



Policy analysis

Reducing anthropogenic subsidies can curb density of overabundant predators in protected areas

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ABSTRACT

Protected areas safeguard biodiversity and provide opportunities for human recreation. However, abundant anthropogenic food subsidies associated with human activities in protected areas can lead to high densities of generalist predators, posing a threat to rare species at broad spatial scales. Reducing anthropogenic subsidies could curb populations of overabundant predators, yet the effectiveness of this strategy is unclear. We characterized changes in the foraging ecology, body condition, and demography of a generalist predator, the Steller's jay, three years after implementation of a multi-faceted management program to reduce anthropogenic subsidies in a protected area in California. Stable isotope analysis revealed that the proportional contribution of anthropogenic foods to jay diets declined from 88% to 47% in response to management. Overlap between jay home ranges decreased after management began, while home range size, body condition, and individual fecundity remained stable. Adult density in subsidized areas decreased markedly from 4.33 (SE: ± 0.91) to 0.65 (± 0.20) jays/ha after the initiation of management, whereas density in unsubsidized areas that were not expected to be affected by management remained stable (0.70 \pm 0.22 pre-management, 0.58 \pm 0.38 post-management). Thus, the response of jays to management was density-dependent such that reduced densities facilitated the maintenance of individual body condition and fecundity. Importantly, though, jay population size and collective reproductive output declined substantially. Our study provides evidence that limiting anthropogenic subsidies can successfully reduce generalist predator populations and be part of a strategy to increase compatibility of species protection and human recreation within protected areas.

1. Introduction

Protected areas are a foundation for global biodiversity conservation (Bruner et al., 2001; Naughton-Treves et al., 2005; Watson et al., 2014), yet they are also increasingly relied upon to provide recreation and ecotourism opportunities (Balmford et al., 2009; Watson et al., 2014). Human use of protected areas often results in abundant anthropogenic food subsidies for wildlife, which have ecological and evolutionary implications for biodiversity globally (Oro et al., 2013). Spatially and temporally predictable food subsidies can alter many aspects of species ecology (Oro et al., 2013) and threaten species of conservation concern (Kristan and Boarman, 2003). In some cases, access to subsidies improves fitness by boosting fecundity (Prange et al., 2003; Beckmann et al., 2008) or increasing survival (Prange et al., 2003). Indeed, areas with abundant subsidies are typically characterized by higher densities of subsidized species than unsubsidized areas (Beckmann and Berger,

2003; Prange et al., 2003; Shochat, 2004; Rodewald and Shustack, 2008). Elevated densities of subsidized species can modify interspecies interactions like competition and predation (Rodewald et al., 2011; Newsome et al., 2015b; Ciucci et al., 2020), which can lead to increased human-wildlife conflict (Hopkins et al., 2014) and spillover predation (Kristan and Boarman, 2003). Spillover predation occurs when plentiful food resources in one habitat allow predators to achieve high densities and spread into other habitats where they may prey upon rare species (Holt, 1984; West et al., 2019). 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 anthropogenic food subsidies (Marzluff et al., 2001; Newsome et al., 2010), and those capitalizing on anthropogenic food available in heavily-visited sections of protected areas have the potential to spill over into undeveloped areas that provide important habitat for species of conservation concern.

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Several management strategies have been recommended to reduce subsidized predator populations in protected areas, including lethal control of populations and selective removal of problematic individuals (Boarman, 2003; Peery and Henry, 2010). However, these strategies can be challenged by high cost, recolonization by new recruiting individuals, potential for community changes such as mesopredator release when predators are removed, and public opposition to lethal tactics (Goodrich and Buskirk, 1995). An alternative strategy that has been proposed as a potential long-term solution is reducing the availability of anthropogenic food subsidies on the landscape (Peery and Henry, 2010; Hopkins et al., 2014; Walker and Marzluff, 2015). This approach has been used successfully to reduce black bear consumption of anthropogenic foods in Yosemite National Park (Hopkins et al., 2014), but the effectiveness of this management strategy for broader application remains unclear. Furthermore, an understanding of how anthropogenic subsidy reduction affects species ecology, social systems, and density-dependent processes could elucidate the general effectiveness of this strategy.

The Steller's jay (*Cyanocitta stelleri*) is a generalist predator that readily takes advantage of anthropogenic food subsidies (Marzluff and Neatherlin, 2006) and is an important nest predator of the marbled murrelet, a federally threatened seabird (USFWS, 1997; Peery et al., 2004), as well as several songbirds in the Pacific Northwest (Vigallon and Marzluff, 2005). Indeed, one of the most serious threats to the murrelet is low reproductive success, which is largely attributed to high predation rates by corvids such as Steller's jays (Peery et al., 2004; Marzluff and Neatherlin, 2006; Peery and Henry, 2010). Population viability analyses have shown that reducing corvid predation may be the most effective way to recover the marbled murrelet (Peery and Henry, 2010).

Protected areas harbor the majority of remaining nesting habitat for the genetically distinct population of marbled murrelets in central California (Peery et al., 2004; Hall et al., 2009; Halbert and Singer, 2017), and frequent and abundant human visitors and subsequent food subsidies in these areas have been implicated in producing overabundant populations of Steller's jays (Walker and Marzluff, 2015; West et al., 2019). Steller's jay density is high in subsidized campground areas, and jay body condition and fecundity are improved by food subsidies provided by park visitors (West and Peery, 2017), which could result in spillover predation on marbled murrelets (West et al., 2019). In an effort to reduce the effects of jay predation on murrelet populations, California State Parks initiated an intensive visitor education and food management program to reduce food subsidies to Steller's jays. The "Keep it Crumb Clean" campaign (hereafter referred to as "management efforts") began in 2013, and it combines visitor education, improved food management strategies (such as the installation of wildlife-proof food lockers and trash cans and limiting food waste at dishwashing stations in campgrounds), and enforcement of food policies by rangers and other park staff. This initiative provides a unique opportunity to gauge the effectiveness of visitor education and food management as a general strategy to reduce anthropogenic food subsidies within natural areas and to understand the fitness and demographic consequences of reducing food subsidies to generalist predator species.

Here, we aimed to evaluate (1) the effectiveness of management efforts in reducing anthropogenic food subsidies to jays, and (2) the response of jays in subsidized areas to the reduction of previously abundant subsidies at multiple scales including individual behavior, body condition and fecundity, and emergent population effects. We predicted that management efforts would reduce the amount of anthropogenic food in the diets of jays in subsidized areas. We also used a before-after-control-impact design (Green, 1979) to examine population-level consequences of management efforts on jay density and fecundity using surveys in subsidized and unsubsidized areas. We posed two alternative hypotheses about how jay populations would respond to a reduction in food subsidies: fewer subsidies could result in 1) reduced body condition and fecundity of jays that maintained similar density or 2) reduced density of jays that maintained similar body condition and

fecundity. Under the first hypothesis, in addition to reduced body condition and fecundity, we also predicted that management efforts would result in larger home ranges, as jays would need to travel greater distances to find food when fewer subsidies were available (Marzluff and Neatherlin, 2006; Bautista et al., 2017). Under this hypothesis we also predicted stable or increasing overlap of jay home ranges because territoriality may break down if jays relied upon more dispersed, less defensible food resources after management efforts began (Wilson, 2001; Robb et al., 2008). Additionally under this hypothesis, we predicted that jay density in both subsidized and unsubsidized areas would remain stable. Alternatively, under the second hypothesis, in addition to stable body condition and fecundity, we expected home range size to remain stable and the amount of overlap between home ranges to decrease as food resources may be more easily defensible for remaining territorial jays (Robb et al., 2008). We also predicted that jay density in subsidized areas would decrease in response to management while density in unsubsidized areas would remain comparatively stable. Given the limited number of existing assessments and the broad potential applicability of these types of management efforts, this study will help guide conservation initiatives in protected areas that offer opportunities for outdoor recreation and also provide important habitat for species of conservation concern.

2. Materials and methods

2.1. Study area and time periods

We studied a population of Steller's jays in Big Basin Redwoods State Park (Santa Cruz County, California; hereafter Big Basin) to understand the effects of management efforts on their diet, behavior and fitness, and demography. Big Basin includes approximately 4300 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 (Peery et al., 2004; Halbert and Singer, 2017) and also receives over 100,000 campers per year to its almost 200 campsites (California State Parks, 2017). We collected data related to jay diet and fitness during the breeding season in two distinct time periods: "pre-management" from 2010 to 2013, before management began (West and Peery, 2017), and "post-management" from 2017 to 2019, after management had been implemented for three years. We were primarily interested in changes in jay populations in areas where human food subsidies were abundant in the pre-management period (West and Peery, 2017), so we intensively studied jays in seven heavily-used campgrounds in Big Basin (hereafter referred to as "subsidized areas;" Fig. 1). However, we also collected density and fecundity data (see "density and fecundity" below) in unsubsidized forest areas with less human use that were at least 2 km from campgrounds (hereafter referred to as "unsubsidized areas").

2.2. 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. All jay capture and sampling took place within subsidized areas. 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 (Hope, 1980), and we confirmed all sexes later using extracted DNA from blood samples 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; Hope, 1980) and differences in gape coloration and plumage pattern (Pyle, 1997). We weighed jays,

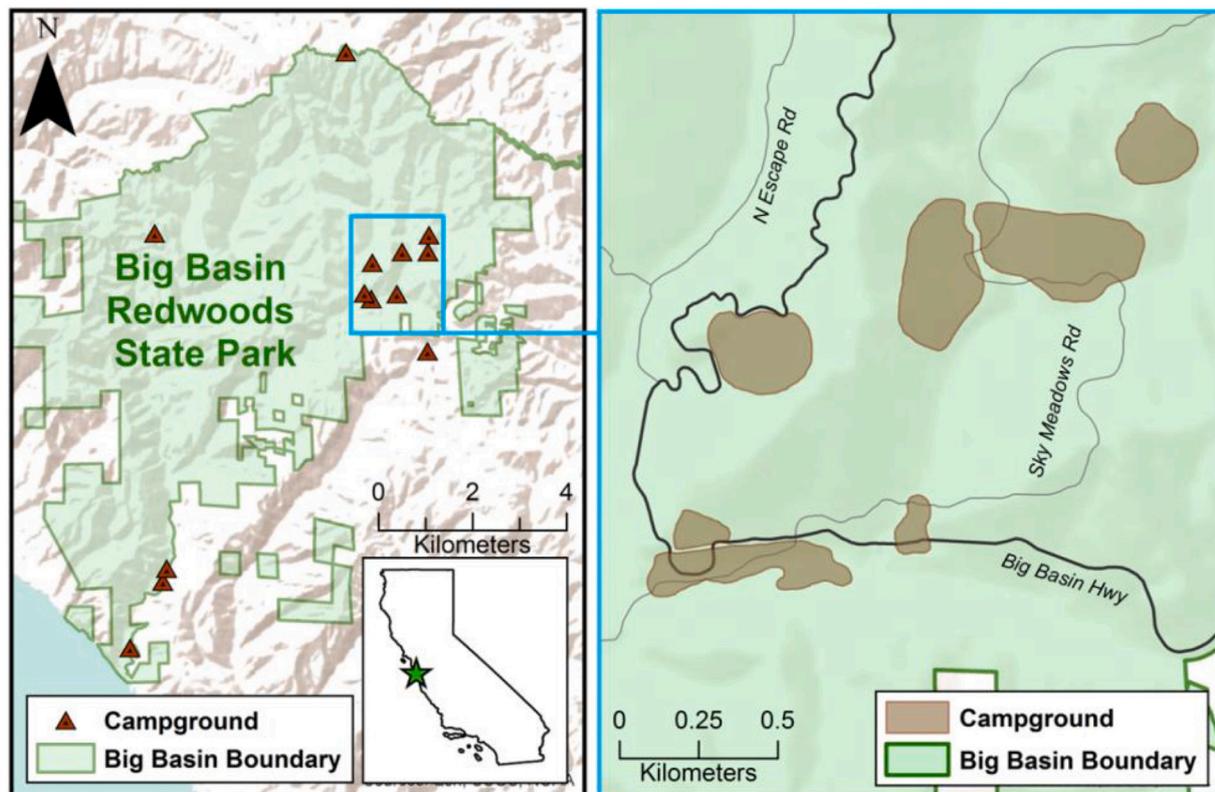


Fig. 1. Map of the study area. The right panel (blue box) shows the campgrounds in which jays were captured. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

measured tarsus length, and collected feather samples from some individuals (see anthropogenic food enrichment and body condition, below). To determine patterns of space use, 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).

2.3. Anthropogenic food consumption

We quantified the consumption of anthropogenic food by Steller's jays living in subsidized areas using stable isotope analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in feathers. To determine if anthropogenic food consumption had changed due to management efforts, we compared (1) the proportion of diet composed of anthropogenic food, and (2) the level of anthropogenic food enrichment between pre- and post-management periods. Because anthropogenically-sourced foods are often made up of corn (a C_4 plant) and corn-based byproducts, 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 also measured $\delta^{15}\text{N}$, which is influenced by a consumer's trophic level with carnivores being more enriched than herbivores in terrestrial landscapes (Kelly, 2000). Analyses of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic ratios have been used effectively to distinguish anthropogenic from natural diet items in this system (West et al., 2016), as well as in other systems (Newsome et al., 2010, 2015a; Hopkins et al., 2014). We clipped approximately 50 mm of a newly grown primary flight feather from each jay captured at the end of the breeding season (early – mid-August) during both time periods. 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 (authors' personal

observations). We also sampled potential diet sources at Big Basin, including invertebrates, berries, acorns, conifer seeds, and anthropogenic foods, approximately every two weeks during the pre-management period (2011–2013). 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 h. We then weighed and sealed approximately 0.5 mg of each feather sample into a tin capsule. Analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was conducted at the University of New Mexico Center for Stable Isotopes 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). We removed one post-management individual from all isotope analyses because it was never seen in subsidized areas after initial capture, and its territory did not coincide with subsidized areas (based on telemetry data).

In order to understand how the overall diet of jays changed after management efforts began, we estimated the proportional contribution of distinct diet sources to adult jay diets using mixing models in the MixSIAR package (version 3.1.11, Stock et al., 2018) in the R statistical environment (R Core Team, 2020). 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 as a diet source 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 estimated to have some 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 Steller's jays: $+3.3\%$ (SD = 0.04) for $\delta^{15}\text{N}$ and $+3.5\%$ (SD = 0.1) for $\delta^{13}\text{C}$ (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 (Table S1). We used management as a fixed effect in our model, which allowed us to estimate diet proportions for each time period separately and calculate the Bayesian 95% credible interval for the difference in proportion of anthropogenic foods in diets among time periods. We specified the generalist ("uninformative") prior and *process x residual* error structure (Stock and Semmens 2016) and ran three Markov chains (length = 1,000,000, burn-in = 500,000, thinning rate = 500), which yielded an effective sample size of 3000 for each time period (calculated with R package coda, Plummer et al., 2006). We examined trace plots, Gelman-Rubin diagnostic values, and the results of the Geweke test for each chain to determine model convergence.

To determine how the level of anthropogenic food enrichment differed due to management efforts, we compared pre- and post-management mean $\delta^{13}\text{C}$ enrichment of adult jays. We first compared $\delta^{13}\text{C}$ enrichment across pre-management years and then across post-management years individually using ANOVA to confirm that $\delta^{13}\text{C}$ enrichment was not different among the years within each period. We then compared $\delta^{13}\text{C}$ enrichment between pre- and post-management periods using a linear mixed model with a random effect for individual. Because sample sizes were equal in the two management periods, we used Satterthwaite's method in the R package lmerTest (Kuznetsova et al., 2017) to obtain a *p*-value for the effect of management. The variance of $\delta^{13}\text{C}$ enrichment was unequal between pre- and post-management periods (determined through visual inspection); however, sample sizes in pre- and post-management periods were equal, and *F*-tests are robust against violation of the homoscedasticity assumption when sample sizes are equal (Blanca et al., 2018). 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 anthropogenic food consumption between pre- and post-management years. Results are presented as mean \pm standard error.

2.4. Home range size and overlap

We used telemetry data to evaluate changes in Steller's jay home range size and in the amount of overlap in home range among individuals living in subsidized areas between pre- and post-management periods. We collected telemetry data from mid-May to early August, a period that largely coincides with the breeding season of the Steller's jay 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. To fully characterize jay home ranges, we varied the time of day we tracked each individual throughout the season and also collected roost locations (between 10 p.m. and 3 a.m.) for each bird 3–4 times per year.

To assess whether jay home range size increased after management efforts began, we calculated the core area and home range size for each jay, which we defined as the 50% and 95% utilization distributions, respectively, using the adehabitatHR package (Calenge, 2006) in the R Statistical Environment (R Core Team, 2020). We were primarily interested in the home range sizes of jays living in subsidized areas, so we used ArcMap 10.3 to identify jays for which $\geq 50\%$ of their core areas overlapped subsidized areas (West et al., 2016; West and Peery, 2017). Because we had a small sample size of females, we only utilized male home range data for this comparison. We log-transformed all home range sizes for normality, and we used a linear mixed model with management as fixed effects and individual as a random effect, and a likelihood ratio test to assess if there was a difference in log-transformed male home range size between pre- and post-management periods.

We also compared overlap between Steller's jay home ranges 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 mean UDOI values and the distribution of UDOI values between the first two years of the study, 2011–2012, and the last year of the study, 2019, as a bookend analysis 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). We compared UDOI between pre- and post-management periods using a Kruskal Wallis test because UDIs were non-normally distributed and variances were not equal in both periods. We also compared mean UDOI values and the distribution of UDOI values from 2017 and 2018 individually to those from 2019 to ensure that utilizing UDOI values from only 2019 did not skew the results from this analysis. Results are presented as mean UDOI \pm standard error.

2.5. Body condition

We assessed the body condition of jays living in subsidized areas in pre- and post-management periods using feather growth bar width. Each feather growth bar consists of a dark band, produced during the day, and a light band, produced at night, that together indicate feather growth over a 24-hour period (Fig. S1). Feather growth is energetically costly; therefore, the width of growth bars is positively correlated with 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 captured in a subsidized area at the end of the breeding season (early to mid-August). In the pre-management period, only 5 rectrices were collected from subsidized areas in Big Basin. However, more rectrices were collected from subsidized areas in Butano State Park, another park located approximately 16 km from Big Basin, where adult jays had similar growth bar width and were similarly enriched in $\delta^{13}\text{C}$ (Table S2; West and Peery, 2017). Therefore, we combined samples from Butano and Big Basin to obtain a larger sample size in the pre-management period. We then scanned or photographed each rectrix 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 width by tarsus length-cubed (an index 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 jays from subsidized areas 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 included random intercepts for year and individual, and we included management as a fixed effect. Results are presented as mean \pm standard error.

2.6. Density and fecundity

To assess the effect of management efforts on the jay population, we used a BACI design to estimate the density of jays in subsidized and unsubsidized areas in the pre- and post-management periods using point count surveys and distance sampling. We conducted monthly 5-min point count surveys at seven points in subsidized areas and seven points in unsubsidized areas during the breeding season (mid-May – mid-August) in pre- and post-management periods. Survey points in subsidized areas were located near the centers of campgrounds, and survey points in unsubsidized areas were located at least 2 km from the

borders of subsidized areas and along roads to facilitate access. 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 (Hope, 1980; Pyle, 1997). 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, 2020). For full distance sampling methods in the pre-management period, see the supplemental methods and West and Peery (2017). In the post-management period, we estimated monthly adult jay density and August juvenile density in subsidized areas for each year in one model, and monthly adult jay density in unsubsidized areas each year in a second model because no juveniles were detected in forest areas in the post-management period. For each model, we evaluated seven potential detection functions using AIC, see supplemental methods for details. We assessed the fit of the top models by examining detection function plots and using a Cramér-von Mises goodness-of-fit test, in which a p -value < 0.05 indicates a poor model fit. After estimating adult densities, we used a two-way ANOVA, with the density estimate for each month and year combination as observations, to test for an interaction effect between management (pre- and post-management) and subsidies (subsidized and unsubsidized).

To evaluate whether management efforts affected jay reproduction, we calculated juvenile to adult ratios for subsidized areas in pre- and post-management periods. 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 estimated density of adults in June (to minimize the effects of post-breeding adult movements) and the estimated density of juveniles in August (which is the peak fledging period) to calculate ratios for both pre- and post-management years (West and Peery, 2017), and we used equations from Peery et al. (2007) to estimate the variance and standard error of the juvenile to adult ratio. Results in all sections are presented as mean \pm standard error, unless otherwise noted. We also estimated the collective number of juvenile jays produced annually in subsidized areas by multiplying estimated juvenile densities by the total combined area of all the subsidized areas in which we worked (42.2 ha; Fig. 1).

3. Results

3.1. Anthropogenic food consumption

We analyzed stable isotopes in feathers from 51 adult Steller's jays both before and after management ($n = 102$ total). Stable isotope analyses of feathers indicated that diets had changed since management efforts began: a larger proportion of the jay diet was made up of anthropogenic foods in the pre- than post-management period (95% credible interval for difference between pre- and post-management: 0.31 to 0.50). Specifically, the mean proportion of anthropogenic foods in the diet of jays in subsidized areas decreased from 0.88 (95% credible interval: 0.73 to 0.97) in the pre-management period to 0.47 (95% credible interval: 0.36 to 0.58) in the post-management period (Fig. 2A). We observed a similar trend in $\delta^{13}\text{C}$ enrichment: jays in the post-management period were 2.4‰ ($\pm 0.27\text{‰}$) less enriched than jays in the pre-management period ($F_{1,99} = 79.87$, $p < 0.001$; Fig. 2B). Additionally, there was no evidence of a difference in $\delta^{13}\text{C}$ enrichment within pre-management years ($F_{3,43} = 0.87$, $p = 0.47$) or within post-management years ($F_{2,45} = 0.28$, $p = 0.76$).

3.2. Home range size and overlap

We calculated home range sizes for 25 male jays in the pre-management period and 42 male jays in the post-management period. There was no difference in home range size between pre-management (6.15 ± 0.79 ha) and post-management (6.35 ± 0.60 ha) periods for jays ($\chi^2 = 0.18$, p -value = 0.67). Before management efforts began, male jays exhibited a high degree of home range overlap (0.65 ± 0.11 ; $n = 35$ pairs), and overlap decreased substantially after management efforts had been implemented (0.10 ± 0.02 ; $n = 46$ pairs; Kruskal Wallis p -value < 0.01 ; Fig. 3). Mean UDOI values in 2017 (0.06 ± 0.01) and 2018 (0.09 ± 0.01) were similar to those from 2019.

3.3. Body condition

We collected body condition data for 54 jays living in subsidized areas ($n = 19$ pre-management, $n = 35$ post-management). Average growth bar width was $4.72 (\pm 0.11)$ and $5.04 (\pm 0.16)$ for jays in pre- and post-management periods, respectively. Our likelihood ratio test indicated that body condition was not affected by management efforts ($\chi^2 = 1.13$, p -value = 0.29).

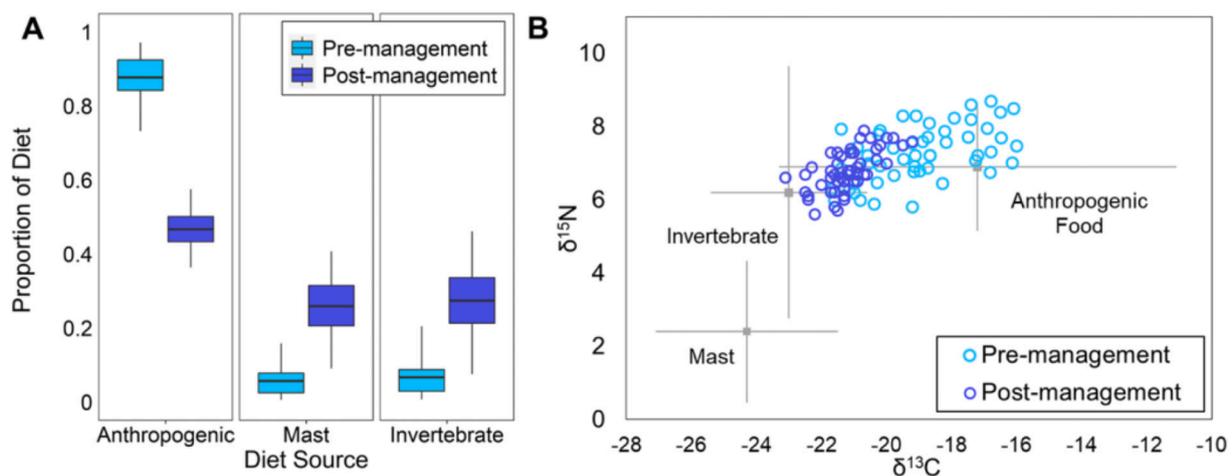


Fig. 2. Jay diet results from stable isotope analysis. (A) Proportional contributions of three diet sources to adult jay diets in pre- and post-management periods. Boxes represent the first and third quartiles, thick lines represent the means, and whiskers represent 95% credible intervals. (B) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope ratios of individual Steller's jay feather samples in pre- and post-management periods. Results are plotted with each potential diet source for reference.

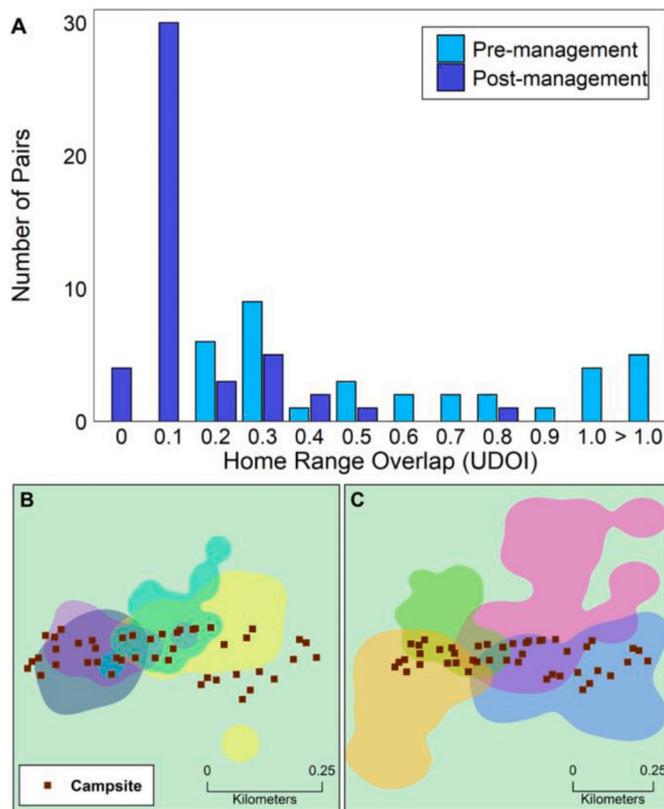


Fig. 3. (A) Results from the Utilization Distribution Overlap Index (UDOI) showing the distribution of home range overlaps between pairs of adult male Steller's jays captured in the same campground in pre- and post-management periods. (B - C) Examples of home ranges for four male Steller's jays in the (B) pre-management and (C) post-management periods. Each differently colored polygon represents the home range (95% utilization distribution) of one jay.

3.4. Density and fecundity

In subsidized areas, the best detection function was the half-normal key function with age as a covariate, and this model fit the data reasonably well (Cramér-von Mises p -value = 0.50). The June density of adult jays in subsidized areas was substantially lower in the post-management period (0.65 ± 0.20 jays/ha) than in the pre-management period (4.33 ± 0.91 jays/ha). In unsubsidized areas, 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). The June density of adult jays in unsubsidized areas was stable between pre-management (0.70 ± 0.22 jays/ha) and post-management (0.58 ± 0.38 jays/ha) periods. Our two-way ANOVA also indicated a significant interaction between management and subsidies ($F_{1,42} = 176.66$, p -value < 0.001, Table S3), which suggests that jay density in subsidized areas declined after management efforts began, while density in unsubsidized areas was relatively stable over the same time period (Fig. 4A).

The August density of juvenile jays in subsidized areas was lower in the post-management period (0.70 ± 0.40 jays/ha) than in the pre-management period (3.3 ± 0.80 jays/ha; Fig. 4A). Juvenile to adult ratios in subsidized areas were slightly higher in the post-management period (1.08 ± 0.33 juveniles/adult) than in the pre-management period (0.76 ± 0.14 juveniles/adult), but the standard errors overlap, indicating that adult jays remaining in subsidized areas after management efforts were implemented had similar fecundity (Fig. 4B). Multiplying estimated juvenile jay densities by the area of subsidized areas indicated that approximately 139 juvenile jays were produced annually in the pre-management period, while only 30 were produced annually in the post-management period.

4. Discussion

Our results indicate that management efforts focused on changing the behavior of visitors to protected areas have reduced anthropogenic food subsidies to Steller's jays, resulting in changes in patterns of space use and density in subsidized areas. Indeed, we observed a substantial reduction in the consumption of anthropogenic foods by jays following the implementation of the visitor education program that led to changes that supported our second hypothesis, specifically that jay density would decrease while body condition and fecundity would remain reasonably stable in subsidized areas. The response of jay populations to management may have been at least partially mediated by the territorial behavior of the jays themselves. The size of jay home ranges did not change between pre- and post-management periods, but the amount of overlap between home ranges decreased, which may suggest that remaining food resources were more easily defensible (Robb et al., 2008) and territorial jays were better able to exclude others from their territories. Despite reduced anthropogenic food consumption, body condition of jays remained similar between pre- and post-management periods, which supports the idea that there was less competition for remaining food resources in the post-management period. It is also possible that anthropogenic foods are of lower nutritional quality than diet sources like mast and arthropods (e.g., Demeyrier et al., 2017; Plaza and Lambertucci, 2017; Townsend et al., 2019), and thus jays in the post-management period maintained high body condition because they ate fewer anthropogenic foods and more mast and arthropods. We note, though, that anthropogenic foods still constituted a significant

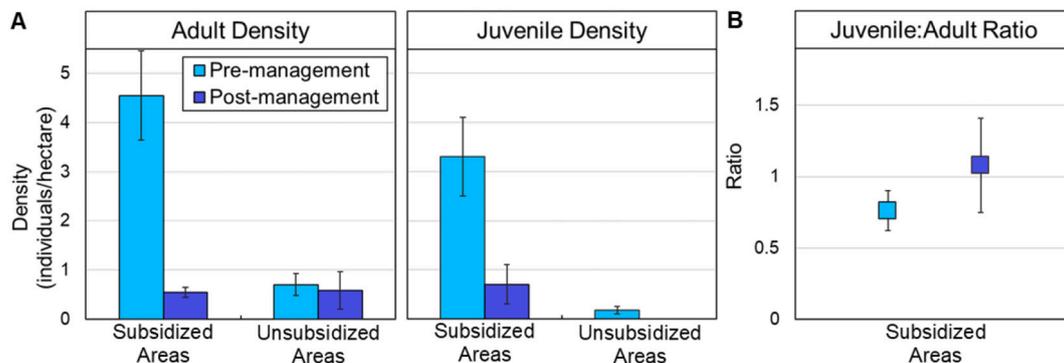


Fig. 4. (A) Jay density estimates from point count surveys in pre- and post-management periods for adults in June and juveniles in August in subsidized and unsubsidized areas. Error bars represent standard errors. No juvenile jays were detected in unsubsidized areas in the post-management period. (B) Estimated juvenile to adult ratios for subsidized areas in pre- and post-management periods.

proportion of jay diets even after management efforts began, indicating that jays remaining in subsidized areas continue to have access to anthropogenic foods despite intensive efforts to eliminate subsidies. Nevertheless, our results provide evidence that management efforts aimed at changing human behavior, when used in tandem with food management and policy enforcement, can constitute a useful conservation tool for reducing the density of subsidized species.

An important limitation of this study is that we could not directly measure the impact of reduced jay densities on murrelet nest success because murrelet nests are difficult and expensive to find and monitor (Peery et al., 2004; Bigger et al., 2006); however, the reduced density of adult and juvenile jays we observed in subsidized areas may lessen the risk of marbled murrelet nest predation by jays. Prior to management efforts, food subsidies at Big Basin were implicated in producing a source population of Steller's jays, where high fecundity resulted in many juvenile jays settling in both subsidized areas and other old-growth areas (West et al., 2019). Importantly, known nest locations of marbled murrelets at Big Basin often coincide with these subsidized areas (Baker et al., 2006), and Steller's jay predation on nests appears to be incidental rather than the result of a specialized search strategy (Vigallon and Marzluff, 2005). Therefore, reducing jay densities in subsidized areas likely lessens the probability of jays coming into contact with and preying on murrelet nests. Further, despite the fact that individual adult fecundity was stable pre- and post-management, there were still significantly fewer juvenile jays being produced overall due to reduced adult densities. Thus, whether subsidized areas in Big Basin still constitute a source population is unclear, but greatly reduced adult and juvenile Steller's jay densities in these areas likely constitute a conservation success for nesting murrelets.

Although we observed reduced densities of Steller's jays in subsidized areas, the long lifespan (Klimkiewicz and Futcher, 1989) and high survival of Steller's jays (West et al., 2019) begs the question: where did all the jays go? Maintenance of fairly high body condition of jays in subsidized areas and the fact that jays are generalist omnivores capable of exploiting a wide variety of foods (Walker et al., 2020) make it unlikely that any jays died of starvation due to reduced availability of anthropogenic subsidies. Stable densities in unsubsidized areas seem to demonstrate that jays did not simply move away from subsidized areas and into other old-growth areas of the park. The remaining possibilities are that jays moved into other, unsurveyed habitats within Big Basin, such as young forest and chaparral, or that jays left Big Basin altogether. Indeed, West et al. (2019) found that a large proportion of radio-tagged juveniles and even a small proportion of adults dispersed out of Big Basin and into residential areas, where there are presumably food subsidies available year-round in the form of bird feeders and human refuse. While more work would be necessary to distinguish between these possibilities, we believe the most likely scenario is some combination of all three processes. Thus, the potential for jays to return to campground areas if subsidies become abundant again underscores the importance of continuing visitor education and enforcement initiatives and maintaining infrastructure, such as wildlife-proof food lockers, to ensure that anthropogenic food subsidy availability remains low for jays and other wildlife.

There are two caveats to our study; first, we did not directly measure the availability of anthropogenic food to jays and thus we assume that reduced consumption of anthropogenic foods reflects an actual reduction in availability of this resource to jays. Observations of management efforts and visitor behavior at Big Basin support this assumption, and it seems unlikely that jay food preferences would change when they were able to attain high body condition and fecundity by eating anthropogenic foods (West and Peery, 2017; West et al., 2019). The second caveat is that we did not measure body condition, home ranges, or diets of jays in unsubsidized areas because capturing jays in areas outside of campgrounds is logistically and financially challenging and may still result in small sample sizes (West et al., 2016). This raises the crucial question of whether the changes we observed in jay space use and diet in subsidized

areas were due to management efforts or another factor that we did not measure. To our knowledge, no significant changes occurred related to levels of human use or habitat conditions in either subsidized or unsubsidized areas during the study period. However, our study area experienced an unusually severe drought during the jay breeding seasons from 2012 to 2015 (Griffin and Anchukaitis, 2014; Tortajada et al., 2017), which 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 unsubsidized areas, as those utilizing subsidized areas may be buffered from drought effects by the predictable availability of anthropogenic food (Shochat et al., 2006). This is the opposite of the pattern we observed – jay density in subsidized areas decreased over time, while density in unsubsidized forest areas was stable. Second, drought conditions may have caused jays in subsidized areas to rely more on anthropogenic food resources, resulting in the high $\delta^{13}\text{C}$ enrichment we observed in the pre-management period. However, we collected isotope data from two drought years and two average 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 conducted in the Sierra Nevada, California (~300 km from our study site) concurrently with our study found that Steller's jay abundance was not affected by high ambient 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, and, thus, management efforts are the most likely explanation for the changes we documented.

Collectively, our study provides evidence that visitor education can be part of a broader solution to support protected areas' dual mandate to provide the public with recreational opportunities while also protecting biodiversity. Our findings have broad applicability outside our study system: utilization of anthropogenic food subsidies by predators is a global phenomenon that has consequences for the behavior, fitness, and abundance of predators, as well as for the conservation of at-risk species and human-wildlife conflict (Newsome et al., 2015b). Generally, human behaviors that stem from lack of information or lack of outdoor skills, such as intentionally or unintentionally feeding wildlife, are the most amenable to change in response to education programs (Manning, 2003); however, 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). Indeed, even changing intentions often may not engender genuine behavior change (Webb and Sheeran, 2006). Instead, combining education and enforcement, as well as making compliance with policies easier (e.g., by providing wildlife-proof food lockers) has been shown to be more effective at changing problematic human behaviors (Duncan and Martin, 2002; Manning, 2003; Baruch-Mordo et al., 2011). 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 people to feel connected to nature and personally invested in its conservation (Pyle, 2003; Kareiva, 2008; Balmford et al., 2009). Therefore, effective management of protected areas depends on multi-faceted strategies to make species protection and human recreation more compatible.

Ethical considerations

All appropriate guidelines for humane and ethical use of animals in research were followed, and research was conducted under IACUC protocol A005411-R01-A01 and scientific collection permit SC-13714.

CRedit authorship contribution statement

All authors contributed to the conceptualization of the study, E.H. West and K. Brunk collected the field data, E.H. West and K. Brunk conducted analyses, K. Brunk wrote the original draft, and all authors contributed substantially to reviewing and editing the manuscript.

Declaration of competing interest

The funders of this study played no role in the study design, analyses, interpretation of results, or writing of this manuscript. The authors certify there are no known conflicts of interest associated with this publication.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109081>.

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