, and a light bar, produced at night, that together indicate the amount of feather growth over a 24-hour period. Feather growth is energetically costly and therefore the width of growth bars is an indicator of the nutritional status of a bird during feather growth, with wider growth bars indicating better body condition (Grubb 2006). We collected a newly grown rectrix from each jay at the end of the breeding season (early to mid-August). We then scanned each feather to obtain a high-quality image, and three independent observers measured ten individual growth bars from each feather using the program ImageJ (Schneider et al. 2012) to calculate an average growth bar width for each bird. We took the average of measurements from all observers for each feather, and we standardized growth bar width by dividing the growth bar average by tarsus length-cubed (a measure of body volume) to correct for body size. Finally, we multiplied all values by 100,000 for ease in reporting the results. To understand how body condition had been affected by jay management, we compared average growth bar width of campground jays in pre-management and post-management periods using linear mixed models and a likelihood ratio test. Because we had a priori knowledge that growth bar width may vary among years (West and Peery 2017), we used year and individual as random effects and management as a fixed effect, and we also computed a profile confidence interval for the effect of management.

RESULTS

Human food enrichment

We analyzed stable isotopes in feathers from 38 adult Steller's jays in pre-management years, and 37 adult Steller's jays in post-management years. Stable isotope analyses of feathers indicated that jay diets had changed since the campaign began. The proportion of human foods in the diet of jays decreased from 0.65 (95% credible interval: 0.55-0.77) in the pre-management period to 0.42 (95% credible interval: 0.32-0.53) in the post-management period (Figure 2). We observed a similar trend in $\delta^{13}C$ enrichment, as jays were less enriched in the post-management period. Jays in the post-management period were, on average, 2.18‰ (95% CI: 1.57-2.78‰; $F_{1,73} = 50.95$, $p < 0.001$; Figure 3) less enriched than jays in the pre-management period. Additionally, there was no evidence of a difference in $\delta^{13}C$ enrichment among pre-management ($F_{3,43} = 0.87$, $p = 0.47$) or post-management years ($F_{2,45} = 0.28$, $p = 0.76$).

Density and reproduction

In campgrounds, we found that the density of jays was lower in the post-management period than in the pre-management period. The best model used the hazard rate key function, included month and year as covariates, and fit the data reasonably well (Cramér-von Mises p-value = 0.65). The estimated June density of adult Steller's jays in pre-management years was 4.33 (±0.91) jays/hectare (West and Peery 2017), while in post-management years the density was 0.65 (±0.20) jays/hectare. Detection probabilities for adults were slightly higher in the pre-management than post-management period (pre: 0.54 ± 0.13, post: 0.40 ± 0.04). The estimated August density of juvenile Steller's jays in pre-management years was 3.30 (± 0.80), while in post-management years the density was 0.70 jays/hectare (± 0.41).

In forest areas, jay density was comparatively stable between pre- and post-management periods. The model with the half-normal key function and with month and year as covariates had the lowest AIC and fit the data reasonably well (Cramér-von Mises p-value = 0.37). In the pre-management period, the estimated jay density was 0.70 (± 0.22) jays/hectare (West and Peery 2017), while in post-management years, we estimated jay density as 0.58 (± 0.38) jays/hectare. We also estimated a lower detection probability in post-management years than in pre-management years (pre: 0.58 ± 0.09, post: 0.22 ± 0.08).

Juvenile to adult ratios indicated that reproduction per jay may have increased in campgrounds between pre- and post-management periods. In the pre-management period, the estimated juvenile to adult ratio was 0.76 and in the post-management period it was 1.07. In forests, the pre-management juvenile to adult ratio was 0.21, but in the post-management period, we never detected a juvenile jay at a forest point and therefore the juvenile to adult ratio would be estimated as zero.

Home range size and overlap

We radio-tagged 50 jays in the pre-management period and obtained an average of 34.4 locations for each individual. We radio-tagged 65 jays in the post-management period and collected home range data from 64 (one radio-tagged jay was predated early in the season in 2019). We collected an average of 29.56 locations from each individual in the post-management period. From these locations we calculated home range sizes for 35 jays in the pre-management period and 45 jays in the post-management period.

There was no difference in log-transformed home range size between pre-management (6.16 ± 0.80 hectares) and post-management (6.35 ± 0.60 hectares) periods for male jays ($F_{1, 65} = 0.18$, $p = 0.67$). Log-transformed home range size was different between sexes in pre-management years ($F_{1, 45} = 7.54$, $p = 0.008$), but not in post-management years ($F_{1,61} = 0.59$, $p = 0.44$).

Space use in campground areas changed between pre- and post-management periods. In the pre-management period, jays exhibited a high degree of home range overlap (median UDOI = 0.03; n = 35 pairs), while in the post-management period jays exhibited a lower degree of home range overlap (median UDOI= 0.48; n = 46 pairs; Figure 4).

Body condition

We used feather growth bar width as a proxy for body condition for 54 jays (n = 19 pre-management, n = 35 post-management). Average growth bar width was 4.72 (SE: 0.11) and 5.04 (SE: 0.16) for jays in pre- and post-management periods, respectively. Our likelihood ratio test and profile confidence intervals indicated that growth bar width was not affected by management ($\chi^2 = 1.13$, p-value = 0.29, 95% CI: -0.35 – 0.86).

DISCUSSION

Our results suggest that visitor education, policy enforcement, and food management at Big Basin has reduced human food subsidies to Steller's jays, resulting in changes to jay density and patterns of space use in campgrounds. Jay density in subsidized campground areas decreased after management, while density in unsubsidized forest areas was stable over the same time period, as we had anticipated if management was successful. While the size of jay territories in campgrounds did not change between pre- and post-management, the amount of overlap between territories decreased, perhaps indicating that jays were utilizing more evenly distributed resources rather than clumped, campsite-based anthropogenic food. We found no changes in body condition of jays between pre- and post-management periods, although average growth bar width was slightly wider in the post-management period. Other studies have found that adult body condition may not be very sensitive to consumption of human food (i.e., "junk food"; Salleh Hudin et al. 2016, Townsend et al. 2019), but that demographic rates like reproductive success can be negatively affected by human food consumption in corvids (Shawkey et al. 2004, Meyrier et al. 2017) and other passerines (Chamberlain et al. 2009, Seress et al. 2020) in urban areas. Our results suggest that reduction of abundant human food subsidies was associated with lower abundance of jays in campground areas and that remaining jays are relying more upon natural food resources, which may result in stable or increased body condition. Notably, we also observed an increase in fecundity in campgrounds, as measured by juvenile:adult ratios, which may further support this idea.

There are two caveats to our study. The first is that we did not directly measure the availability of human food to jays. By not doing so we assume that reduced consumption of human foods reflects an actual reduction in availability of this resource to jays. Anecdotal evidence from the park supports this assumption, and Marzluff and Neatherlin (2006) found that jays within 1 km of human settlements frequently utilized anthropogenic subsidies while those >5 km from settlements never utilized anthropogenic subsidies and instead foraged significantly more on mast. We observed a similar pattern – post-management jays that ate less human food had diets rich in mast, including berries, fruits, and seeds. The second caveat is that because capturing jays in forest areas is logistically and financially challenging, often necessitates lethal sampling, and can result in small sample sizes (West et al. 2016), we did not measure body condition, home ranges, or diets of jays in unsubsidized areas. This raises the crucial question of whether the changes we observed in jay space use and diet in campgrounds were due to jay management or potentially due to some other unmeasured factor. To our knowledge, no significant changes occurred related to levels of human use or habitat conditions in either campground or unsubsidized forest areas during the study period. However, our study area experienced an unusually severe drought during jay breeding seasons from 2012-2015 (Griffin and Anchukaitis 2014, Tortajada et al. 2017) that could have resulted in some of the patterns we observed. We believe this scenario is unlikely for several reasons. First, drought conditions would be more likely to negatively affect jays in forest areas, as those utilizing campgrounds may be buffered from drought effects by the predictable availability of human food (Shochat et al. 2006). This is the opposite of the pattern we observed – jay density in campgrounds decreased over time, while density in unsubsidized forest areas was stable. Second, drought conditions could have caused jays in campground areas to rely more upon human food resources, resulting in the high $\delta^{13}C$ enrichment we observed in the pre-management period. However, we collected isotope data from two drought years and two normal years in the pre-management period and did not detect a difference in enrichment among any of the four years, indicating drought likely did not affect the diets of Steller's jays in this study. Finally, a study examined the responses of Steller's jays, and many other bird species, to both high temperatures and water deficit during the same drought in the Sierra

Nevadas, California, and found that Steller’s jay abundance was not affected by temperature and responded positively to water deficit (Roberts et al. 2019). For these reasons it seems unlikely that the drought was responsible for the patterns we observed.

Overall, our results indicate that the Crumb Clean Campaign appears to have reduced the amount of human food consumed by jays and the density of jays, which may ultimately reduce the risk of marbled murrelet nest predation. We note that while the post-management density of jays in campground areas was similar to that in unsubsidized forest areas, the diet of post-management jays in campgrounds was comprised of more human foods than those in forest areas during the pre-management period (Figure 3), indicating that campground jays continue to have access to human foods despite intensive efforts to eliminate subsidies. Additionally, the jays that remained in campgrounds continued to reproduce at high rates and maintain similar body condition and home range sizes as before management began. Nevertheless, our results provide evidence that management efforts aimed at changing human behavior, when used in tandem with policy enforcement and trash management, can constitute a useful conservation tool to reduce the density of target species.

Based on evidence from this study, educating users of natural areas can be part of a broader solution that may also include completely excluding humans from some areas. Indeed, uninformed behaviors, such as intentionally or unintentionally feeding wildlife, are the most amenable to change in response to information and education programs (Manning 2003). Importantly, though, education alone has proven to be an ineffective management tool in other situations (George and Crooks 2006, Gore et al. 2008, Baruch-Mordo et al. 2011, Dietsch et al. 2018) and even changing intentions often may not engender actual behavior change (Webb and Sheeran 2006). However, combinations of education strategies and enforcement have shown to be more effective at changing problematic human behaviors (Manning 2003, Baruch-Mordo et al. 2011). Therefore, we join others in recommending collaborations between social scientists and wildlife managers to create effective programs for educating humans and protecting wildlife (Baruch-Mordo et al. 2009, Dietsch et al. 2018). Human visitation to protected areas is increasing globally (Balmford et al. 2009), and we are just beginning to comprehend the suite of potential impacts this may have on wildlife (Miller et al. 1998, Liu et al. 2001, Reed and Merenlender 2008, Larson et al. 2016, Bötsch et al. 2018). However, human recreation in natural areas is also important – these spaces provide benefits to human health and well-being (Frumkin 2001, MacKerron and Mourato 2013) and essential opportunities for humans to feel connected to nature and personally invested in its conservation (Pyle 2003, Kareiva 2008, Balmford et al. 2009). Therefore, it is essential that we continue to seek ways to increase the compatibility of species protection and human recreation in protected areas.

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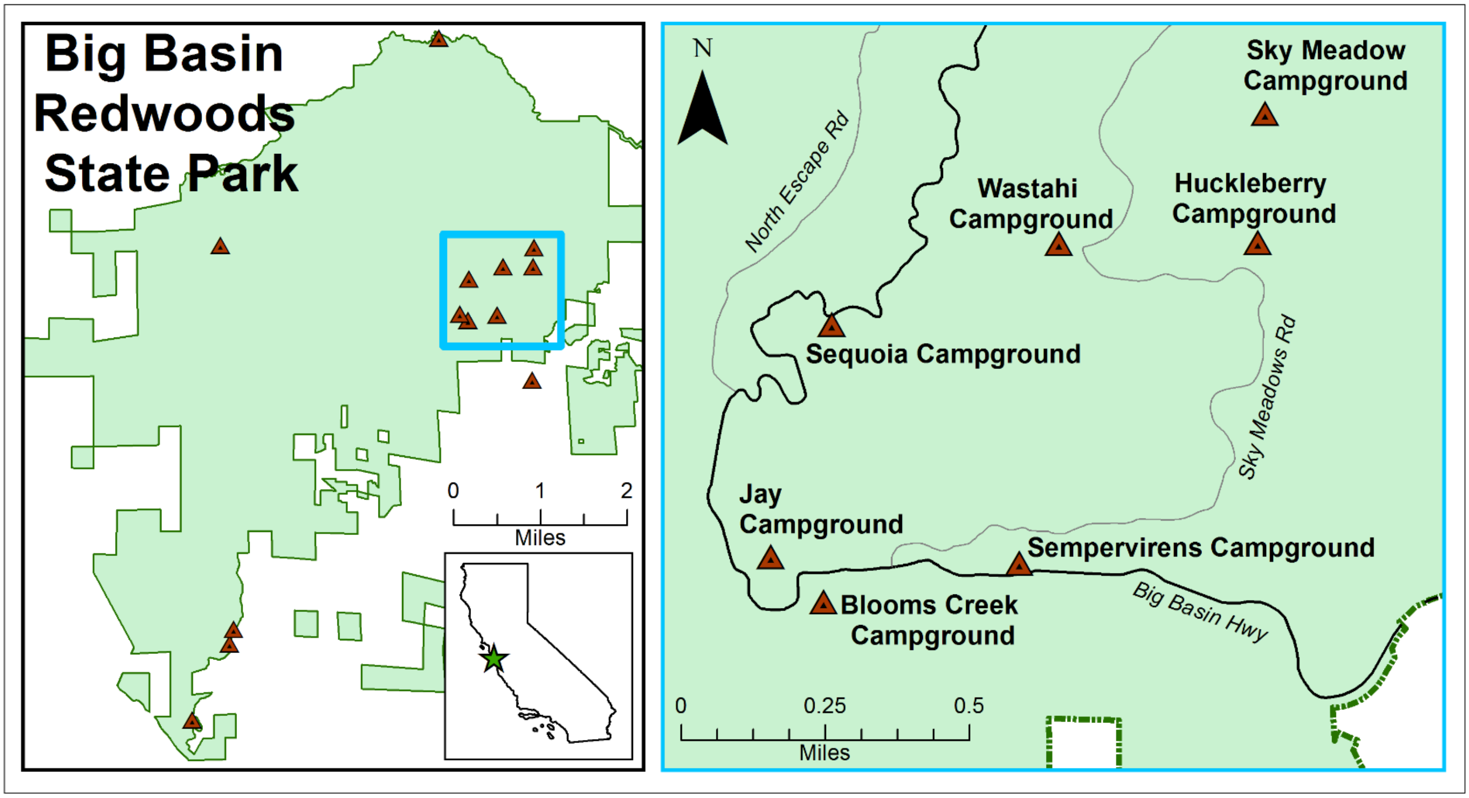

Figure 1. Map of the study area. Campgrounds are denoted by brown triangles. The inset area (blue box) shows capture locations of campground and periphery jays.

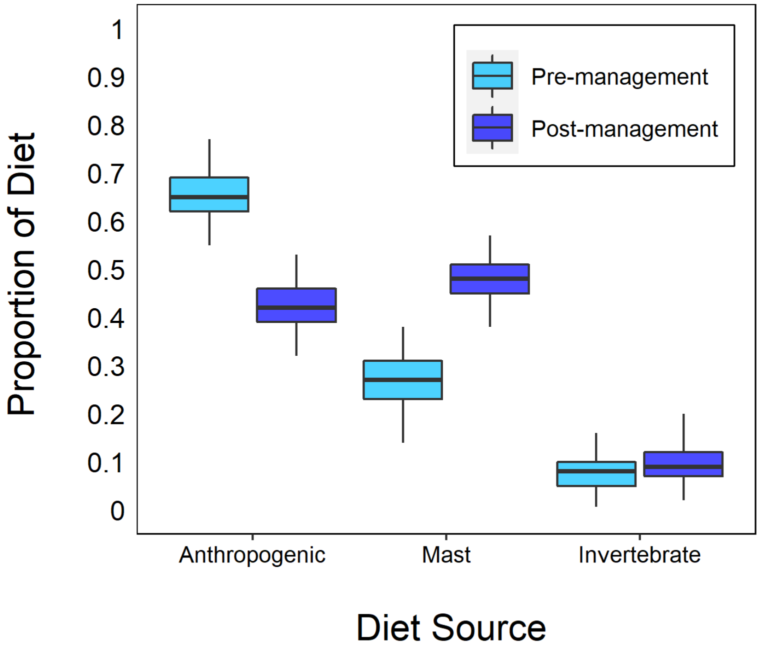

Figure 2. Proportional contributions of three diet sources to adult jay diets in pre- and post-management periods. Boxes represent the first and third quartiles, thick lines represent the medians, and whiskers represent 95% credible intervals.

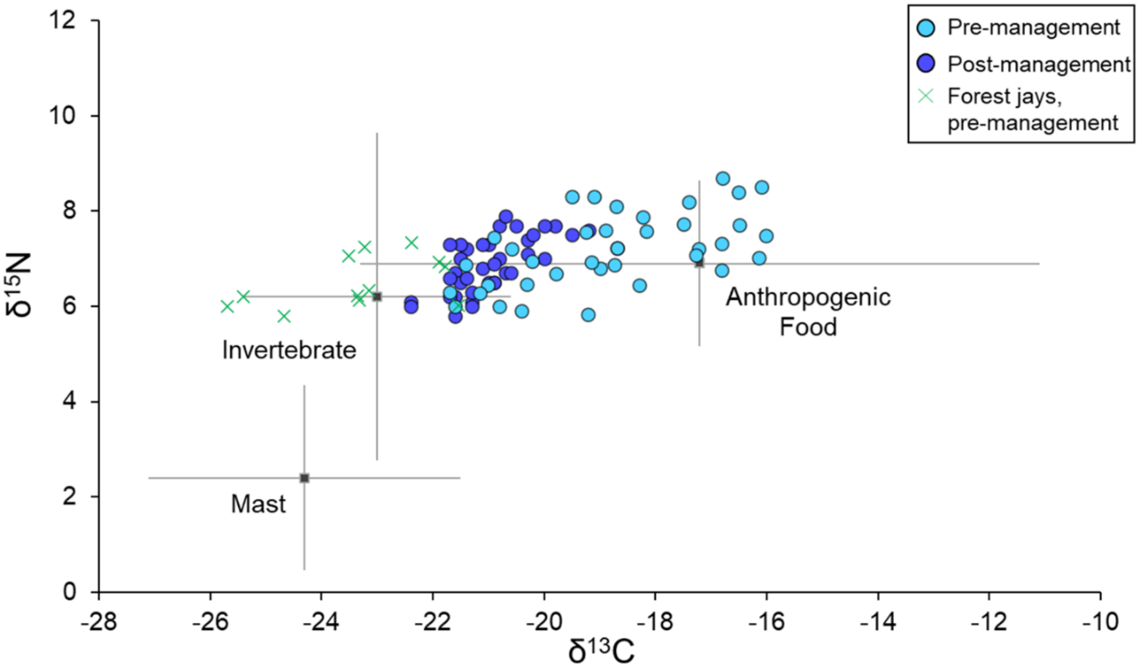

Figure 3. $\delta^{13}C$ and $\delta^{15}N$ isotope ratios of individual Steller's jay feather samples in pre- and post-management periods. Results are plotted with each potential diet source and the isotope results from forest jays in the pre-management period for reference.

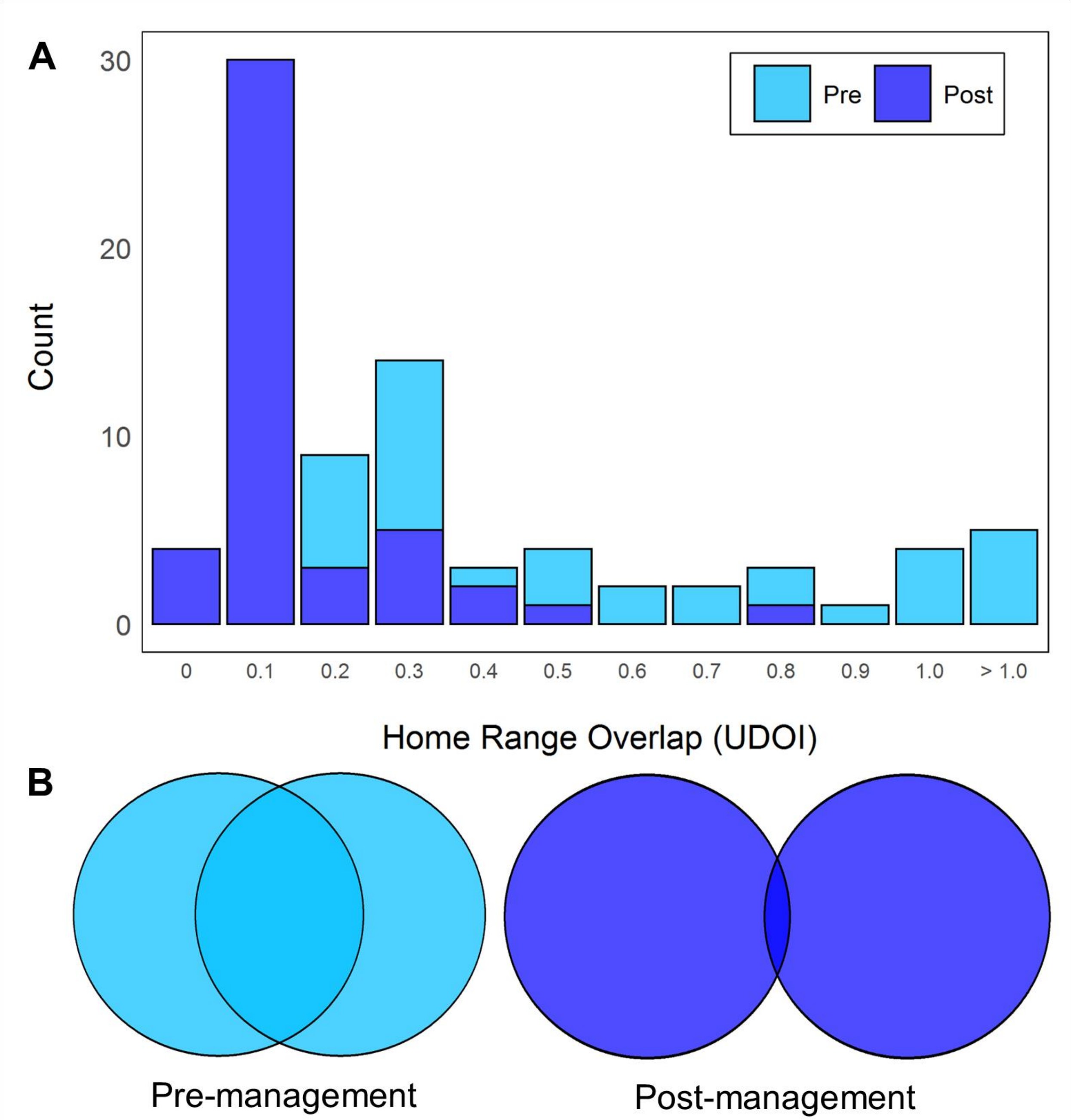

Figure 4. (A) Pairwise index of home range overlap between male Steller's jays captured in the same campground in pre- and post-management periods. (B) Visual representation of the median home range overlap between pairs of male jays in the pre-management and post-management period, respectively.