Marbled murrelet conservation and Steller's jay ecology and management
in coastal redwood forests

by

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Dedication

To Milo, Charles, Lenny, and Karl. You know what you did.

Table of Contents

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MARBLED MURRELET CONSERVATION AND STELLER'S JAY ECOLOGY AND

MANAGEMENT IN COASTAL REDWOOD FORESTS

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Under the supervision of Professor M. Zachariah Peery and Professor Anna Pidgeon

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Dissertation Abstract

The Marbled Murrelet (*Brachyramphus marmoratus*) is a small, federally threatened seabird native to the western coast of North America that ranges from the Aleutians to central California. Murrelets are old-growth forest specialists during the breeding portion of their life history, and historic loss of old-growth forest throughout much of the murrelet's range has resulted in greatly reduced murrelet populations, especially in the southern-most extent of the murrelet's range. In central California, approximately 85% of old-growth forests have been lost due to timber harvest of economically valuable old-growth trees. Much of the remaining old-growth forest is either on private property, where murrelets are at the mercy of local forest management strategies, or protected in national and state parks. Additionally, in the fragmented old-growth that remains, murrelets often experience elevated rates of nest predation, largely by corvids such as Common Ravens (*Corvus corax*) and Steller's Jays (*Cyanocitta stelleri*). Indeed, low reproductive success has been implicated in the ongoing decline of murrelet populations, even though much of their remaining nesting habitat has been protected. Habitat protected for murrelet breeding, such as state parks, is also often important for human recreation. Human use of these protected areas has led to increased densities of corvids that take advantage of readily available human food subsidies. Abundant human food subsidies potentially put murrelets at greater risk of nest predation and also affect the ecology and behavior of

corvids. The first two-thirds of this dissertation examines the effectiveness of conservation measures to protect nesting habitat for marbled murrelets and to control populations of overabundant murrelet nest predators. The last third focuses on understanding how human food subsidies affect the behavioral ecology of subsidized nest predators.

In my first chapter, I assess the effectiveness of a Habitat Conservation Plan (HCP) that was created to protect important nesting habitat for the Marbled Murrelet on private lands owned by a timber company in Humboldt County, California. I compared trends in occupancy and abundance over 17 years between private areas protected by the Habitat Conservation Plan and publicly-owned reference areas. Old-growth forests were smaller and more fragmented in private HCP areas than public reference areas, likely contributing to the consistently lower occupancy and abundance we found on private land. However, trends in occupancy were stable and similar between private HCP and public reference areas. Additionally, I found that inland murrelet counts declined at a similar rate between private HCP and public reference areas over time, potentially indicating a reduction in breeding effort over time. Thus, I found that habitat protected under the HCP was not of the same high quality as habitat protected in public reference areas, but the HCP apparently did not exacerbate the decline of murrelet populations. This work provides an essential assessment of habitat conservation efforts for murrelets on private land, and it highlights the importance of including reference areas when assessing conservation policies. The limitations of this study also emphasize the need for more rigorous experimental designs and careful assessments of conservation policies going forward.

In my second chapter, I evaluate the effects a visitor education and trash management campaign had on Steller's jay populations living in highly human-subsidized campground areas nestled in the old growth forest of central California where jays have the potential to predate

marbled murrelet nests. I compared Steller's jay populations in two time periods, pre-management and post-management, to understand how management had affected human food consumption, body condition, space use, density, and fecundity. I found that management successfully reduced the amount of human food consumed by Steller's jays and the density of Steller's jays in subsidized campground areas. While overlap between jay home ranges was substantially reduced by management, jays remaining in subsidized campground areas maintained similar home range sizes and high individual body condition and fecundity. Overall, jay density and collective reproductive output declined substantially after management efforts were implemented, which likely reduces the risk of predation of murrelet eggs and nestlings. Human food subsidies are a global phenomenon that impact almost every aspect of species' ecology and human-wildlife interactions. This work indicates that human education and trash management can effectively reduce human food subsidies to wildlife and ultimately make wildlife protection and human recreation in protected areas more compatible.

In my third chapter, I dig more deeply into the effects of human food subsidies on Steller's jay ecology and behavior. Territorial species are often predicted to under-match local food resources, meaning that individuals in high-quality habitat achieve higher fitness than those in low-quality habitat. In this chapter, I asked how Steller's jay populations in subsidized campground areas are able to under-match locally abundant human food subsidies, despite the presence of mechanisms like high density, compressed territories, and frequent agonistic behaviors that should decrease individual fitness and lead to resource matching. I examined the distribution of fitness among individuals in high-quality, subsidized habitat, by categorizing jays into dominance classes and characterizing individual consumption of human food, body condition, fecundity, and core area size and spatial distribution. I found that jays of all dominance classes achieved similar fitness, as measured by body condition and fecundity. However, the most dominant individuals maintained

smaller core areas that overlapped with subsidized campground areas more. Thus, it appears that dominant jays do not exclude subordinates from human food subsidies, but they may monopolize space in subsidized areas and thereby prevent population densities from increasing to the point of matching available human food subsidies. This work suggests that abundant anthropogenic foods have the potential to de-couple dominance from fitness and that incomplete exclusion of subordinate individuals may be a common mechanism underpinning high densities of synanthropic species in subsidized habitats.

Overall, the work in this dissertation provides a few of the missing puzzle pieces to help form a more cohesive picture of murrelet conservation and management, but I also believe this work has both basic and applied implications beyond murrelets, jays, and coastal redwoods. The first chapter is a useful case study for the strengths and limitations of assessing conservation policies. Conservation strategies are more defensible and the expenditure of conservation dollars more justifiable when we rigorously assess the effectiveness of conservation measures and work to improve them over time. The second chapter demonstrates the utility of a simple but effective conservation technique (i.e., visitor education) than could be widely applied within and outside of protected areas to reduce human-wildlife conflict and to limit the impact of highly dense populations of subsidized predators on other species. Finally, the third chapter integrates classical ideas about habitat selection into a highly human-modified environment and provides useful insights into how human food subsidies can shape ecology from the individual to the population level. As human impacts continue to expand across the globe, understanding how classic ecological theory applies, or does not apply, to human-dominated landscapes will be valuable as well as fascinating.

"Instructions for living a life:

Pay attention.

Be astonished.

Tell about it."

— Mary Oliver

Chapter 1: Assessing the effectiveness of a forest Habitat Conservation Plan for a threatened seabird, the Marbled Murrelet

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Abstract

Habitat Conservation Plans (HCPs) commonly facilitate habitat conservation on private land in the United States, yet the effectiveness of individual HCPs is rarely evaluated. Here, we assess the effectiveness of a high-profile HCP created by a lumber company to protect old-growth forest used for breeding by Marbled Murrelets (*Brachyramphus marmoratus*) on private land. We used 17 years of HCP-monitoring data to compare trends in murrelet occupancy and inland counts between private HCP areas and public reference areas over time. Based on occupancy models applied to audio-visual survey data, average occupancy was higher in public reference areas (0.85; 85% CI: 0.79-0.90) than in private HCP areas (0.46; 85% CI: 0.38-0.54). Numerically, trends in occupancy were slightly positive in public areas ($\hat{\bar{\lambda}}$=1.01; 85% CI: 0.94-1.08) and slightly negative in private areas ($\hat{\bar{\lambda}}$=0.97; 85% CI: 0.87-1.06), but confidence intervals did not preclude stable occupancy on both ownerships. Based on generalized linear mixed models applied to inland radar survey data, murrelet counts in private HCP areas (LS mean=8.7; 85% CI: 6.2-12.2) were lower than those in public reference areas (LS mean=14.8; 85% CI: 10.1-21.7), but confidence intervals overlapped. Murrelet counts declined by 12-17% annually on both ownerships over the study period based on the top model, but a closely competing interactive model suggested more rapid declines in public reference (14-20%) than in private HCP (10-15%) areas. Both models indicated that murrelet counts were negatively related to sea surface temperature, suggesting that warm ocean conditions negatively affect murrelet breeding effort. Collectively, these results suggest that while HCP habitat may be lower quality than public reference areas, the HCP has likely not exacerbated ongoing declines of murrelets in the region. This work highlights the importance of including reference areas when evaluating conservation policies.

Introduction

There is growing recognition of the need to empirically evaluate the effectiveness of conservation policies (Ferraro and Pattanayak 2006, Fisher et al. 2013, Baylis et al. 2016, Ribas et al. 2020). Even common biodiversity conservation policies are rarely evaluated with the same rigor as ecological hypotheses, leading to uncertainty about the effectiveness of these measures and conservation investments (Ferraro and Pattanayak 2006).One common conservation tool in the United States is the Habitat Conservation Plan (HCP) policy under the Endangered Species Act (ESA). The ESA protects habitat for listed threatened and endangered species on both federal and non-federal land, including land owned by private citizens, which is where species are most vulnerable to habitat loss (Eichenwald et al. 2020). However, because restrictions on land use imposed by the ESA can promote perverse incentives for private landowners, such as the pre-emptive removal of habitat or listed species from private land (Wilcove et al. 1996, Brook et al. 2003, Lueck and Michael 2003), the HCP policy was developed to promote partnerships between private landowners and the federal government to address the conservation of listed species. Incidental take permits issued with approved HCPs allow development and other land management activities to continue if threats to listed species are minimized and mitigated to the maximum extent practicable, for example by conserving a portion of important habitat or seasonally restricting activities that could impact the covered species. Because of the flexibility they provide to landowners, HCPs have become a common tool for managing listed species on non-federal land in the United States, with more than 1,000 approved HCPs covering more than 18.5 million hectares (USFWS 2016). Despite the frequent application of this policy, assessments of the effectiveness of individual plans are rare (Shilling 1997). Thus, whether HCPs constitute an effective mechanism for increasing landowner flexibility without impacting the viability of listed species remains a critical, unanswered question (Harding et al. 2001, Schwartz 2008).

Understanding the effectiveness of individual HCPs is challenging for at least two reasons. First, many HCPs lack adequate monitoring programs (Harding et al. 2001), and even when monitoring has been performed, few HCPs have been implemented for a sufficient duration to detect changes in populations, which can take decades (Kareiva et al. 1999). Second, the geographic ranges of listed species usually exceed the area governed by individual HCPs such that listed species are affected by broad-scale environmental factors (e.g., climate change) beyond the activities allowed under the HCP. Further, in some cases, population declines of listed species may be an *a priori* expectation because of persistent, large-scale environmental stressors. Therefore, rather than only monitoring populations within HCP areas, also monitoring populations within a control or reference area that experiences similar broad-scale environmental conditions would allow for more rigorous evaluations of HCP impacts on species.

The Marbled Murrelet (*Brachyramphus marmoratus*) is a federally threatened seabird that, in the conterminous U.S., nests almost exclusively in old-growth forests (Hamer and Nelson 1995) and forages in the nearshore waters of the Pacific Ocean (Raphael et al. 2015). Murrelet breeding and abundance are negatively affected by fragmentation and loss of breeding habitat resulting from management activities like harvest of economically-valuable old-growth trees (Raphael et al. 2002a, Zharikov et al. 2007, Betts et al. 2020). Additionally, murrelet populations are affected by a myriad of broad-scale environmental processes. For example, higher murrelet reproductive success has been linked to cooler ocean conditions and concomitant high availability of prey, such as krill and juvenile rockfish (Meyer et al. 2002, Becker et al. 2007, Raphael et al. 2015). Loss of nesting habitat due to timber harvest in old-growth forests and declines in prey abundance at sea have both been implicated in murrelet population declines (Carter and Erickson 1992, Becker and Beissinger 2006, Betts et al. 2020). Therefore, the effects of broad-scale oceanic factors on murrelets can complicate

the assessment of local breeding habitat management and conservation strategies, such as those included in an HCP, if reference areas are not also monitored.

Here, we utilized a 17-year dataset of Marbled Murrelet inland surveys to evaluate the effectiveness of private conservation areas created as part of a high-profile HCP to protect murrelet breeding habitat on private land in northwestern California. To assess this HCP, we utilized murrelet occupancy and inland count data collected from HCP conservation areas, as well as nearby protected public areas that were not part of the HCP. These data were collected as part of an effectiveness monitoring program implemented with the HCP. Because murrelets in public and private areas were affected by similar broad-scale oceanic factors, we used these protected public areas as a baseline to evaluate the utility of the HCP conservation areas for protecting murrelet breeding habitat. Importantly, protected public areas were larger and had higher occupancy and inland counts than HCP conservation areas at the inception of the HCP (see Bigger et al. 2006a) and, thus, here we compare *trends* in murrelet occupancy and inland counts between HCP sites and protected public sites as our metric to assess the effectiveness of the HCP. We predicted that if the HCP conservation areas were effective, then trends in murrelet occupancy and counts would not be different between private HCP areas and public reference areas, or trends in private HCP areas would be more positive. This monitoring program provides a key opportunity to compare murrelet inland habitat use between areas characterized primarily by differences in forest management and protection afforded by an HCP. By evaluating a prominent HCP for Marbled Murrelets, we aim to provide insights into the effectiveness of HCPs as a conservation policy, and an example framework for more rigorous evaluations of HCPs in the future.

Methods

Study Area

The Pacific Lumber Company, located in northwestern California, completed and implemented a 200,000-acre, multi-species HCP that includes Marbled Murrelets in 1999. Prior to the HCP, extensive harvest of old-growth forest took place beginning in the late 1800s. This HCP, and the subsequent transfer of 3,024 hectares of old-growth forest known as the Headwaters Forest Grove to the federal government, helped resolve a highly public, decade-long forest management controversy. After the transfer, two of the few large remaining tracts of unharvested old-growth forest in northern California were officially protected within the newly created Headwaters Forest Reserve (managed by the Bureau of Land Management) and the already preserved Humboldt Redwoods State Park (managed by the California Dept. of Parks and Recreation). Additionally, on private land subject to the HCP, six of the remaining stands of old-growth forest (~2,671 hectares total) were designated as Marbled Murrelet Conservation Areas (MMCAs), in which timber harvesting was prohibited except to accelerate murrelet habitat development (Figure 1). Forests outside of the MMCAs, including small amounts of potentially occupied murrelet nesting habitat, remained subject to timber management activities. In 2008, ownership of the land subject to the HCP was transferred to the Humboldt Redwood Company, which manages the property, no longer harvests any old-growth trees or stands, and continues to fulfill the requirements of the HCP. Forests on both public and private land experienced a similar history of mixed use and are composed mainly of coastal redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*) in the overstory and tanoak (*Notholithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), salal (*Gaultheria shallon*), and western sword fern (*Polystichum munitum*) in the understory. Habitat within both ownerships is characterized by a mosaic of forest types, including varying degrees of

unharvested old-growth and partially harvested (residual) old-growth, as well as second-growth forest.

We used two protected public areas, Headwaters Forest Reserve (3,024 hectares) and Humboldt Redwoods State Park (21,448 hectares; hereafter collectively referred to as "public"; Figure 1), as reference sites to compare trends in murrelet occupancy and inland counts between non-HCP and HCP areas. Within HCP areas, we conducted murrelet surveys at four MMCA sites: Bell-Lawrence MMCA (193 hectares), Shaw-Gift MMCA (531 hectares), Allen Creek MMCA (928 hectares), and Cooper Mill Creek MMCA (308 hectares; hereafter collectively referred to as "private"; Figure 1). We note that the MMCAs were the only areas monitored for murrelet occupancy and abundance on private land; no murrelet monitoring surveys took place on HCP land outside of the MMCAs. Thus, we compare murrelet trends on public reference sites to those on MMCAs, rather than broadly to all of the land subject to the HCP. This is a valuable comparison, though, because the creation of MMCAs was the focal strategy for murrelet protection within the HCP. While no timber harvest took place within the MMCAs during the life of the HCP, it is possible that historic (prior to 1999) selective harvesting of large, old trees on private land or timber harvest at the edges of the MMCAs could result in delayed murrelet abandonment of private HCP areas given this species' long life span and presumed nest site fidelity (Meyer et al. 2002). Additionally, the MMCAs constitute smaller and less-contiguous old-growth habitat that may be less suitable for murrelet breeding. Therefore, we expected to see more negative trends in occupancy dynamics and inland counts in the MMCAs than in public reference areas if the MMCAs, and thus the HCP, were not effective for promoting continued murrelet breeding on private land.

Survey Methods

We used two independent survey methods to monitor murrelet use of inland breeding habitats annually. Inland audio-visual surveys yield information about the presence and potential breeding status of murrelets, and radar surveys provide information about the abundance of murrelets flying inland and can be used as an index of the size of the potential breeding population (Peery et al. 2004a). We used audio-visual surveys from 2000-2016 to determine trends in murrelet occupancy dynamics and radar surveys from 2002-2018 to assess trends in inland murrelet counts. Audio-visual and radar surveys on both ownerships each year were conducted by the same set of surveyors, all of whom were trained and evaluated annually in Marbled Murrelet survey techniques, as suggested by Pacific Seabird Group protocols.

Audio-visual Surveys

Marbled Murrelets were monitored from 2000-2016 using audio-visual surveys at 33 survey stations ($n = 27$ private, $n = 6$ public; Figure 1). Survey stations were placed in good murrelet habitat and positioned to maximize surveyors' ability to see murrelets because occupancy was determined based on visual observations. Survey station placement and audio-visual surveys were conducted according to the standard protocol for monitoring this species at inland locations (Ralph et al. 1994, Pacific Seabird Group 1998). While the Marbled Murrelet monitoring protocol was revised in 2003, per the requirement of the HCP, Humboldt Redwood Company continued to monitor murrelets according to the protocol that was in place when monitoring began to ensure consistency in monitoring throughout the study period. Surveys took place during the breeding season, between April 15 and August 5 each year. Station visits were spread throughout the nesting season such that visits to an individual survey station were at least six and no more than thirty days apart, and at least one survey took place in the last two weeks of July or the first week of August. Surveys began 45 minutes

before and continued until 75 minutes after sunrise. During each survey, surveyors considered stations to be unoccupied when no murrelets were detected and occupied when they observed certain behaviors such as circling above the canopy, flying below the canopy, or landing on a branch. While these behaviors are not necessarily indicative of a current nesting attempt, they are considered indicators of habitat that is important for breeding (Bahn 1998, Pacific Seabird Group 1998). Because it is unclear whether murrelets observed flying over a station but not circling (i.e. flyovers) are utilizing habitat near the station, we considered stations where only flyovers were recorded as unoccupied. Surveyors visited each survey station five times per season or until an occupied behavior was observed, after which no further surveys were conducted.

Audio-visual survey analysis.

Occupancy and Detection Covariates. We used two categorical station-level covariates to describe habitat in our study area. *Ownership* was a categorical covariate indicating whether a survey station was located on private (HCP) or public (non-HCP) land, which we used to test the effect of the HCP conservation areas on occupancy dynamics. *Ownership* encompasses many HCP-driven factors that could be related to murrelet occupancy, including habitat differences between public and private land such as amount of old-growth, age of trees, availability of nesting platforms, amount of edge habitat, and patch area. *Habitat* was a categorical covariate that indicated whether a survey station was located within 200-m of unharvested old-growth forest regardless of ownership. Because over half of the private HCP survey stations were located within 200-m of unharvested old-growth (Table S2), we used *habitat* to test whether proximity to old-growth alone, and not ownership per se, was important for determining murrelet occupancy dynamics. We also tested both *ownership* and *habitat* as potential influences on surveyor's ability to detect murrelets because public stations generally had larger tracts of old-growth forest and murrelet detectability has been shown to be positively

correlated with amount of old-growth near a survey station due to changes in murrelet flight behavior near old-growth, like flying more slowly and vocalizing more as they prospect for or maintain a bond with a nest site (Bigger et al 2006b).

We used survey-level covariates to describe factors that may have affected surveyors' ability to detect murrelets during surveys. We considered inclusion of proportion cloud cover (*cloudcov*) and precipitation (*precip*) in detection models because both have been shown to influence murrelet detection during surveys (Naslund and O'Donnell 1995, Bahn 1998). Cloud cover and precipitation data were collected at the beginning of all audio-visual surveys, as most murrelets move inland before sunrise, corresponding with the beginning of the survey period (Rodway et al. 1993, Naslund and O'Donnell 1995, Burger 2001). Cloud cover was estimated as the proportion of the sky obscured by clouds, and precipitation was categorized as none, fog, drizzle, or light rain. We also included quadratic day of year (*DoY*) as a temporal covariate affecting detection probability because we expected that murrelet detections would likely peak late in the breeding season as murrelets flew to and from the nest to provision nestlings and then decline (Naslund 1993, Rodway et al. 1993). Day of year variables were centered and standardized before inclusion. To account for heterogeneity in visibility from each survey station, we asked murrelet surveyors to rank each survey station as low, medium, or high visibility, and we included this as a station-level covariate in detection models (*visibility*). Stations with low visibility were often located in the center of a stand and had little view of the sky, while stations with high visibility were located on a ridge, road or other opening and had a good view of a large swath of sky (S. Chinnici, *pers. observation*). Finally, we also included a continuous station-level covariate for the proportion of forest that was old-growth within 1000-m radius of each survey station (*PropOG*) because murrelet detectability has been shown to be positively correlated with the amount of old-growth forest near survey stations due to changes in murrelet flight behavior, like flying more slowly and vocalizing more near large tracts of old-growth (Bigger et al.

2006b). We used ArcMap 10.3 and Humboldt Redwood Company forest cover maps created in 2002 to delineate old-growth, which we defined as forest that was classified as either unharvested old-growth or residual old-growth with at least 50% canopy cover, and to calculate the proportion of old-growth for each survey station.

Model selection. We used dynamic occupancy modeling in program PRESENCE 2.13.6 to characterize murrelet occupancy dynamics. Dynamic occupancy modeling estimates survey station occupancy over multiple primary survey periods while correcting observations for imperfect detection by using detection/non-detection data from repeated sampling within secondary survey periods (Mackenzie et al. 2003). Our occupancy models estimated three parameters: ψ_1 was the probability of a station being occupied in the first year of surveys (initial occupancy), γ_t was the probability of an unoccupied site being colonized in year t (colonization), and ε_t was the probability of an occupied site becoming unoccupied in year t (temporary or local extinction; Mackenzie et al. 2003). We note again that for murrelets, colonization and local extinction represent changes in occupied behaviors, not necessarily whether stations were used for breeding. Our primary sampling periods, t, were breeding seasons (i.e. April 15 to August 5), and our secondary sampling periods were approximately three-week windows within each breeding season (April 15-May 6; May 7-May 29; May 30-June 20; June 21-July 13; and July 14-August 5). If a site was visited multiple times within a secondary sampling period, we randomly selected one survey to include in analysis. We also parameterized detection probability as in MacKenzie et al. 2003, where p represented the probability of detecting murrelet occupancy, given that a site was occupied.

We first chose the best modeling structure for detection probability (p). To do so, we assessed the effect of combinations of several covariates (*ownership*, *habitat*, *DoY*, *precip*, *cloudcov*, *visibility*, *PropOG*) on within-year detection, and then assessed temporal variation in detection

probability among years by comparing a null model with no time trend, a model with an annual

effect (*year*), a model with a linear time trend (*T*), and a model with a logarithmic time trend (*lnT*).

We examined several different possible time trends because re-growth of trees near survey stations

could impact visibility and result in decreasing detection probabilities over time, but if a trend was

present, it could be linear or non-linear. When evaluating competing detection models, we allowed

colonization (γ_t) and local extinction (ε_t) to vary by year, and we allowed initial occupancy (ψ_1) to vary

by ownership. We ranked models using Akaike's Information Criterion (AIC) and AIC model

weights (Burnam and Anderson 2002).

To directly compare occupancy trends between private HCP areas and public reference

areas, we used the best detection model and fit one model for each ownership using year-specific

colonization and local extinction. We used these models to obtain derived estimates of annual

occupancy (ψ_t) and annual rate of change in occupancy (λ_t) for each ownership (Mackenzie et al.

2003, MacKenzie et al. 2018). We then calculated the geometric mean of the rate of change in

occupancy ($\hat{\bar{\lambda}}$) for each ownership, where $\hat{\bar{\lambda}} = 1$ indicates stable occupancy over the 16-year survey

period and $\hat{\bar{\lambda}} < 1$ indicates a decline in occupancy over time (Jones et al. 2018). We calculated

variance for $\hat{\bar{\lambda}}$ using the delta method (Powell 2007).

Lastly, to characterize differences in occupancy dynamics between public reference stations

and private HCP stations, we examined the effects of temporal and habitat covariates on

colonization (γ_t) and local extinction (ε_t), while using the best detection model. Because public

stations were known to have higher occupancy when the HCP was implemented (Bigger et al.

2006a), we allowed initial occupancy (ψ_1) to vary by ownership for all models. We tested (1) a null

model with no covariate effects on colonization or local extinction; (2) models with *ownership* or

habitat effects on colonization, local extinction, or both; (3) models with *ownership* or *habitat* and an

annual (*year*) effect on colonization, local extinction, or both; and (4) additive and interactive effects between time trends (*T*, *lnT*) and *ownership* or *habitat* effects on colonization, local extinction, or both (37 models total; Table S1). If an interactive model between a time trend and ownership was well-supported, it would indicate that differences exist in occupancy trends between ownerships. We used models with *habitat* to understand if proximity to old-growth, rather than ownership per se, was the important factor determining trends in colonization and local extinction. We again ranked models using Akaike's Information Criterion (AIC) and AIC model weights (*w*; Burnam and Anderson 2002), and we calculated variances of dynamic occupancy probabilities and covariate effects using the delta method (Powell 2007). After selecting the best model, we assessed goodness of-fit using parametric bootstrapping (100 simulations) within program PRESENCE, followed by an analysis of deviance to assess the amount of variation in occupancy explained by the covariates in the best-supported model. Analysis of deviance compares the difference in deviance between a constant (null) model and the model of interest to the difference in deviance explained by the constant (null) model and a global (most complex) model, and hence provides an estimate of r^2 (Skalski et al. 1993, Tempel et al. 2016). The constant model for our analysis of deviance included the best detection structure and only intercepts for initial occupancy (ψ_1), colonization (γ_t), and local extinction (ϵ_t). The global model included the habitat covariates from the top-ranked model and was fully time varying for colonization and local extinction, while using the same structure for detection as the top-ranked model (Tempel et al. 2016, Jones et al. 2018).

We are confident that our study meets the assumptions of these types of models. In particular, we assumed 1) the true occupancy state of each survey station did not change within a breeding season because occupied behaviors are strong indicators of breeding behavior, 2) the detection histories observed at stations were independent of one another because occupied behaviors are a local phenomenon, and 3) there were no false detections of murrelets during surveys

because personnel were well-trained in conducting murrelet surveys. We report all results with 85% confidence intervals to ensure compatibility with AIC model selection (Arnold 2010), and we report model effect sizes using odds ratios (Jones and Peery 2019).

Radar Surveys

We used radar surveys from 2002-2018 to assess inland murrelet counts at 14 survey stations ($n = 8$ private, $n = 6$ public; Figure 1). Radar survey stations were located within forest stands or along riparian corridors that led to potential breeding areas, as murrelets are known to fly through corridors to reach inland breeding sites (Nelson and Hamer 1995). Radar stations were positioned such that the radar unit had unobstructed scanning areas of the forest stands or flyways being surveyed. Radar surveys were conducted from 75 minutes prior to 75 minutes after sunrise. Each station was surveyed 4 times per year between April 15 and August 5 from 2002 to 2018, except in 2009 which had a reduced sampling effort and was excluded from this study. Repeat visits to a radar station were at least 9 days apart. Radar surveyors utilized a Furuno® FR-1510 Mark-3 high-performance X-band radar that transmits 9410 ± 30 MHz with a peak power output of 12 kW. This radar used a 2-meter antenna mounted onto a pickup truck approximately 3.5m above ground-level. The antenna was set to rotate 24 times per minute and to scan a circular area with a 1.5-kilometer radius. Pulse length was set at 0.07 µsec. During each survey, the total number of murrelet detections was counted. Radar targets traveling at least 64-kilometers per hour and leaving an echo trail of ≥3 blips after 4 antenna sweeps were classified as murrelets (Cooper et al. 2001). Because single and small groups of murrelets flying within a few meters of each other appear as a single echo on a radar screen (Burger 1997), each echo trail was counted as a single detection. An overlap in radar ranges for some survey stations could have led to some murrelets being double-counted when

those stations were surveyed the same morning, so to prevent double-counting, we randomly

removed one survey on mornings when overlapping stations were surveyed simultaneously.

Radar survey analysis. We analyzed murrelet counts obtained from radar surveys with a

generalized linear mixed model (GLMM) in the 'lme4' package (Bates et al. 2015) in the R statistical

environment (R Core Team 2020). Because our count data were overdispersed, we used a negative

binomial distribution with a logarithmic link to correct for overdispersion. We were interested in

determining (1) if there was a negative trend over time in murrelet counts, and if so, (2) if that

negative trend was different between public and private land. Thus, with the goal of keeping models

as simple as possible due to the limited number of survey stations, we compared two models: 1) a

full model including *ownership*, linear year (*T*) and an interaction effect between them, and 2) a

reduced model without the interaction effect. We compared these two models using AIC (Burnham

and Anderson 2002). We included sea surface temperature (SST) in our model because at-sea

conditions influence the proportion of murrelets that fly inland to breed in a given year (Peery et al.

2004a). While there are many oceanic factors we could have used, including lag effects from oceanic

conditions the previous year (e.g., Betts et al. 2020), we chose SST because of prior murrelet work

conducted in California. Generally, cooler average SSTs lead to better foraging conditions (Becker

and Beissinger 2003), and prey availability has been linked to breeding success in Marbled Murrelets

(Becker et al. 2007). Sea surface temperature data (°C) were averaged from NOAA buoys 46022 –

(Eel River - 17NM West-Southwest of Eureka, CA) and 46027 (St. George's - 8NM West

Northwest of Crescent City, CA) for the months of January through April (pre- and early-breeding

season) for each year (2002-2018). We also included quadratic day of year in the model because

murrelet activity likely peaks and then tapers off each year (Mack et al. 2003). SST and day of year

variables were centered and standardized before inclusion in the model. We also included *surveyor* as

a fixed effect to account for any variation in counts that may have existed among surveyors. Finally, we also included a random slope and intercept for each survey station over time.

After we completed modeling, we examined diagnostic plots including a QQ plot, a residual plot, and individual plots regressing model residuals against each explanatory variable to ensure that our model adequately met GLMM assumptions for our purposes. We also ensured that the overdispersion parameter, calculated as the Pearson Chi-square divided by the degrees of freedom, was reasonably close to one. We then used our GLMM to estimate the number of murrelets counted per survey in each year and we characterized slopes of inland murrelet counts on each ownership using the 'emmeans' package (Lenth 2020). Finally, we also conducted a power analysis using the 'simr' package (Green and Macleod 2016) to estimate our power to detect a difference in trends between public and private land, given our survey design and observed data.

Results

Occupancy Modeling of Audio-visual Data

We conducted 1,968 audio-visual surveys from 2000-2016, with an average of 125 surveys per year (range 97-142). We detected murrelet occupancy at an average of 34% of private HCP stations and 82% of public reference stations annually (Figure 2A). On average, public stations had a higher proportion of old-growth forest within a 1000-m radius of survey stations (public: 0.71 (SE = 0.11), private: 0.20 (SE = 0.02)). A full description of annual observed occupancy and habitat covariates for each survey station is available in Table S2 of the Supplemental.

Detection probabilities throughout the study ranged from 0.10 to 0.79, which are similar to those published by others for audio-visual surveys (e.g., Cooper and Blaha 2002, Bigger et al. 2006b). The top model for detection parameters included within-year effects of *ownership* and quadratic day

of year (Table S3) and a linear year effect (T; Table S4). Detection probability was higher on public than on private land ($\beta_{ownership} = 1.17$, 85% CI: 0.88 – 1.45). The inclusion of a linear year effect indicated that detection probabilities declined over time ($\beta_T = -0.09$, 85% CI: -0.11 – -0.06), which could have been due to re-growth of trees and vegetation at survey stations that reduced visibility or due to changes in murrelet behavior (e.g. less circling or less calling, making birds harder to detect).

Our fully time-varying models with year-specific colonization and local extinction revealed that over the 16-year study period, average occupancy at public reference sites was 0.85 (85% CI: 0.79 – 0.90), while average occupancy at private HCP sites was 0.46 (85% CI: 0.38 – 0.54). Occupancy in public reference areas was consistently higher than occupancy in private HCP areas (Figure 2B). Numerically, trends in occupancy were slightly positive at public reference sites ($\hat{\bar{\lambda}} = 1.01$, 85% CI: 0.94 – 1.08) and slightly negative at private HCP sites ($\hat{\bar{\lambda}} = 0.97$, 85% CI = 0.87 – 1.06; Figure 3) but estimates for both ownerships had wide confidence intervals and, thus, there was no strong evidence for a trend in occupancy on either ownership.

Our modeling of colonization and local extinction dynamics indicated that ownership and either a linear or log-linear time trend were important factors in determining colonization dynamics and that ownership and a linear or log-linear time trend were important in determining local extinction dynamics (Figure 4; Table S5). The top model was additive and included ownership and a log-linear time trend for both colonization and local extinction:

$$logit(\gamma_t) = 0.78 - 1.41(lnT) + 1.52(Ownership_{public})$$

$$logit(\varepsilon_t) = -0.41 - 0.78(lnT) - 1.08(Ownership_{public})$$

This model indicated that the odds of colonization increased by a factor of 4.57 (85% CI for odds ratio: 1.46 – 14.30) regardless of the year for public reference areas compared to private HCP areas (Figure 4A), and the odds of colonization declined on both ownerships by a factor of 0.25 per log-year (85% CI for odds ratio: 0.14 – 0.44; Figure 4A). This model also indicated that the odds of local

extinction decreased by a factor of 0.34 (85% CI for odds ratio: 0.12 – 0.94) for public reference

areas compared to private HCP areas (Figure 4B), and the odds of local extinction declined on both

ownerships by a factor of 0.46 per log-year (85% CI for odds ratio: 0.25 – 0.85; Figure 4B). This

model received 0.38 of model weight, covariates in this model explained 59% of the variation in

colonization and local extinction rates according to analysis of deviance, and our goodness-of-fit test

did not indicate any issues with model fit (P = 0.37). A model that included ownership and an

additive linear time trend (T) was within 1 AIC of the top model and received 0.23 of model weight,

but this model produced very similar estimates of colonization and local extinction as the top model

(Table S6).

GLMM of Radar Data

We completed 814 radar surveys from 2002-2018 (n = 346 public, n = 468 private). We counted an

average of 29.3 (SE: 1.57, range: 0 to 135) and 14.2 (SE: 0.68, range: 0 to 109) murrelets per 2.5-hour

survey at all stations in public reference and private HCP areas, respectively, over the entire study

period. Generally, average annual murrelet counts were higher in public reference areas than in

private HCP areas (Figure 5A). The full (ownership by year interaction) and reduced (additive

ownership and year effects) models had similar AIC scores: the reduced model was ranked higher,

but the full model had some support (ΔAIC: 0.4; likelihood ratio test: χ^2 = 2.39; P = 0.12), and we

therefore report parameter estimates and effect sizes from both models. There was no evidence of

overdispersion for the full model.

The reduced model without the interaction effect estimated the least-squares mean of

murrelet counts in private HCP areas as 8.7 (85% CI: 6.2 – 12.2), while that for public reference

areas was 14.8 (85% CI: 10.1 – 21.7). Similarly, the coefficient for ownership indicated that murrelet

counts in private HCP areas were 0.41 times those in public reference areas (85% CI: 0.08 – 0.65; P = 0.11). The linear year term (*T*) indicated that annual rate of change in counts was 0.86 (85% CI: 0.83 – 0.88), which means counts were declining on both ownerships by approximately 14% annually (85% CI: 12 – 17%; P < 0.01). The reduced model also indicated that each 0.8 degree increase in SST was associated with a 13% decline in murrelet inland counts (85% CI: 10 – 16%; P < 0.01); thus, years with warmer ocean temperatures were associated with lower murrelet counts. The full model indicated that the estimated annual rate of change in counts in public reference areas was 0.83 (85% CI: 0.80 – 0.86), corresponding with an approximate 17% annual decline in counts (85% CI: 14 – 20%; *P* < 0.01; Figure 5). Additionally, the interaction effect for this model revealed an approximate 5% annual difference in trends in murrelet counts between public and private land (85% CI: 1 – 10%; *P* = 0.11; Figure 5B), suggesting that average murrelet counts may be declining faster in public reference areas than in private HCP conservation areas. Thus, the estimated annual rate of change in private HCP areas was 0.88 (85% CI: 0.85 – 0.90), corresponding to an approximate 13% annual decline in murrelet counts (85% CI: 10% – 16%). Similar to the reduced model, the full model also estimated a negative relationship between SST and murrelet counts such that each 0.8 degree increase in SST was associated with a 13% decrease in inland radar counts (85% CI: 11 – 17%, *P* < 0.01; Figure 6). All coefficient estimates and standard errors are presented in Supplemental Table S7.

Our power analysis indicated that the power to detect a 10% annual difference in trends between ownerships over time was high (estimated power = 96.9%; 95% CI: 95.6 – 97.9%) given our study design. However, power to detect the observed 5% annual difference in trends between ownerships was limited (estimated power = 61.5%; 95% CI: 58.4 – 64.5%). Thus, we suggest that, while counts of inland flying murrelets declined substantially over the study period, the extent to which they declined more on public areas is uncertain.

Discussion

Our results present a nuanced understanding of how conservation areas set aside as part of a high-profile HCP have affected murrelet occupancy and abundance in the context of broad-scale environmental factors. Generally, public areas seem to represent better murrelet habitat – occupancy was consistently higher, colonization was more likely, local extinction was less likely, and murrelet counts were higher in public reference areas. However, these differences existed at the outset of the HCP, and we therefore focused on trends in occupancy and inland counts to evaluate the effectiveness of the HCP in conserving murrelets. Models with additive effects for ownership had consistently more support than those that included interactions, except that murrelet counts were potentially declining more slowly in private HCP conservation areas than in public reference areas. Taken together, this evidence suggests that the HCP has likely not exacerbated negative trends in occupancy and inland counts for the Marbled Murrelet. While HCP conservation areas may not be appreciably contributing to murrelet population recovery due to relatively low occupancy and abundance, the minimum requirement for HCPs is that they do not appreciably reduce the likelihood of survival and recovery of the species. Another important consideration is that habitat within the HCP conservation areas will likely improve over time as forests mature into more suitable habitat, and retaining as much breeding habitat as possible will likely benefit the recovery of the marbled murrelet, which has lost approximately 85% of its breeding habitat in California (USFWS 1997). Most of the extant high-quality nesting habitat in California is now protected within parks, reserves, or other conservation areas (Falxa and Raphael 2016), and thus, factors affecting murrelets at sea, nest predation, and historic and ongoing habitat loss are likely responsible for continued murrelet declines in California (Betts et al. 2020).

Despite the declines we observed in murrelet inland counts in our study area, regional population estimates from at-sea surveys (the standard protocol for censusing murrelet population size) off the coast of southern Oregon and northern California increased from 2000-2017 (Pearson et al. 2018). This apparent discrepancy is likely due to the fact that inland radar counts do not reflect regional population size, but more likely represent breeding effort and the size of the potential breeding population, including nonbreeders and failed breeders (Peery et al. 2004a, Barbaree et al. 2014, Lorenz et al. 2017). Thus, the decline we observed in inland radar counts is likely indicative of a long-term decline in local murrelet breeding effort. The decline we observed in colonization over time on both landownerships further supports this explanation. Indeed, dispersal of murrelets from Oregon or Washington into coastal areas near our study site could have resulted in high regional population estimates at-sea near our study area even while, locally, murrelet breeding effort declined. Murrelets are known to temporarily disperse long distances, which can contribute to changes in at-sea populations (Hébert and Golightly 2008, Peery et al. 2008, Hall et al. 2009, Vásquez-Carrillo et al. 2013), and there is evidence that large movements at sea may indicate low breeding propensity for murrelets (Lorenz et al. 2017). It seems likely that murrelets have fidelity for nesting areas (Hébert et al. 2003, Piatt et al. 2007, Lorenz et al. 2019), and murrelet populations have experienced an approximate 30% decline in Washington, Oregon, and California (Miller et al. 2012). Thus, temporary immigration seems more likely than a permanent increase in regional population size offshore from our study area and is consistent with our inland survey results.

Differences in occupancy and abundance between public and private land are likely attributable, at least in part, to differences in amount and configuration of habitat. The HCP conservation areas consisted of smaller and less contiguous old-growth patches than public reserves, meaning there was a higher edge to core ratio. Smaller patch size, and therefore less core habitat, has been shown to negatively impact other interior forest species (Valente and Betts 2019), and although

some ambiguity exists about the effect of habitat fragmentation on murrelet occupancy and breeding success (Meyer and Miller 2002, Meyer et al. 2002, Raphael et al. 2002b, Zharikov et al. 2006, 2007; Burger and Page 2007, Malt and Lank 2009), it seems unlikely that murrelets have high breeding success in highly fragmented landscapes. Murrelets may be susceptible to edge effects including reduced epiphyte availability (van Rooyen et al. 2011), increased exposure to heat and evaporative water loss (Meyer and Miller 2002), and higher abundance of nest predators (Zharikov et al. 2007). In particular, the potential for nest predation by corvids increases in fragmented habitat (Malt and Lank 2007), and murrelets are sensitive to corvid predation (Peery et al. 2004b, Peery and Henry 2010, Raphael et al. 2002b, Luginbuhl et al. 2001, Malt and Lank 2009). On both ownerships, we found that colonization decreased over the study period, likely because of declining breeding effort but, surprisingly, local extinction also decreased over time. This could be a result of low-quality sites being abandoned by murrelets first, resulting in higher fidelity at sites that remained occupied, which presumably contain higher-quality breeding habitat. We note that we cannot infer differences in actual breeding success related to landownership because neither monitoring technique indicates whether a detected murrelet actually nested or more importantly, successfully reproduced. More detailed nest-level work would need to be done to explore breeding success within HCP conservation areas and whether conservation areas could constitute population sinks for murrelets.

There are a few important limitations of our study. The first is that this is a retrospective analysis of survey data collected from an HCP effectiveness monitoring program where treatments (i.e., public and private) were not randomly assigned and survey stations were not randomly placed across the landscape. The small number of stations surveyed for both analyses resulted in the wide confidence intervals we calculated for several model parameters. Therefore, our results should be interpreted with some caution and the understanding that larger sample sizes or a more rigorous experimental design would allow stronger conclusions to be drawn about the effect of the HCP

conservation areas on murrelet populations. However, our dataset is also unique in its longevity and in the parallel monitoring of public reference areas for direct comparison. The second caveat is that associating murrelets detected by radar with specific habitat is potentially flawed, as radar detections do not guarantee that murrelets are utilizing habitat near a survey station. However, radar surveys are a highly recommended method for monitoring inland habitat use by murrelets because they result in higher detection probabilities and more accurate counts than audio-visual surveys (Burger 2001, Bigger et al. 2006a, b). Additionally, there is little other suitable murrelet nesting habitat located near our study area (Raphael et al. 2011; S. Chinnici, *pers. observation*), so murrelets are unlikely to be transiting through our study area to get to other areas. While radar counts on public land may be inflated if murrelets are detected flying through Headwaters Forest Reserve on their way to use habitat within the MMCAs, we find this scenario unlikely because radar counts at Headwaters Forest Reserve were lower than those in Allen Creek and Bell Lawrence MMCAs, for example.

Finally, we reiterate that murrelet surveys on private land were only conducted within the habitat set aside for murrelets (i.e., the MMCAs), so the effect of the HCP on the occupancy status of any murrelets utilizing private land outside those specific areas remains unknown. While some seasonal restrictions exist to minimize the effects of timber harvest on murrelets that breed outside the MMCAs, these conservation areas were the main protective measure outlined in the HCP for murrelets and the majority of suitable murrelet habitat is protected within them. Therefore, this study still provides vital information about how the HCP has affected Marbled Murrelet populations. Moreover, this multi-species HCP also covers 16 additional species, including fish, amphibians, a reptile, birds, and mammals. The focal species are anadromous salmonids, including Coho (*Oncorhynchus kisutch*) and Chinook (*Oncorhynchus tshawytscha*) Salmon, the Northern Spotted Owl (*Strix occidentalis caurina*), and the Marbled Murrelet. The individual conservation plans of the HCP each include a habitat-based approach with an effectiveness monitoring component. Aquatic

effectiveness monitoring for the salmonids and other species has indicated that riparian conditions may be improving following significant impacts during first-cycle logging. Monitoring indicates that the invasive Barred Owl (*Strix varia*) is negatively impacting Northern Spotted Owl occupancy and reproduction as is the case throughout the range of the Northern Spotted Owl (Gutiérrez et al. 2007).

Similar long-term trends in murrelet occupancy and inland counts in public reference and private HCP areas over time and the negative relationship between SST and inland counts underscore the importance of monitoring reference areas when evaluating an HCP. In fact, there is general need for conservation to better implement rigorous experimental designs and counterfactual analyses to assess the success of conservation policies (Ferraro and Pattanayak 2006, Baylis et al. 2016). However, in light of the lack of funding for conservation initiatives, including even quasi-experimental reference sites in HCP monitoring is an important step in the right direction. We hope that this study will prompt more thorough evaluations of other large-scale HCPs and careful consideration when designing monitoring programs of future HCPs to improve the rigor of such evaluations. Given the importance of habitat protection and the high risk of habitat loss on private land (Eichenwald et al. 2020), thorough evaluations of HCPs and other private land conservation initiatives are essential to ensure conservation on private land is successful.

Acknowledgments

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Tables

Table 1. Covariates used to model detection probability (p), initial occupancy (ψ_1), colonization (γ), and local extinction (ε). Each 'x' indicates that the effect of the covariate was tested for the parameter.

Covariate	Variable Type	Definition	Parameters		
			p	Ψ_1	γ, ε
cloudcov	Continuous	Percent cloud cover	x		
precip	Categorical	Precipitation condition	x		
DoY	Continuous	Day of year (quadratic)	x		
visibility	Categorical	Visibility at each survey station, ranked by murrelet surveyors	x		
PropOG	Continuous	Proportion of habitat within a 1000-m radius of the survey station that is old-growth forest	x		
ownership	Categorical	Whether a site is on private (HCP) or public (reference) land	x	x	x
habitat	Categorical	Whether a site is located within 200-m of unharvested old-growth or has only residual old-growth within 200-m	x		x

Figure Captions

Figure 1. Map of the study area. Surveyed private (HCP) sites included Allen Creek, Bell Lawrence, Cooper Mill, and Shaw Gift MMCAs. Surveyed protected public (non-HCP) sites included the Headwaters Forest Reserve and Humboldt Redwoods State Park.

Figure 2. A: The proportion of sites where murrelet occupancy was observed, without correcting for detection. B: Derived annual estimates of occupancy for stations on public and private land over time from fully time-varying models (see methods). Error bars represent 85% confidence intervals.

Figure 3. Derived annual rate of change in occupancy (λ_t) for both ownerships from the fully-time varying models. Error bars represent 85% confidence intervals calculated using the delta method. The horizontal dotted line denotes $\lambda = 1$, which represents stable occupancy between years.

Figure 4. Occupancy dynamics from the top occupancy model, which included ownership and an additive log-linear time trend on both (A) colonization and (B) local extinction. Shaded areas represent 85% confidence intervals.

Figure 5. Radar survey and analysis results. (A) Dots and 85% error bars represent the observed number of murrelets counted per radar survey, averaged across stations on public and private land each year. Lines represent GLMM-derived estimates of average murrelets counted per radar survey given the observed values of all model parameters for stations on public and private land each year, with bootstrapped 85% confidence intervals. (B) GLMM-derived effect plot for the interaction between ownership and linear year showing the mean number of murrelets counted per radar survey on each ownership while all other model parameters were held at their median values, with bootstrapped 85% confidence intervals. GLMM-derived estimates in A and B are from the full model including the interaction effect between ownership and year.

Figure 6. The relationship between sea surface temperature and murrelet inland counts. (A) Observed sea surface temperatures and associated murrelet counts, with 85% confidence intervals. (B) GLMM-derived effect plot for sea surface temperature showing the mean number of murrelets counted per radar survey at each sea surface temperature, while all other model parameters were held at their median values, with bootstrapped 85% confidence intervals. Estimates were derived from the full model including the interaction effect between ownership and year.
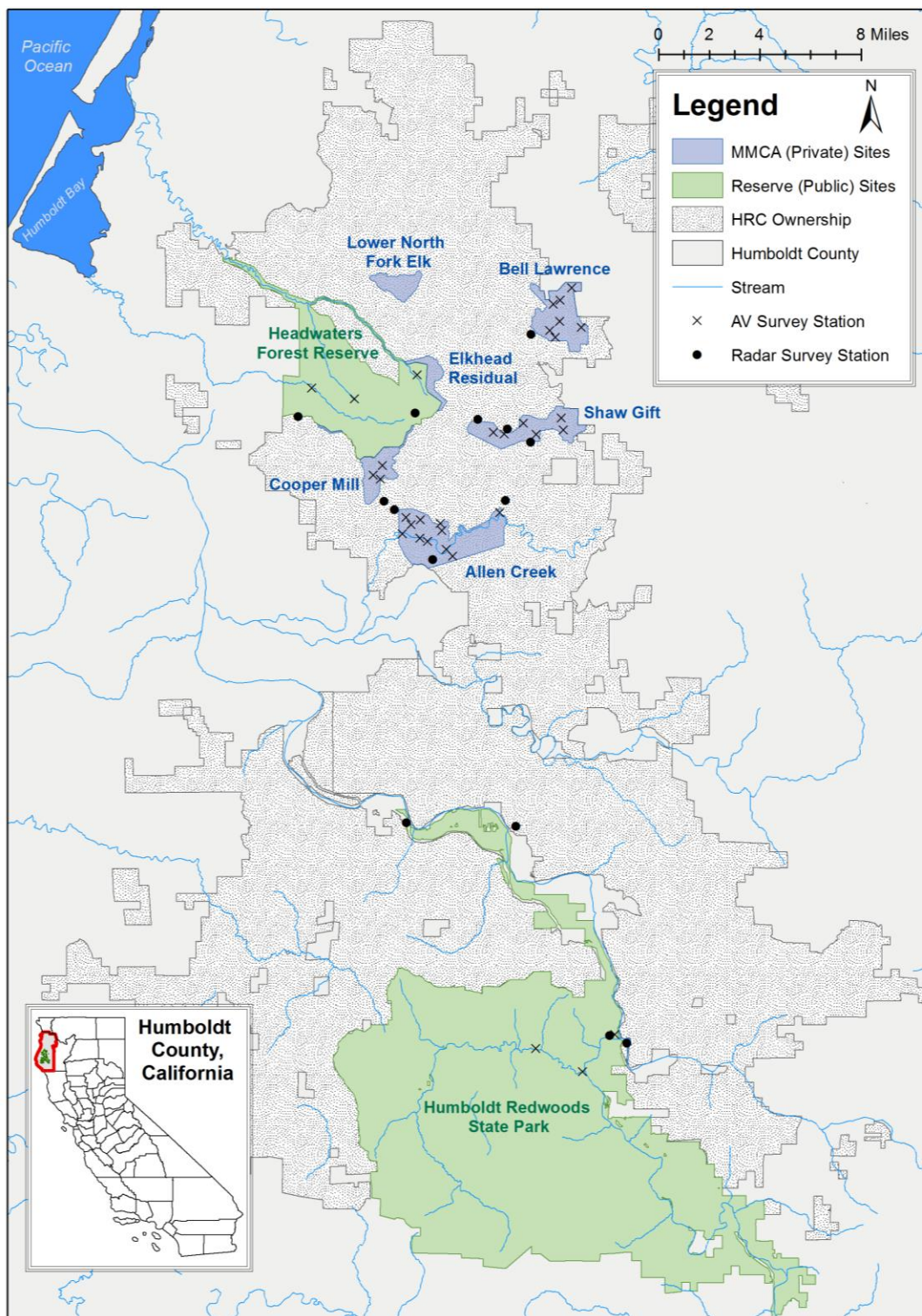
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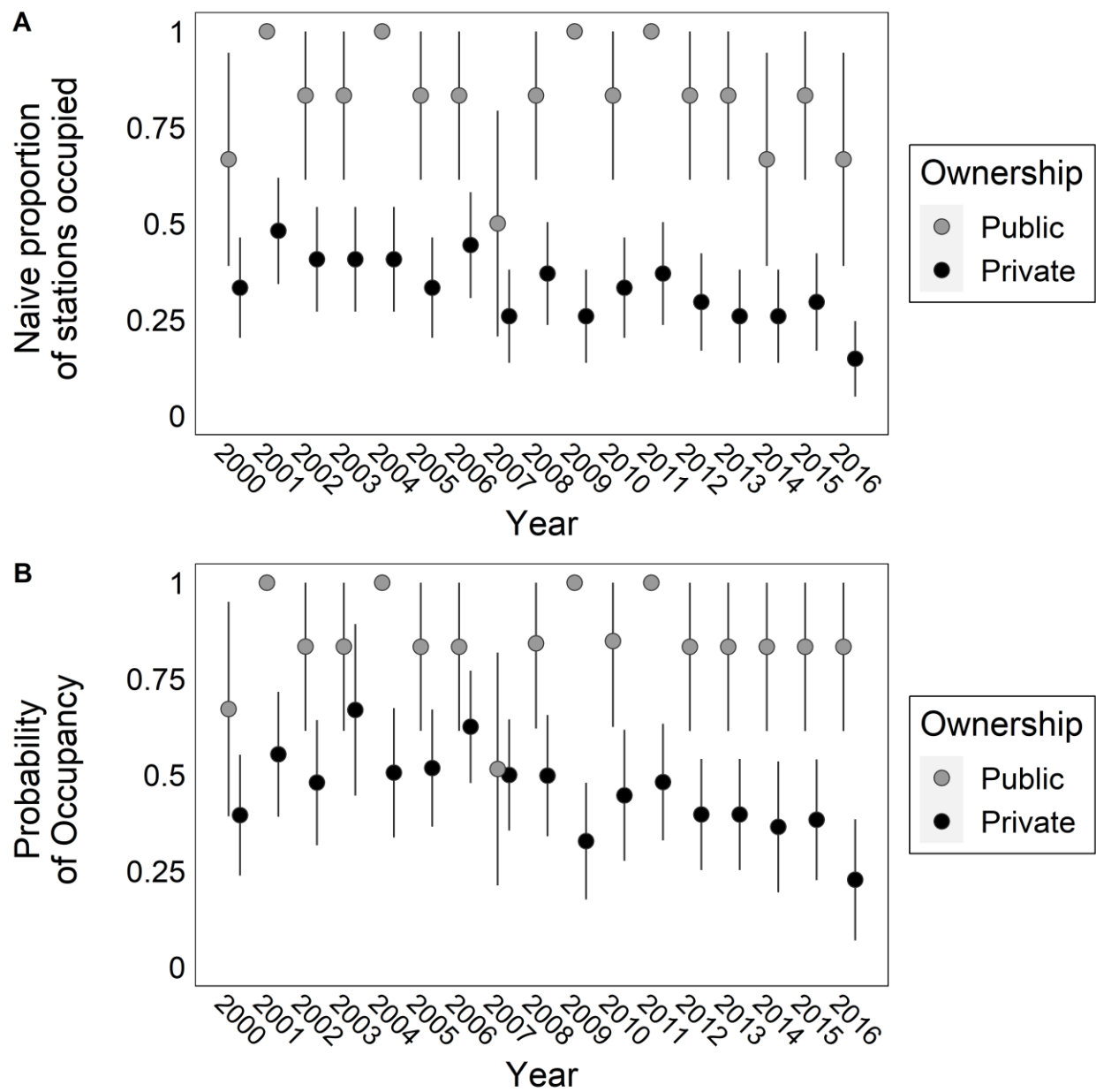
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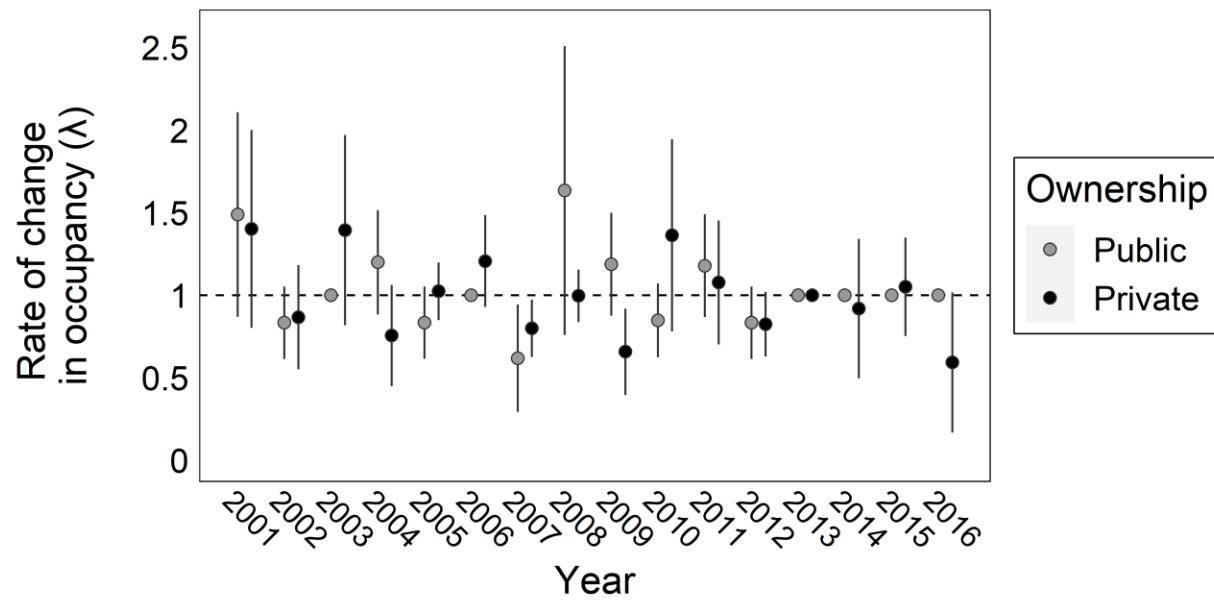
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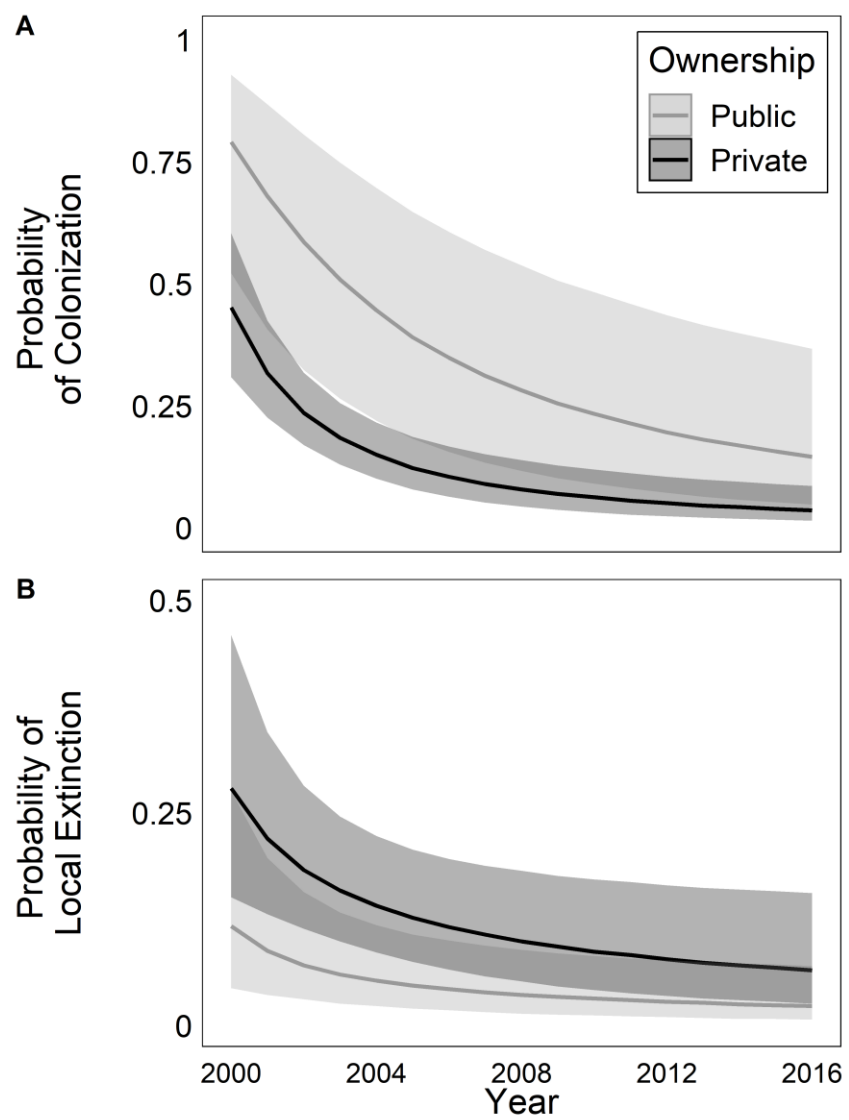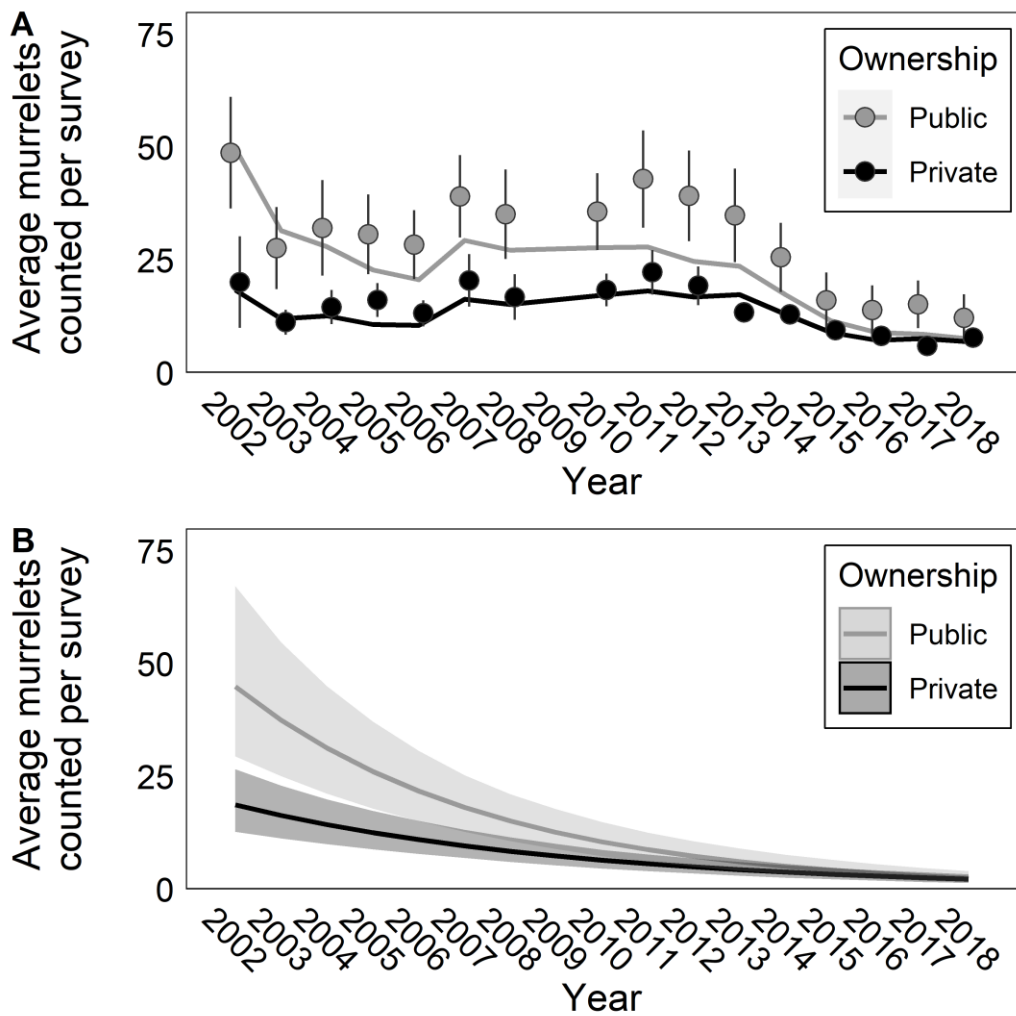
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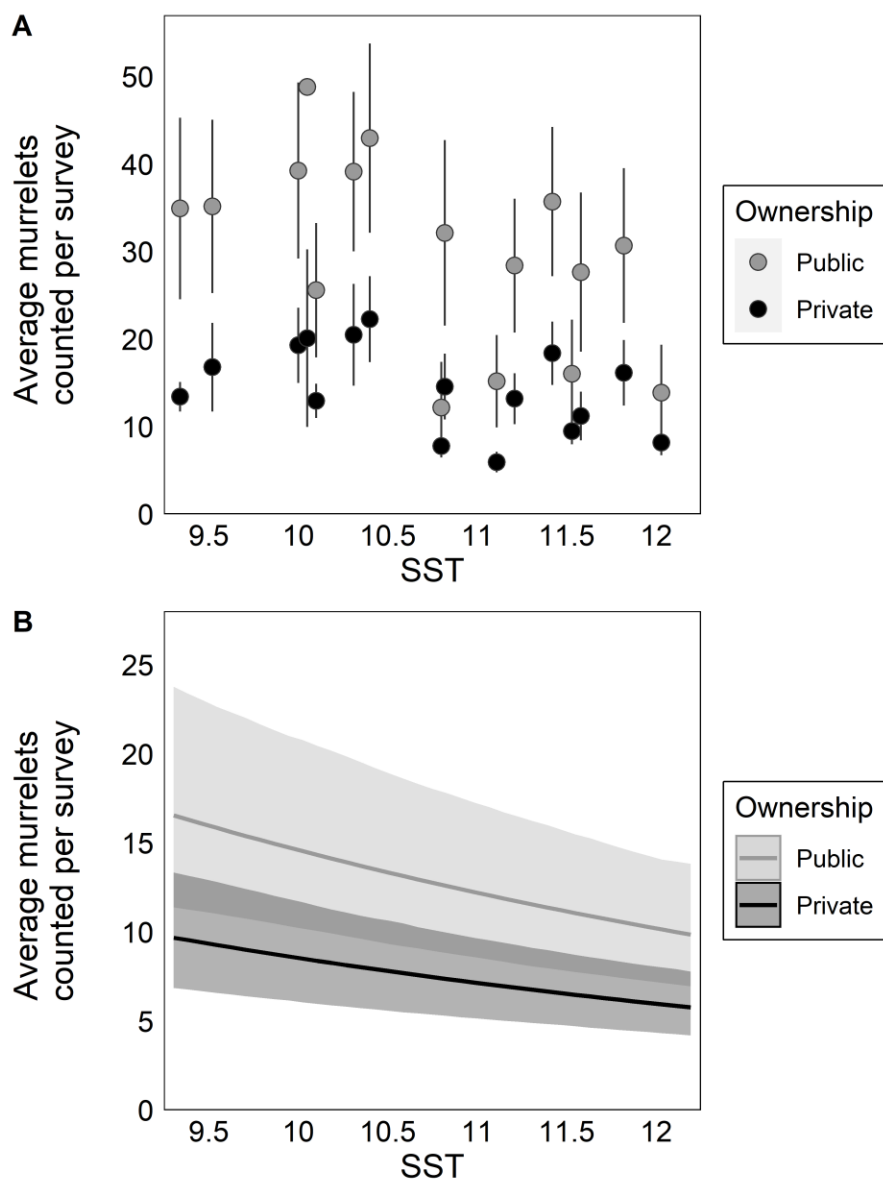
Figure 6

Supplementary Materials

Table S1. All the candidate models for colonization (γ) and local extinction (ε) tested within our occupancy modeling framework. Models with (.) indicate that they did not include covariates. We ran each model with the best model for detection (p) and an ownership effect on initial occupancy (ψ_1).

Model
$\gamma(.)$, $\varepsilon(.)$
$\gamma(own)$, $\varepsilon(.)$
$\gamma(own + year)$, $\varepsilon(.)$
$\gamma(own + T)$, $\varepsilon(.)$
$\gamma(own + lnT)$, $\varepsilon(.)$
$\gamma(own * T)$, $\varepsilon(.)$
$\gamma(own * lnT)$, $\varepsilon(.)$
$\gamma(.)$, $\varepsilon(own)$
$\gamma(.)$, $\varepsilon(own + year)$
$\gamma(.)$, $\varepsilon(own + T)$
$\gamma(.)$, $\varepsilon(own + lnT)$
$\gamma(.)$, $\varepsilon(own * T)$
$\gamma(.)$, $\varepsilon(own * lnT)$
$\gamma(own)$, $\varepsilon(own)$
$\gamma(own + year)$, $\varepsilon(own + year)$
$\gamma(own + T)$, $\varepsilon(own + T)$
$\gamma(own + lnT)$, $\varepsilon(own + lnT)$
$\gamma(own * T)$, $\varepsilon(own * T)$
$\gamma(own * lnT)$, $\varepsilon(own * lnT)$
$\gamma(hab)$, $\varepsilon(.)$
$\gamma(hab + year)$, $\varepsilon(.)$
$\gamma(hab + T)$, $\varepsilon(.)$
$\gamma(hab + lnT)$, $\varepsilon(.)$
$\gamma(hab * T)$, $\varepsilon(.)$
$\gamma(hab * lnT)$, $\varepsilon(.)$
$\gamma(.)$, $\varepsilon(hab)$
$\gamma(.)$, $\varepsilon(hab + year)$
$\gamma(.)$, $\varepsilon(hab + T)$
$\gamma(.)$, $\varepsilon(hab + lnT)$
$\gamma(.)$, $\varepsilon(hab * T)$
$\gamma(.)$, $\varepsilon(hab * lnT)$
$\gamma(hab)$, $\varepsilon(hab)$
$\gamma(hab + year)$, $\varepsilon(hab + year)$
$\gamma(hab + T)$, $\varepsilon(hab + T)$
$\gamma(hab + lnT)$, $\varepsilon(hab + lnT)$
$\gamma(hab * T)$, $\varepsilon(hab * T)$
$\gamma(hab * lnT)$, $\varepsilon(hab * lnT)$

Table S2. Habitat covariates and observed annual occupancy state for each survey station. In the observed occupancy state columns, "1" indicates a station was occupied and "0" indicates it was unoccupied by murrelets.

Survey Station ID	Site	Ownership	Habitat	*PropOG*	Observed Occupancy State																
					2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
HM0104	Allen Creek	Private	Old-growth	0.24	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HM0105	Allen Creek	Private	Old-growth	0.23	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
HM0107	Allen Creek	Private	Old-growth	0.33	1	1	1	1	1	1	1	0	1	1	1	1	0	1	0	0	0
HM0109	Allen Creek	Private	Old-growth	0.36	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0
HM0111	Allen Creek	Private	Old-growth	0.32	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
HM0124	Allen Creek	Private	Old-growth	0.26	1	0	0	0	1	1	1	0	1	1	1	0	1	1	0	0	1
HM1013	Allen Creek	Private	Residual	0.02	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0
HM1106	Allen Creek	Private	Residual	0.14	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
HM1107	Allen Creek	Private	Residual	0.04	0	1	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0
HM2501	Allen Creek	Private	Old-growth	0.30	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
HM2502	Allen Creek	Private	Residual	0.23	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
HM0201	Bell Lawrence	Private	Old-growth	0.14	0	0	1	1	0	0	1	1	1	1	0	1	0	0	0	0	1
HM1203A	Bell Lawrence	Private	Old-growth	0.29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HM1204	Bell Lawrence	Private	Old-growth	0.36	1	1	1	0	1	1	1	0	1	0	0	1	0	1	0	0	0
HM1206	Bell Lawrence	Private	Old-growth	0.32	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	1	0
HM1306	Bell Lawrence	Private	Residual	0.16	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
HM2301	Bell Lawrence	Private	Old-growth	0.12	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HM2302	Bell Lawrence	Private	Old-growth	0.09	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
HM0804B	Cooper's Mill	Private	Residual	0.14	0	0	0	1	0	1	0	1	1	0	1	1	1	0	1	0	0
HM0808	Cooper's Mill	Private	Residual	0.18	0	1	0	1	0	0	1	0	0	0	1	1	1	1	0	0	0
HM0813	Cooper's Mill	Private	Residual	0.18	0	1	1	1	0	0	1	0	0	0	1	0	0	0	1	1	0
HM0405	Shaw Gift	Private	Old-growth	0.35	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	1	0
HM0413	Shaw Gift	Private	Old-growth	0.36	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
HM0503	Shaw Gift	Private	Residual	0.03	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HM0707	Shaw Gift	Private	Old-growth	0.10	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0

HM0906	Shaw Gift	Private	Residual	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HM2401	Shaw Gift	Private	Residual	0.11	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CM0105A	HFR	Public	Old-growth	0.27	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1
CM0207	HFR	Public	Old-growth	0.82	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
DM0103	HFR	Public	Old-growth	0.56	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
ZM0101	HRSP	Public	Old-growth	0.98	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
ZM0108	HRSP	Public	Old-growth	1.00	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
ZM0110	HRSP	Public	Old-growth	0.63	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0

Table S3. AIC table for detection models including within-year habitat and survey covariates. Models with (.) indicate no covariates. Occupancy structure was: ψ_1(*ownership*), γ(*year*), ε(*year*).

Detection Structure	Δ AIC	w_i	K
p(DoY + own)	0.00	0.998	38
p(DoY + vis)	12.50	0.002	38
p(own)	21.57	0	36
p(own + precip)	21.62	0	37
p(own + cloudcov)	21.92	0	37
p(own + precip + cloudcov)	23.00	0	38
p(DoY + habitat)	25.21	0	38
p(vis)	29.98	0	36
p(DoY + propOG)	30.26	0	38
p(vis + precip)	31.25	0	37
p(vis + cloudcov)	31.79	0	37
p(DoY)	32.32	0	37
p(DoY + precip)	32.35	0	38
p(vis + precip + cloudcov)	33.23	0	38
p(DoY + cloudcov)	34.04	0	38
p(DoY + precip + cloudcov)	34.35	0	39
p(habitat)	47.85	0	36
p(habitat + precip)	48.38	0	37
p(habitat + cloudcov)	49.11	0	37
p(habitat + precip + cloudcov)	50.20	0	38
p(propOG)	51.51	0	36
p(propOG + precip)	51.96	0	37
p(.)	52.26	0	35
p(propOG + cloudcov)	52.82	0	37
p(precip)	52.90	0	36
p(cloudcov)	53.57	0	36
p(propOG + precip + cloudcov)	53.80	0	38
p(precip + cloudcov)	54.72	0	37

Top Model AIC: 1514.33

DoY - quadratic day of year, *own* – ownership (public or private), *vis* – visibility, *precip* – precipitation, *cloudcov* – cloudcover, *propOG* – proportion old-growth, *habitat* – old-growth or residual

Table S4. AIC table for detection models including among-year temporal covariates. Occupancy structure was: ψ_1(*ownership*), γ(*year*), ε(*year*).

Detection Structure	Δ AIC	w_i	K
p(DoY + own + T)	0	0.600	39
p(DoY + own + lnT)	0.86	0.390	39
p(DoY + own + year)	11.23	0	54
p(DoY + own)	11.48	0	38

Top Model AIC: 1502.85

Table S5. AIC table for covariate structures in dynamic occupancy models. Models with (.) indicate that they did not include covariates. Detection structure was: $p(jd + own + T)$, and initial occupancy structure was: $\psi_1(own)$.

Covariate Structure	Δ AIC	w_i	K
γ(own + lnT), ε(own + lnT)	0	0.380	13
γ(own + T), ε(own + T)	0.97	0.234	13
γ(own + lnT), ε(.)	2.19	0.127	11
γ(own * lnT), ε(own * lnT)	3.42	0.069	15
γ(own + T), ε(.)	3.99	0.052	11
γ(own * lnT), ε(.)	4.08	0.049	12
γ(own * T), ε(own * T)	4.56	0.039	15
γ(own * T), ε(.)	5.93	0.020	12
γ(hab + lnT), ε(hab + lnT)	7.57	0.009	13
γ(hab + lnT), ε(.)	7.8	0.008	11
γ(hab + T), ε(hab + T)	9.09	0.004	13
γ(hab * lnT), ε(.)	9.8	0.003	12
γ(hab + T), ε(.)	9.84	0.001	11
γ(hab * lnT), ε(hab * lnT)	11.48	0.001	15
γ(hab * T), ε(.)	11.82	0.001	12
γ(own), ε(own)	12.56	0.001	11
γ(hab * T), ε(hab * T)	13.03	0	15
γ(own), ε(.)	14.19	0	10
γ(.), ε(own)	14.32	0	10
γ(.), ε(own + lnT)	15.61	0	11
γ(.), ε(own + T)	15.78	0	11
γ(.), ε(own * lnT)	17.57	0	12
γ(.), ε(own * T)	17.68	0	12
γ(.), ε(.)	19.09	0	9
γ(own + year), ε(.)	19.9	0	25
γ(hab), ε(.)	20.73	0	10
γ(.), ε(hab)	21.01	0	10
γ(.), ε(hab + lnT)	21.7	0	11
γ(.), ε(hab + T)	21.73	0	11
γ(hab), ε(hab)	22.73	0	11
γ(.), ε(hab * lnT)	23.52	0	12
γ(.), ε(hab * T)	23.62	0	12
γ(hab + year), ε(.)	29.05	0	25
γ(.), ε(own + year)	31.57	0	25
γ(own + year), ε(own + year)	36.81	0	41
γ(.), ε(hab + year)	39.91	0	25
γ(hab + year), ε(hab + year)	48.46	0	41

Top Model AIC: 1458.00

Table S6. All untransformed beta coefficients for the top two competitive occupancy models of audiovisual survey data.

	Top Model		
Parameter	**Covariate**	**Estimate**	**SE**
Initial Occupancy (ψ_1)	(intercept)	-0.47	0.45
Initial Occupancy (ψ_1)	Ownership	1.20	1.00
Colonization (γ_t)	(intercept)	0.78	0.66
Colonization (γ_t)	lnT	-1.41	0.40
Colonization (γ_t)	Ownership	1.52	0.79
Local Extinction (ε_t)	(intercept)	-0.41	0.79
Local Extinction (ε_t)	lnT	-0.78	0.43
Local Extinction (ε_t)	Ownership	-1.08	0.70
Detection (p)	(intercept)	-0.56	0.20
Detection (p)	T	-0.09	0.02
Detection (p)	Day of year	0.29	0.08
Detection (p)	Day of year^2	0.11	0.08
Detection (p)	Ownership	1.17	0.20
	Competitive Model		
Parameter	**Covariate**	**Estimate**	**SE**
Initial Occupancy (ψ_1)	(intercept)	-0.46	0.45
Initial Occupancy (ψ_1)	Ownership	1.20	1.00
Colonization (γ_t)	(intercept)	-0.33	0.41
Colonization (γ_t)	T	-0.21	0.07
Colonization (γ_t)	Ownership	1.52	0.77
Local Extinction (ε_t)	(intercept)	-0.95	0.51
Local Extinction (ε_t)	T	-0.13	0.07
Local Extinction (ε_t)	Ownership	-1.10	0.69
Detection (p)	(intercept)	-0.51	0.20
Detection (p)	T	-0.09	0.02
Detection (p)	Day of year	0.30	0.08
Detection (p)	Day of year^2	0.12	0.08
Detection (p)	Ownership	1.15	0.20

Table S7. All untransformed beta coefficients for fixed effects in the full and reduced GLMMs models for inland count data. The dependent variable for both models is log(Count).

Full Model				
Parameter	**Estimate**	**SE**	**Z-value**	**P-value**
Intercept	4.97	0.33	15.19	<0.01
Ownership$_{Private}$	-0.93	0.39	-2.36	0.02
T	-0.18	0.03	-7.24	<0.01
SST (scaled)	-0.14	0.03	-5.73	<0.01
Surveyor$_{DWL}$	-1.06	0.13	-8.16	<0.01
Surveyor$_{DB}$	-1.11	0.11	-10.06	<0.01
Surveyor$_{TD}$	-1.58	0.17	-9.23	<0.01
Surveyor$_{JTC}$	-0.63	0.19	-3.29	<0.01
Surveyor$_{KGR}$	-0.28	0.22	-1.29	0.20
Surveyor$_{MCS}$	-2.08	0.83	-2.50	0.01
Surveyor$_{MKT}$	-0.39	0.13	-3.06	<0.01
Surveyor$_{RLS}$	0.12	0.35	0.33	0.74
Surveyor$_{SEM}$	0.08	0.19	0.42	0.68
Day of Year	0.00	0.02	0.20	0.84
Day of Year^2	0.13	0.02	5.23	<0.01
Ownership$_{Private}$:T	0.05	0.03	1.61	0.11
Reduced Model				
Parameter	**Estimate**	**SE**	**Z-value**	**P-value**
Intercept	4.74	0.31	15.30	<0.01
Ownership$_{Private}$	-0.53	0.33	-1.59	0.11
lin.year	-0.15	0.02	-8.04	<0.01
SST.scl	-0.14	0.03	-5.74	<0.01
Surveyor$_{DWL}$	-1.06	0.13	-8.16	<0.01
Surveyor$_{DB}$	-1.11	0.11	-10.05	<0.01
Surveyor$_{TD}$	-1.58	0.17	-9.25	<0.01
Surveyor$_{JTC}$	-0.63	0.19	-3.31	<0.01
Surveyor$_{KGR}$	-0.28	0.22	-1.29	0.20
Surveyor$_{MCS}$	-2.09	0.83	-2.51	0.01
Surveyor$_{MKT}$	-0.39	0.13	-3.08	<0.01
Surveyor$_{RLS}$	0.12	0.35	0.34	0.74
Surveyor$_{SEM}$	0.08	0.19	0.42	0.67
Day of Year	0.01	0.02	0.22	0.83
Day of Year^2	0.13	0.02	5.26	<0.01

Chapter 2: Reducing anthropogenic subsidies can curb density of overabundant predators in protected areas

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Citation

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, 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/hectare after the initiation of management, whereas density in unsubsidized areas that were not expected to be affected by management remained stable (0.70 ± 0.22 pre-management, 0.58 ± 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 fitness. 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 can be part of a strategy to increase compatibility of species protection and human recreation within protected areas.

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.

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 fitness, 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 fitness of jays that maintained similar density or 2) reduced density of jays that maintained similar fitness. Under the first hypothesis, we

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 body condition and fecundity would decrease and that jay density in both subsidized and unsubsidized areas would remain stable. Alternatively, under the second hypothesis, 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 body condition and fecundity would remain stable, but 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.

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; hereafter Big Basin) to understand the effects of management efforts on their diet, behavior and fitness, and demography. 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 (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;" Figure 1). However, we also collected density and reproduction data (see "density and reproduction" below) in unsubsidized forest areas with less human use that were at least 2 km from campgrounds (hereafter referred to as "unsubsidized 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. 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, 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).

Anthropogenic food consumption

We quantified the consumption of anthropogenic food by Steller's jays living in subsidized areas

using stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ 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

$\delta^{15}N$, which is influenced by a consumer's trophic level with carnivores being more enriched than

herbivores in terrestrial landscapes (Kelly 2000). Analyses of $\delta^{13}C$ and $\delta^{15}N$ 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 50mm 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 hours. We then weighed and

sealed approximately 0.5 mg of each feather sample into a tin capsule. Analysis of $\delta^{13}C$ and $\delta^{15}N$

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 2018). 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 $\delta^{15}N$ and +3.5‰ (SD = 0.1) for $\delta^{13}C$ (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 (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 $\delta^{13}C$ enrichment of adult jays. We first compared $\delta^{13}C$ enrichment across pre-management years and then across post-management years individually using ANOVA to confirm that $\delta^{13}C$ enrichment was not different among the years within each period. We then compared $\delta^{13}C$ 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 $\delta^{13}C$ 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 ± standard error.

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 2018). 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 ≥ 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 UDOIs 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 ± standard error.

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 (Figure 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 $\delta^{13}C$ (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 ± standard error.

Density and reproduction

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-minute 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 2018). 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 ± 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; Figure 1).

Results

Anthropogenic food consumption

We analyzed stable isotopes in feathers from 51 adult Steller's jays both before and after management. 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 (Figure 2A). We observed a similar trend in $\delta^{13}C$ enrichment: jays in the post-management period were 2.4‰ (± 0.27‰) less enriched than jays in the pre-management period ($F_{1,99} = 79.87$, $p < 0.001$; Figure 2B). Additionally, there was no evidence of a difference in $\delta^{13}C$ enrichment within pre-management years ($F_{3,43} = 0.87$, $p = 0.47$) or within post-management years ($F_{2,45} = 0.28$, $p = 0.76$).

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 hectares) and post-management (6.35 ± 0.60 hectares) periods for jays (χ^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; Figure 3). Mean UDOI values in 2017 (0.06 ± 0.01) and 2018 (0.09 ± 0.01) were similar to those from 2019.

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 (± 0.11) and 5.04 (± 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 (χ^2 = 1.13, p-value = 0.29).

Density and reproduction

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/hectare) than in the pre-management period (4.33 ± 0.91 jays/hectare). 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/hectare) and

post-management (0.58 ± 0.38 jays/hectare) periods. Our two-way ANOVA also indicated a significant interaction between management and subsidies ($F_{1,42}$ = 176.66, p-value < 0.001), 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 (Figure 4A).

The August density of juvenile jays in subsidized areas was lower in the post-management period (0.70 ± 0.40 jays/hectare) than in the pre-management period (3.3 ± 0.80 jays/hectare; Figure 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 (Figure 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.

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 fitness would remain reasonably stable in subsidized areas. The size of jay territories did not change between pre- and post-management periods, but the amount of overlap between territories decreased, which may suggest that remaining food resources were more easily

defensible (Robb et al. 2008). 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. We note, though, that anthropogenic foods still constituted a significant 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.

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 predating 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? 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.

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 fitness 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 2012-2015 (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 $\delta^{13}C$ 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.

Acknowledgements

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.

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Figure Captions

Figure 1. Map of the study area. The right panel (blue box) shows the campgrounds in which jays were captured.

Figure 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) $\delta^{13}C$ 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 for reference.

Figure 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.

Figure 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 forest areas in the post-management period. (B) Estimated juvenile to adult ratios for subsidized areas in pre- and post-management periods.
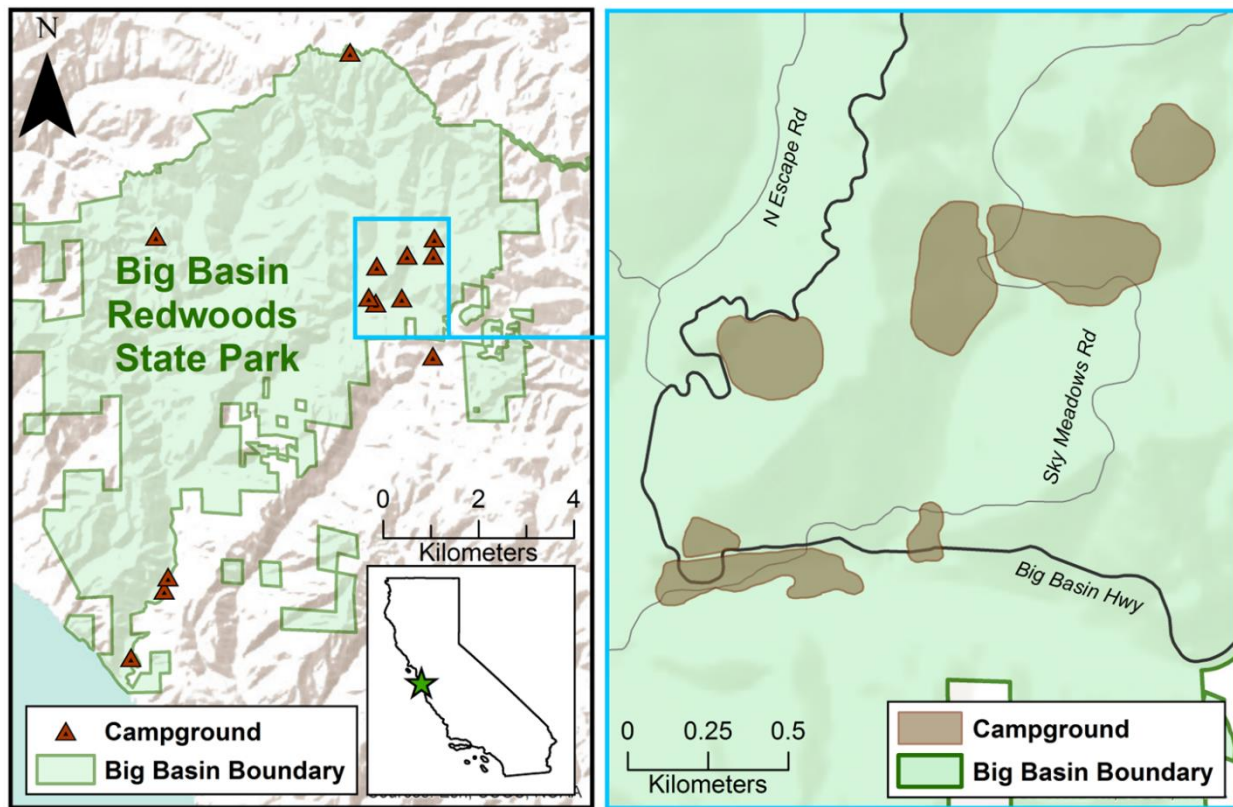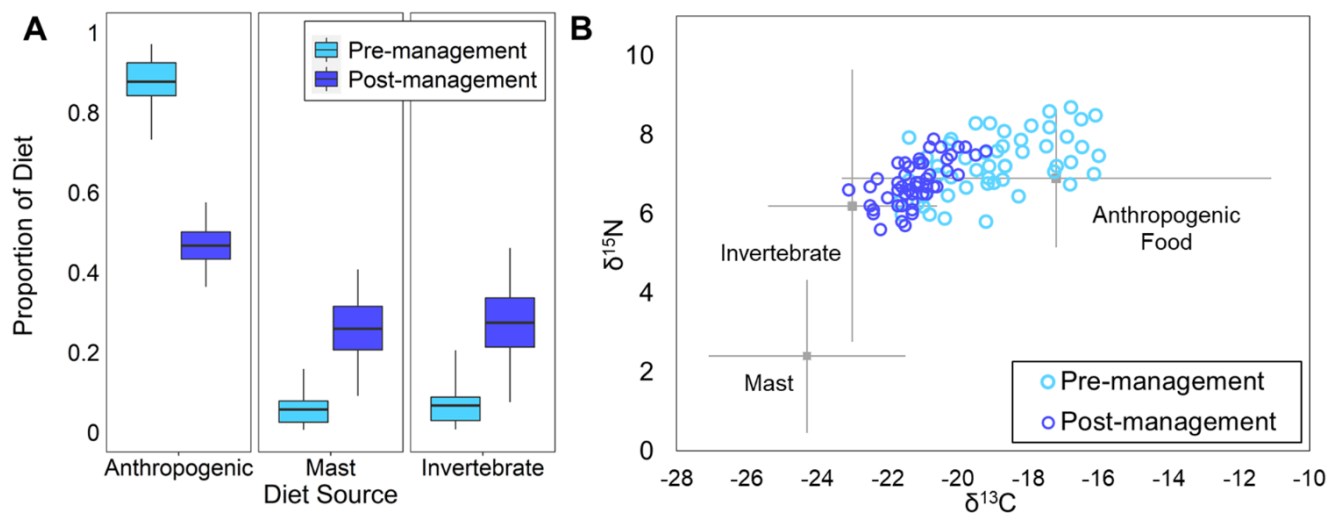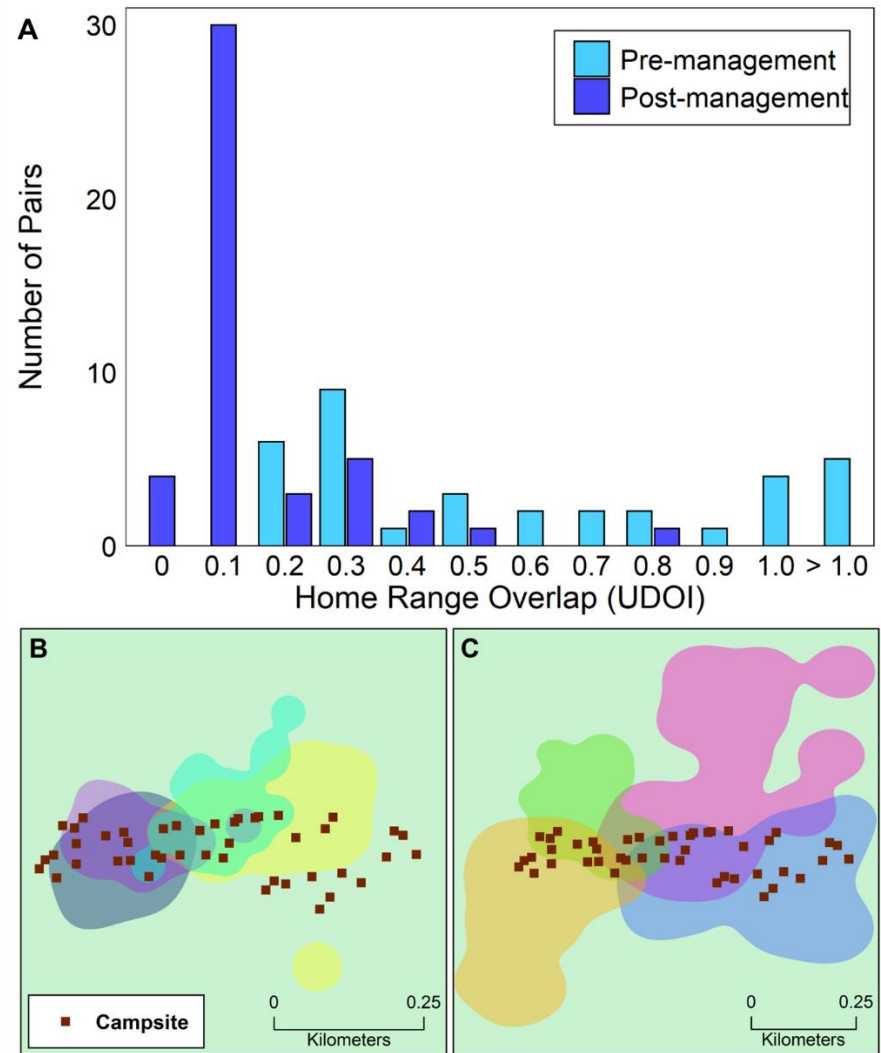
Figure 1

Figure 2

Figure 3

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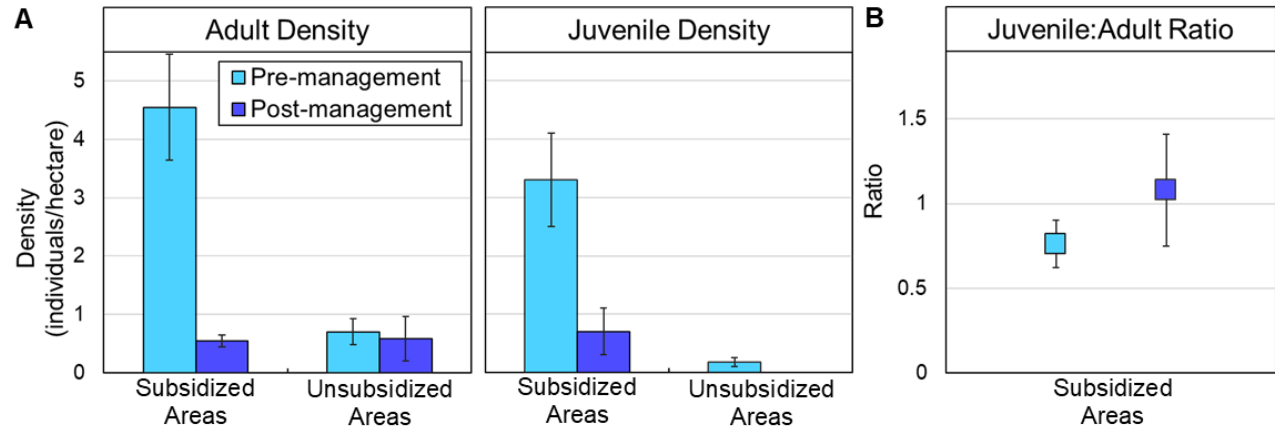
Supplementary Materials

Table S1. Sample sizes and mean stable isotope signatures and elemental concentrations of Steller's jay diet sources (adapted from West et al. 2016).

Diet Source	n	$\delta^{13}C$ (‰) Mean	SD	$\delta^{15}N$ (‰) Mean	SD	Elemental Concentration (wt%) C	N
Mast	38	-27.8	2.7	-0.9	1.9	43.9	0.9
Invertebrate	151	-26.5	2.3	2.9	3.4	50.3	10.2
Anthropogenic	45	-20.7	5.5	3.6	1.7	44.6	3.2

Table S2. Mean $\delta^{13}C$ enrichment and growth bar width for jays captured in campgrounds in Butano and Big Basin State Parks in the pre-management period. We combined rectrices from the two parks to get a higher sample size for the pre-management period.

State Park	$\delta^{13}C$ enrichment (‰)		Growth bar width (standardized)	
	Mean	95% CI	Mean	95% CI
Big Basin	-19.0	-20.07 to -19.21	4.67	4.11 to 5.23
Butano	-19.64	-19.40 to -18.51	4.73	4.51 to 4.95
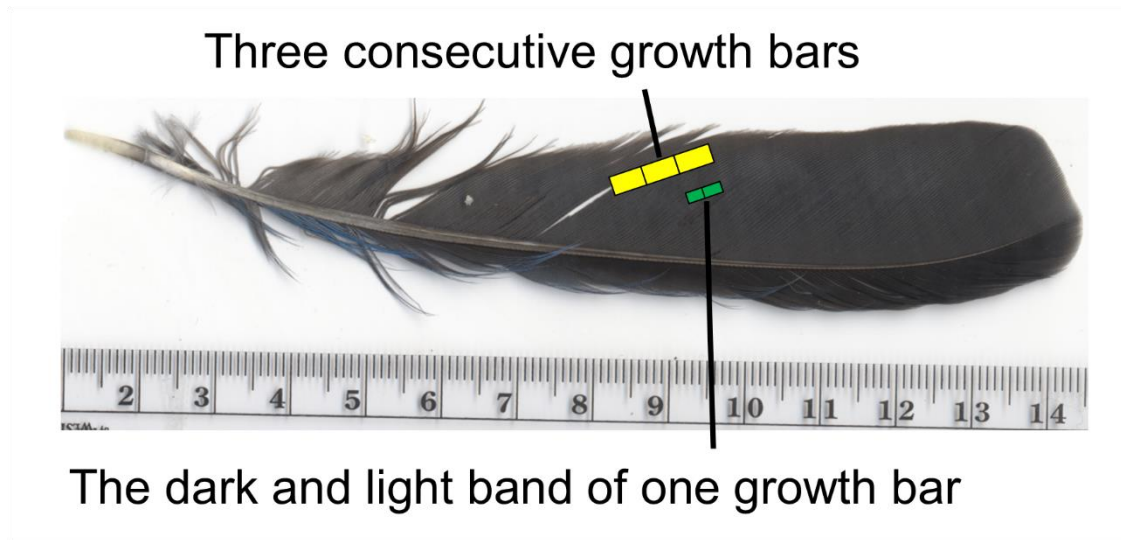
Figure S1. An example of a Steller's jay rectrix with growth bars. One feather growth bar (green block) consists of a dark band (produced during the day) and a light band (produced at night). The yellow block shows three consecutive growth bars.

Supplemental methods – Distance sampling

Pre-management. In the pre-management period, adult and juvenile jay densities in campground and forest areas were estimated in four separate models: adult campground jays, juvenile campground jays, adult forest jays, and juvenile forest jays. All models were implemented in Program Distance. Five detection functions were compared, each using month and year as covariates: half-normal cosine, half-normal hermite-polynomial, uniform cosine, hazard-rate cosine, and hazard-rate simple polynomial. Detection functions were ranked using AIC, and the top models all fit the data reasonably well (i.e. χ^2 goodness-of-fit $P > 0.05$ for all models).

Post-management. For the campground jay model, we compared five detection functions with transformations and no covariates: half-normal cosine, half-normal hermite-polynomial, uniform cosine, hazard-rate cosine, and hazard-rate simple polynomial; and two detection functions with age as a covariate: half-normal and hazard-rate.

For the unsubsidized forest jay model, we compared the same five detection functions with transformations, and the same two detection functions with covariates, but with month and year as covariates, rather than age.

Chapter 3: Failed despots and the equitable distribution of fitness in a subsidized species

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Abstract

Territorial species are often predicted to adhere to an ideal despotic distribution and under-match local food resources, meaning that individuals in high-quality habitat achieve higher fitness than those in low-quality habitat. However, conditions such as high density, territory compression, and frequent territorial disputes in high-quality habitat are expected to cause habitat quality to decline as population density increases and, instead, promote resource matching. We studied a highly human-subsidized and under-matched population of Steller's jays (Cyanocitta stelleri) to determine how under-matching is maintained despite high densities, compressed territories, and frequent agonistic behaviors, which should promote resource matching. We examined the distribution of fitness among individuals in high-quality, subsidized habitat, by categorizing jays into dominance classes and characterizing individual consumption of human food, body condition, fecundity, and core area size and spatial distribution. Individuals of all dominance classes consumed similar amounts of human food and had similar body condition and fecundity. However, the most dominant individuals maintained smaller core areas that had greater overlap with subsidized habitat than those of subordinates. Thus, we found that 1) jays attain high densities in subsidized areas because dominant individuals do not exclude subordinates from human food subsidies and 2) jay densities do not reach the level necessary to facilitate resource matching because dominant individuals monopolize space in subsidized areas. Our results suggest that human-modified landscapes may decouple dominance from fitness and that incomplete exclusion of subordinates may be a common mechanism underpinning high densities and creating source populations of synanthropic species in subsidized environments.

Introduction

Ecological theory predicts that the distribution of individuals in landscapes with heterogeneously distributed food resources is a function of habitat selection strategies, mediated by social system (Fretwell and Lucas 1969). For territorial species, habitat selection is often influenced by unequal competitive abilities, and organisms are predicted to adhere to an ideal despotic distribution (Fretwell 1972; Calsbeek and Sinervo 2002). Under an ideal despotic distribution, dominant ('despotic') individuals exclude subordinates from high-quality habitat containing relatively abundant food resources, compelling them to instead use lower-quality habitat with fewer food resources. In these situations, territorial exclusion is predicted to result in the under-exploitation of food resources in high-quality habitat (i.e., resource under-matching) such that individual fitness is greater in high- than in low-quality habitat (Fretwell 1972; Kennedy and Gray 1993). Under this scenario, the most dominant individuals are predicted to secure the highest quality territories and gain a fitness benefit from doing so (Carpenter and MacMillen 1976; Gill and Wolf 1977; Calsbeek and Sinervo 2002).

The predictions of the ideal despotic distribution and resource under-matching have held for some territorial species (Andren 1990; Lin and Batzli 2001; Calsbeek and Sinervo 2002), but certain conditions can lead to the breakdown of the ideal despotic distribution and instead promote resource matching. Territoriality, a prerequisite of the ideal despotic distribution, can break down when food resources are abundant and the cost of defending them outweighs the benefit gained by excluding subordinates (Carpenter and MacMillen 1976; Hixon 1980). Additionally, high densities of competitors can lead to territory compression (or 'shrinkage') and to more frequent territorial disputes, which can decrease individual fitness in high-quality habitat (Pusenius and Schmidt 2002; Ridley et al. 2004; Haché et al. 2013). Both of these processes could lead to departures from the expectations of the ideal despotic distribution and instead promote resource matching, where habitat

quality declines as population density increases until fitness becomes equivalent between high- and low-quality habitats (Pulliam and Caraco 1984; Fagen 1987; Tregenza 1995). Thus, the defensibility of resources plays a key role in determining the extent to which social systems, and specifically territoriality, shape the distribution and fitness of individuals. While the classic concept of the ideal despotic distribution may sometimes be unrealistic for natural populations (Kennedy and Gray 1993), it provides a useful starting point for testing ideas about how the distribution of resources facilitates habitat selection strategies and the distribution of organisms, especially in human-modified systems.

Human food subsidies are one example of an often abundant and stable resource that may be difficult to defend and could affect habitat selection and the distribution of fitness. Human food subsidies are a global phenomenon with myriad ecological and evolutionary consequences for biodiversity (Oro et al. 2013; Newsome et al. 2015). Landscapes that are highly influenced by human activity are often an abundant source of such subsidies (Marzluff and Neatherlin 2006; Oro et al. 2013), which can alter territorial behavior (Evans et al. 2010; Scales et al. 2011; Hardman and Dalesman 2018) and space use (O'Donnell and DelBarco-Trillo 2020). Human food subsidies also commonly promote high densities and fitness of synanthropic species (Marzluff et al. 2001; Prange et al. 2003; Shochat 2004). Because synanthropes often utilize human food subsidies, they can provide valuable opportunities for understanding how these subsidies affect habitat selection and social systems and, ultimately, influence individual and population-level fitness.

Here, we studied a population of Steller's jays (Cyanocitta stelleri), a common territorial and synanthropic bird species in the forests of western North America, that are under-matched to abundant human food resources in subsidized habitats (i.e., campgrounds). In this system, average body condition and fecundity are higher in subsidized campground areas than unsubsidized habitats

away from campgrounds (West and Peery 2017). However, resource under-matching in this system is contrary to expectations, as exceptionally high population density, compressed and overlapping territories, and frequent agonistic interactions between jays (West and Peery 2017) should theoretically reduce the benefit of settling in resource rich environments and facilitate similar fitness outcomes between subsidized and unsubsidized habitats (Ridley et al. 2004; Shochat et al. 2006). Additionally, Steller's jays typically exhibit incomplete territoriality, in which individuals are most dominant at the center of their territory and less dominant towards the periphery (Brown 1963), and this social system may promote departures from the expectations of the ideal despotic distribution and resource under-matching.

To understand how resource under-matching persists in this system, we assessed how individual subsidy consumption, fitness, and space use varied as a function of social dominance within high-quality, subsidized habitat. We hypothesized that Steller's jays attained high densities in subsidized areas because dominant individuals did not exclude subordinates from subsidies, as the cost of doing so would outweigh the benefits (Carpenter and MacMillen 1976). Thus, we predicted similar levels of human food subsidy consumption and fitness (body condition and fecundity) between dominant and subordinate jays. Further, we hypothesized that under-matching could persist if dominant individuals monopolized breeding sites that overlapped with campgrounds and prevented at least some subordinate jays from nesting in highly subsidized areas. This partial exclusion could allow subsidized campground areas to support dense populations of fit jays, but also prevent so many jays from using campgrounds that the population would match abundant food resources. Testing these predictions will help elucidate mechanisms promoting the commonly observed phenomenon of high densities of synanthropic species in human-dominated, subsidized landscapes. Further, as the impacts of human food subsidies are unlikely to diminish in the future,

understanding how habitat selection strategies and social systems are modified under their influence is important for conservation and predicting wildlife distributions into the future.

Methods

Study system and sampling. We studied populations of Steller's jays in two campgrounds within Big Basin Redwoods State Park, Santa Cruz County, California (hereafter Big Basin; Figure 1), to test our hypotheses about resource under-matching. Because of the availability of human food subsidies and previously established high fitness of jays utilizing campground areas, we considered campgrounds to be high-quality habitat and surrounding forest areas to be of lower quality (West and Peery 2017; West et al. 2019). We collected data during three breeding seasons, mid-May – mid-August, in 2017, 2018, and 2019. We captured and banded jays with unique color combinations for individual recognition and to assess individual fitness (see next sections). We used call playback and a combination of mist nets (Avinet Research Supply) and live traps (Havahart and homemade) to capture jays during all three years of the study. To characterize jay space use, we also deployed radio transmitters (Model A1070, Advanced Telemetry Systems) on jays using backpack-style harnesses made of 0.1" natural tubular spectra tape (Bally Ribbon Mills) in each year of the study.

To examine jay space use, we tracked each radio tagged jay to determine their precise location (± 10 m) 25-35 times per season. We allowed at least two hours between relocations of the same individual to ensure independence between relocations (Swihart and Slade 1985), and we varied the time of day during which we tracked individuals. We also collected roost locations (between 2200 and 0300) to ensure that we fully characterized jay home ranges. We tracked birds by searching on foot with telemetry equipment and marked jay locations using a handheld GPS unit. Observations of jays and jay behavior throughout the breeding season allowed us to assess the

breeding status of jays and determine the identities of socially monogamous jay pairs. We only used male jays for these analyses because female jays are generally subordinate to males (Brown 1963), and our sample size of uniquely identified females did not allow dominance assessment.

Defining dominance classes. We classified jays into dominance classes by conducting controlled feeding trials (hereafter 'behavior trials') at picnic tables. Because jays have site-based dominance where territorial defense typically weakens as distance from the nest site increases (Brown 1963), we determined a dominance ranking of jays at individual picnic tables dispersed throughout the entire campground to ensure we fully captured spatial variation in dominance for each individual. During each trial, we placed approximately 10 peanuts at the center of a picnic table and then observed jays as they interacted with conspecifics to exploit the food source (Brown 1963, West and Peery 2017). We recorded every banded individual present at each trial, the winner and loser of each interaction, and the aggression level of each interaction on a 0-5 scale. An aggression level of zero indicated that individuals did not interact when feeding at the same time on a table, and so no winner was recorded. Aggression levels were defined as follows: 1: one jay wing-flapped and vocalized with an 'aap' or 'wek' call at another; 2: one jay displaced another; 3: one jay chased another; 4: jays aggressively sidled with one another but did not make contact; 5: jays physically fought with one another (West and Peery 2017). We evaluated the results of behavior trials to determine the most dominant bird at each table. To be considered dominant at a table, an individual had to win at least 3 interactions at that table. At each table, an individual was considered dominant if it won the most interactions at that table or if it always won interactions against the bird that won the most interactions. In cases where there was not a consistent winner between two individuals that consistently won against all other individuals, or where consistent winners did not interact with one

another, we classified the bird with the higher average aggression score in contests that they won as dominant. In cases where individuals' wins and aggression scores tied, both were considered dominant at a given table. An individual was also considered dominant at a given table if it was the only individual (with the exception of its mate) to appear for two or more 15-minute trials at a specific table on different days. There were occasionally tables at which not enough interactions occurred to determine a dominant bird. We conducted between one and six trials at each of 49 picnic tables in Bloom's Creek Campground and 65 picnic tables in Huckleberry Campground each year.

We determined dominance for each year separately because dominance and core areas could shift from year to year. Within each year, we overlaid core areas (see below for core area delineation methods) in ArcMap (version 10.7; ESRI 2019) with the results of the behavior trials at each picnic table, and then classified jays into three social classes. 'High' dominance included individuals that were dominant at tables within and outside their core area, 'medium' dominance included individuals that were dominant only within their core area, and 'low' dominance included individuals that were not dominant anywhere within the campground (Figure 2).

Human food subsidy consumption. We evaluated individual consumption of human food subsidies using stable isotope analysis of $\delta13C$ in primary feathers. $\delta13C$ is a useful indicator of human food consumption because human foods are often made up of corn (a C4 plant) and corn byproducts, making them enriched in the heavy isotope of carbon. This makes them isotopically distinguishable from natural prey items in western North America because primary production in this area is driven by native C3 plants (Newsome et al. 2010; West et al. 2016). We clipped approximately 50 mm of the most recently grown new primary flight feather from each captured jay

at the end of the breeding season (early-mid August) at least 40 days after the conclusion of behavior trials. Because feathers incorporate the isotopic signature of the diet during periods of feather growth (Hobson and Clark 1992) and a primary feather takes approximately 30 days to grow, these feather samples represented breeding season diet but were not contaminated by any peanut consumption that occurred during the behavior trials. We rinsed feather samples thrice in 2:1 Chloroform:Methanol solution to remove surface contaminants and then homogenized them using scissors. Homogenized feathers were dried for approximately 72 hours at 55°C. Analysis of δ13C was conducted at the University of New Mexico Center for Stable Isotopes using a Thermo Scientific Delta V mass spectrometer connected to a high-temperature conversion elemental analyzer and a Costech 4010 elemental analyzer. We report δ13C results as parts per mil (‰) ratio relative to the international standard, Vienna-Pee Dee Belemnite limestone. We examined the relationship between dominance class and human food subsidy consumption using a linear mixed model with individual as a random effect because we captured some of the same individuals in multiple years of the study. We used δ13C as the continuous response variable and categorical dominance class (i.e., low, medium, high) as the fixed effect. We also included year as a fixed effect to correct for some heteroscedasticity in the residuals. Results are presented as the estimated marginal mean averaged over the three years of the study and a 95% confidence interval.

Fitness metrics. To understand how fitness was distributed among birds in different dominance classes, we collected data on body condition (i.e., body mass and growth bar width) and annual fecundity. We conducted analyses using the 'lme4' package (version 1.1-21; Bates et al. 2015) and compared means between dominance classes when necessary using the 'emmeans' package (version 1.6.1; Lenth 2021) in the R Statistical Environment (R Core Team 2020).

We measured two indices of body condition: body mass and growth bar width. We measured body mass using a Pesola scale when birds were recaptured at the end of the breeding season (early-mid August). We standardized body mass for body size using tarsus length cubed, an index of body volume (West and Peery 2017). We measured tarsus length using calipers during the same capture event at which body mass was measured. We then multiplied these values by 10,000 for ease in reporting results. We first evaluated body mass among the dominance classes using a linear mixed model with individual as a random effect. However, the variance of the random effect was estimated as zero, and thus we removed it and simply used a two-way ANOVA. Standardized body mass was the continuous response variable, and we used dominance class and year as categorical factors. We did not include an interaction effect between dominance class and year because there was no reason to expect a different relationship between body mass and dominance among years.

We used growth bar width as another indicator of individual body condition. A feather growth bar consists of one dark band produced during the day, and one light band, produced at night (Wood 1950). Together, one set of bands constitutes feather growth in a 24-hour period (Wood 1950; Grubb 2006). Feather growth is energetically costly, and therefore the ability to grow feathers faster (i.e., wider growth bars) is positively correlated with nutritional status (Grubb 1991). We collected the newest newly grown rectrix, determined by molt pattern and presence of feather sheaths, from each jay recaptured at the end of the breeding season, at least 40 days after the conclusion of behavior trials. Growth bars reflect nutrition during the time of feather growth and thus, because we took a newly grown feather, growth bar width was not contaminated by any peanuts that may have been consumed during the behavior trials. We standardized growth bar width by body size using tarsus length cubed, as we did for body mass, and multiplied it by 100,000 for ease in reporting. We then used a linear mixed model with individual as a random effect to assess the

relationship between dominance class and growth bar width. We used standardized growth bar width as the continuous response variable and we used dominance class and year as additive fixed effects. Results are presented as the estimated marginal mean averaged over the three years of the study and a 95% confidence interval.

We estimated annual fecundity (i.e., number of fledglings produced) for individual jays by either locating and monitoring nests until the young fledged (n = 4) or by following radio-tagged birds and observing how many fledglings they interacted with (e.g. begging or feeding behavior; n = 47). Fledgling Steller's jays follow and receive food from their parents for 30 days or more after fledging (Walker et al. 2020; EHW and KB pers. observations), so it was possible to determine nest success and number of fledglings by closely observing both members of the pair after nesting was completed. When possible, we also banded juveniles so that we could discern identities when we observed family groups on multiple occasions.

We treated annual fecundity two different ways for analysis. We first considered annual fecundity as continuous and compared the mean number of fledglings per male per year among dominance classes using a linear mixed model with individual as a random effect. The variance of the random effect was estimated to be zero, so we removed it from the model and assumed independence among all annual fecundity estimates. Due to small sample sizes and non-normality in the distribution of fecundity data, we used a Kruskal-Wallis test for the final comparison of mean annual fecundity between dominance classes. In our second approach, we treated fecundity as a binary indicator of nest success by grouping birds according to whether they successfully fledged offspring or not. We then conducted a chi-squared test to determine if there was any relationship between ordinal dominance class and nest success.

Space use. To characterize jay space use, we delineated home ranges and core areas for each radio-tagged individual. We defined a home range as the 95% Utilization Distribution for each individual jay (West et al. 2016), and we analyzed relocation data using the adehabitatHR package (Calenge 2006) in the R Statistical Environment (R Core Team 2020). Next, we delineated core areas following methods from Vander Wal and Rodgers (2012). Specifically, we plotted each jay's utilization distribution area against the isopleth volume (Figure S1) and identified the isopleth at which the slope was closest to one (Vander Wal and Rodgers 2012). This point represents the threshold at which proportional home range area begins to increase at a greater rate than the probability of use, and we used that isopleth to define the borders of each jay's core area (Vander Wal and Rodgers 2012). We chose this method, rather than using an arbitrary 50% utilization distribution, in an effort to ensure that our core areas accurately represented the areas that received the greatest use (see Appendix S1 for a comparison of methods). Finally, we removed seven individuals from all further analyses because their core areas did not overlap campground areas, so we could not accurately assess their dominance class.

We originally planned to examine both core area size and home range size in relation to dominance class, but because these two measurements were highly positively correlated ($r = 0.97$), we only considered core area size. We log-transformed core area size to meet the assumption of normal distribution and then used a linear mixed model with individual as a random effect to examine the relationship between dominance class and core area size. The variance of the random effect was estimated as zero, so we removed it from the model and used a two-way ANOVA with dominance class and year as categorical factors. Results are presented as the estimated marginal mean averaged over the three years of the study and a 95% confidence interval.

To compare the spatial distribution of core areas in relation to high-quality habitat, we calculated the proportion of overlap between each individual's core area and the campground area. To delineate the campground boundary, we created a 10-m buffer around each campsite and used the minimum bounding geometry tool in ArcMap (version 10.7.1; ESRI 2019) to create minimum convex hull polygons around the two campgrounds. We calculated the area of overlap between individual core areas and campgrounds and then divided by the total area of individual core areas to determine the proportion of each individual's core area that overlapped with the campground. Steller's jays in their first breeding season rarely breed (Brown 1963, West and Peery 2017), and we observed that some of these individuals utilized a strategy of being subordinate 'floaters' in which they maintained a high degree of overlap with campground areas. Our hypotheses were restricted to territorial, breeding jays, and we therefore included only individuals known to be in at least their second breeding season in this analysis. To test whether highly dominant individuals had more overlap with campgrounds than subordinates, we conducted a two-way ANOVA, with the proportion of core area overlap with campgrounds as the response, and dominance class and year as explanatory variables.

Results

Defining dominance classes. Across the three years of the study, we classified 17 males as low dominance, 15 males as medium dominance, and 21 males as high dominance. In 2017, we conducted 152 behavior trials and recorded a total of 1057 dyadic interactions (83% with aggression score >0); in 2018, we conducted 151 behavior trials and recorded 1544 dyadic interactions (81% with aggression score >0); and in 2019, we conducted 183 behavior trials and recorded 1509 dyadic interactions (87% with aggression score >0). On average, low dominance males won 15% of all

interactions (aggression score >0) in which they were involved, medium dominance males won 59%, and high dominance males won 75%. When high dominant males lost interactions, it was most often to other high dominance males (72% of losses). Indeed, considering only tables at which they were dominant, the dominant individual won 96% of the interactions in which they were involved, on average.

Human food subsidy consumption. We measured the human subsidy consumption of 45 individuals (n = 16 low dominance, n = 12 medium dominance, and n = 17 high dominance). Jays with low dominance ($\delta 13C$ = -21.2 ± 0.22‰), medium dominance (-21.2 ± 0.25‰), and high dominance (-21.0 ± 0.21‰) all had similar levels of subsidy consumption ($\delta 13C$; p-value for all pairwise comparisons > 0.83; Figure 3A). There was no evidence of any difference in subsidy consumption among years (p-value for all comparisons > 0.50).

Fitness metrics. We measured body mass of 35 individuals (n = 14 low dominance, n = 8 medium dominance, and n = 13 high dominance). Body mass ranged from 110-127 g, while tarsus length ranged from 40.2-46.5 mm. Standardized body mass ranged from 11.5-18.6. Estimated marginal mean body mass for each dominance class was very similar (low: 15.0 ± 0.36, medium: 15.0 ± 0.47, high: 14.9 ± 0.37), and thus we found no evidence for a difference in body mass between dominance classes (p-value for all comparisons > 0.98). However, average body mass was higher in 2018 (estimated marginal mean = 16.0 ± 0.37) than in 2017 (14.4 ± 0.39; $t30$ = 3.04, p = 0.01) and 2019 (14.5 ± 0.43; $t30$ = 2.73, p = 0.03; Figure 3B).

We measured the average feather growth bar width of 42 individuals (n = 14 low dominance, n = 10 medium dominance, and n = 18 high dominance). Average growth bar width ranged from 2.1-5.3 mm, and standardized growth bar width ranged from 3.90-7.55. Estimated marginal mean growth bar width was similar for each dominance class (low: 5.14 ± 0.28, medium: 5.67 ± 0.32, high: 5.29 ± 0.25), and we found no evidence of differences between any groups (p-value for all comparisons > 0.39; Figure 3C). We also found no evidence for differences among years (p-value for all comparisons > 0.17).

We determined annual fecundity for 47 jays (n = 16 low dominance, n = 13 medium dominance, n = 18 high dominance) across the three years of the study. Fecundity estimates ranged from 0 to 4 fledglings, with 4 fledglings observed only once. Average annual fecundity estimates were quite similar for low (1.31, SE = 0.31), medium (1.15, SE = 0.34), and high (1.44, SE = 0.30) dominance individuals. Our Kruskal-Wallis test confirmed there were no differences in average number of fledglings among dominance classes (H(2) = 0.37, p-value = 0.83), and Chi-squared tests also confirmed that distributions were independent even when fecundity data were considered as binary (i.e., success/failure; Chi-squared = 0.63, df = 2, p-value = 0.73; Figure 4).

Space use. We delineated core areas for 53 individuals (n = 17 low dominance, n = 15 medium dominance, n = 21 high dominance). Core areas had a high amount of overlap (Figure 2) and core area size varied considerably (range: 0.63 to 7.19 ha). Back-transformed estimated marginal mean core area sizes were similar for low (2.82 ± 1.14 ha) and medium (2.57 ± 1.13 ha; $t48 = 0.53$, p-value = 0.86) dominance classes, but there was strong evidence that high dominance individuals maintained smaller core areas (1.49 ± 1.11 ha) than low ($t48 = 3.77$, p-value < 0.01) and medium ($t48 = 3.18$, p-value < 0.01) dominance individuals (Figure 5A). We also found moderate evidence

that core areas were larger in 2019 than in 2018 ($t48$ = -2.28, p-value = 0.06), but there was no

evidence of a difference between 2017 and 2018 ($t48$ = 1.00, p-value = 0.58) or between 2017 and

2019 ($t48$ = -1.39, p-value = 0.35).

During our study, only a small number of birds in their first breeding season regularly used

campgrounds (n = 5); however, these were all low dominance and had high average overlap between

their core areas and campgrounds (0.78 ± 0.15). We never observed any of these 'floaters' with a

mate or participating in breeding or nesting behaviors, so we present results only for individuals

known to be in at least their second breeding season. We assessed the spatial distribution of core

areas for 39 territorial breeding individuals (n = 8 low dominance, n = 12 medium dominance, n =

19 high dominance). There was strong evidence of a difference in mean overlap of core areas with

the campground among all dominance classes ($F2,34$ = 5.90, p-value < 0.01). Specifically, the core

areas of high dominance individuals (0.75 ± 0.05) overlapped campgrounds more than low (0.45 ±

0.07) dominance individuals ($t34$ = 3.31, p < 0.01). There was also weak evidence for a difference in

overlap between high and medium (0.58 ± 0.06) dominance classes ($t34$ = 2.17, p-value = 0.09), but

there was no evidence of a difference between low and medium dominance classes ($t34$ = 1.39, p-

value = 0.36; Figure 5B). Thus, among territorial breeders, dominant individuals had more core area

overlap with campgrounds on average than subordinate individuals (Figure S2).

Discussion

Our results suggests that, first, jays attain high densities in campgrounds because dominant jays do

not exclude subordinates from human food subsidies. This conclusion is supported not only by

stable isotope analyses, but also by observations both during and outside behavior trials, when we

frequently observed subordinate jays accessing subsidies while dominant jays were chasing other

individuals, caching food resources, or not present. We conclude that human food resources are too abundant and dispersed and dominant jays face too many competitors to be effective despots of abundant human subsidies. Second, our results suggest that jay densities do not reach the level necessary to facilitate resource matching because dominant individuals monopolize space in subsidized campground areas. Dominant individuals had small core areas that spatially overlapped subsidized campgrounds, and subordinate individuals were compelled to use larger areas within and on the periphery of campgrounds. Individuals obligated to use areas even further from campgrounds likely face a tradeoff between traveling to campgrounds to access food subsidies and defending their own territories. Consequently, resource under-matching is maintained because dominant jays monopolize space (e.g., breeding sites) and prevent densities in campground areas from reaching the level necessary to reduce individual fitness and promote resource matching.

While dominance is typically assumed to be positively correlated with fitness (Ellis 1995), the prevalence of readily available human food subsidies appears to have decoupled the link between dominance and fitness such that dominance does not necessarily confer a fitness benefit within campgrounds (Verhulst and Salomons 2004). Dominance is most likely to result in a fitness benefit when resources are scarce (Ellis 1995; Henderson and Hart 1995), and therefore the behavioral strategy of using aggression to maintain dominance may benefit individuals living in resource-poor landscapes, while those living in areas with abundant food subsidies do not glean a fitness benefit from this strategy. We note however, jays are known to engage in a moderate level of extra-pair parentage (Overeem et al. 2014); therefore, there could be cryptic reproductive skew towards dominant males that we were unable to measure in this study. Additionally, we were unable to measure lifetime survival and reproductive success of jays because jays are long-lived (Klimkiewicz and Futcher 1989) relative to the duration of our study. However, jays in subsidized areas have very high annual survival on average (annual survival > 0.92; West et al. 2019). This suggests that even

subordinate birds have a low risk of mortality and may achieve similar lifetime fecundity, considering that annual fecundity estimates were similar.

Adherence to an ideal despotic distribution is the most likely explanation for the persistence of resource under-matching, especially in light of the incomplete territoriality of Steller's jays (Brown 1963). However, we acknowledge that under-matching is the most observed departure from the ideal free distribution in free-living populations and can also occur due to violations of the 'ideal' assumption (Kennedy and Gray 1993). Consequently, the distribution we observed could also be attributable to inability of individual jays to accurately assess habitat quality and therefore under-using high-quality habitat (i.e., because they have imperfect knowledge). While this is often the case for less mobile species (Zollner and Lima 1997; Katz and Scharf 2018), we find this scenario unlikely because jays are highly mobile and have high cognitive abilities (Emery et al. 2007), both of which should enhance their perceptual range and assist them in accurately assessing habitat conditions (Jiao et al. 2020).

Highly dominant individuals maintained small core areas that overlapped significantly with subsidized campground areas. These areas likely provided the most reliable access to human subsidies and, in principle, should be of the highest quality for breeding. This observation is in line with the concept of economic defensibility (Brown 1964; Calsbeek and Sinervo 2002), which proposes that high territory quality is associated with small territory size because resources are highly concentrated and because territory defense is energetically costly (Carpenter and MacMillen 1976; Carpenter 1987). Under an ideal despotic distribution, subordinate individuals are predicted to use more space to meet their nutritional needs (Calsbeek and Sinervo 2002; Sells and Mitchell 2020), which we also observed in our study area. Subordinate individuals had larger core areas that were more peripheral to campgrounds than those of highly dominant individuals, a phenomenon that was

suggested by West and Peery (2017). Therefore, we theorize that subordinate individuals likely breed on the periphery of campgrounds and in effect, 'commute' into campgrounds to take advantage of readily available food subsidies (see also Figure S2). While commuting jays on the periphery of campgrounds maintained similar fitness to dominant jays, individuals compelled to live even further from campgrounds may experience high energetic costs and increased exposure to predation if they frequently accessed human subsidies. These factors could reduce adult survival or affect provisioning of offspring and, subsequently, offspring quality (Ghalambor and Martin 2001; Eggers et al. 2008). Hence, jays breeding far from campgrounds likely do not make frequent foraging forays into campgrounds; and consequently, jay abundance in subsidized areas remains too low to result in density-dependent reductions in individual fecundity or body condition. This idea is also supported by the observation of West et al. (2016) that jays radio-tagged 1-2 km away from campgrounds were only rarely seen in campgrounds.

More broadly, our results suggest that incomplete territorial exclusion could be a common mechanism explaining the high densities of synanthropic species that are often observed in subsidized habitats (Marzluff et al. 2001; Beckmann and Berger 2003; Prange et al. 2003). The 'credit card hypothesis' (Shochat 2004) proposes that high densities are achieved when populations over-match human food resources, meaning that only the most dominant individuals monopolize breeding opportunities while subordinates survive and contribute to density estimates in subsidized areas without actually reproducing. While we find this hypothesis intriguing, our results, and those of (Rodewald and Shustack 2008), demonstrate that synanthropes can achieve high densities in subsidized areas without over-matching food subsidies and subsequently experiencing reductions in individual fitness. Indeed, in our study, all territorial breeding individuals that utilized human food subsidies were able to achieve elevated body condition and similar annual fecundity (see also West and Peery 2017), despite high densities in subsidized areas. Further, high densities coupled with high

reproduction resulting from imperfect territoriality suggest that subsidized populations may constitute source, rather than, sink populations (as proposed by Shochat 2004) that can also influence the demographics of unsubsidized areas (West et al. 2019). Given that urbanization continues to expand and encroach upon protected areas (Mcdonald et al. 2008; Wood et al. 2014) that provide important habitat for biodiversity (Naughton-Treves et al. 2005; Watson et al. 2014; Pacifici et al. 2020), source populations of synanthropes in subsidized areas like cities, suburbs, and campgrounds have the potential to threaten the viability of rare species using areas purportedly set aside for conservation via mechanisms like predation and competition.

Acknowledgements

Ethical Considerations

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

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Figure Captions

Figure 1. Map of the study area.

Figure 2. Core areas of individual jays overlaid with picnic tables in Huckleberry Campground in 2019. Picnic table color matches the color of the core area of the bird that was dominant at the table. One example each of a high, medium, and low dominance bird are labeled. Gray tables represent sites where we did not record enough interactions to determine dominance.

Figure 3. (A) The amount of anthropogenic food subsidies in the diet of individual jays in each dominance class, as measured by $\delta13C$ concentrations in feathers. Each circle represents one individual. (B) Estimated marginal mean body mass and 95% confidence interval for jays in each dominance class. Colored dot represents the mean over all years, and the estimated marginal means for each year of the study are shown in gray. (C) Estimated marginal mean growth bar width and 95% confidence interval for jays in each dominance class. Colored dot represents the mean over all years, and the estimated marginal means for each year of the study are shown in gray.

Figure 4. (A) Number of offspring fledged by adults in each dominance class over all years of the study. (B) Estimated marginal mean core area sizes for jays in each dominance class, averaged over the three years of the study (to scale). Inner- and outer-most squares represent 95% confidence intervals around the mean (gray line). (C) Mean proportion of core areas that overlapped with campgrounds for each dominance class. Error bars represent 95% confidence intervals. Letters denote significance.
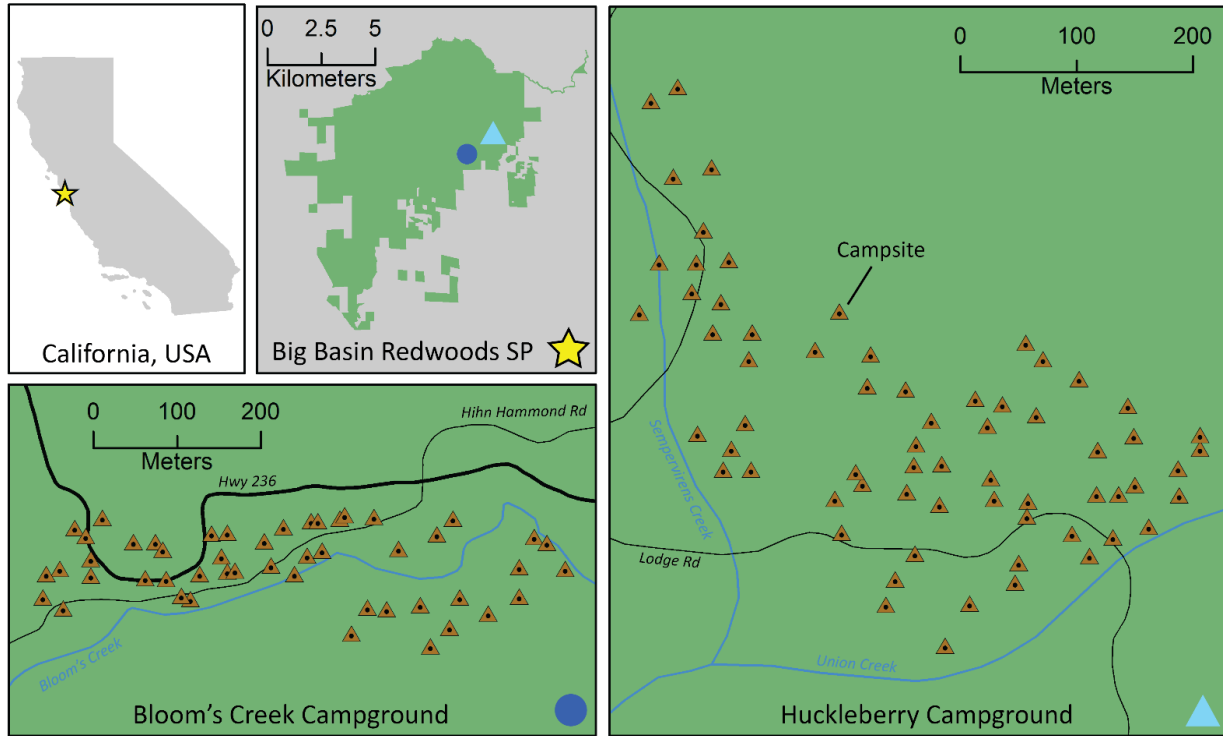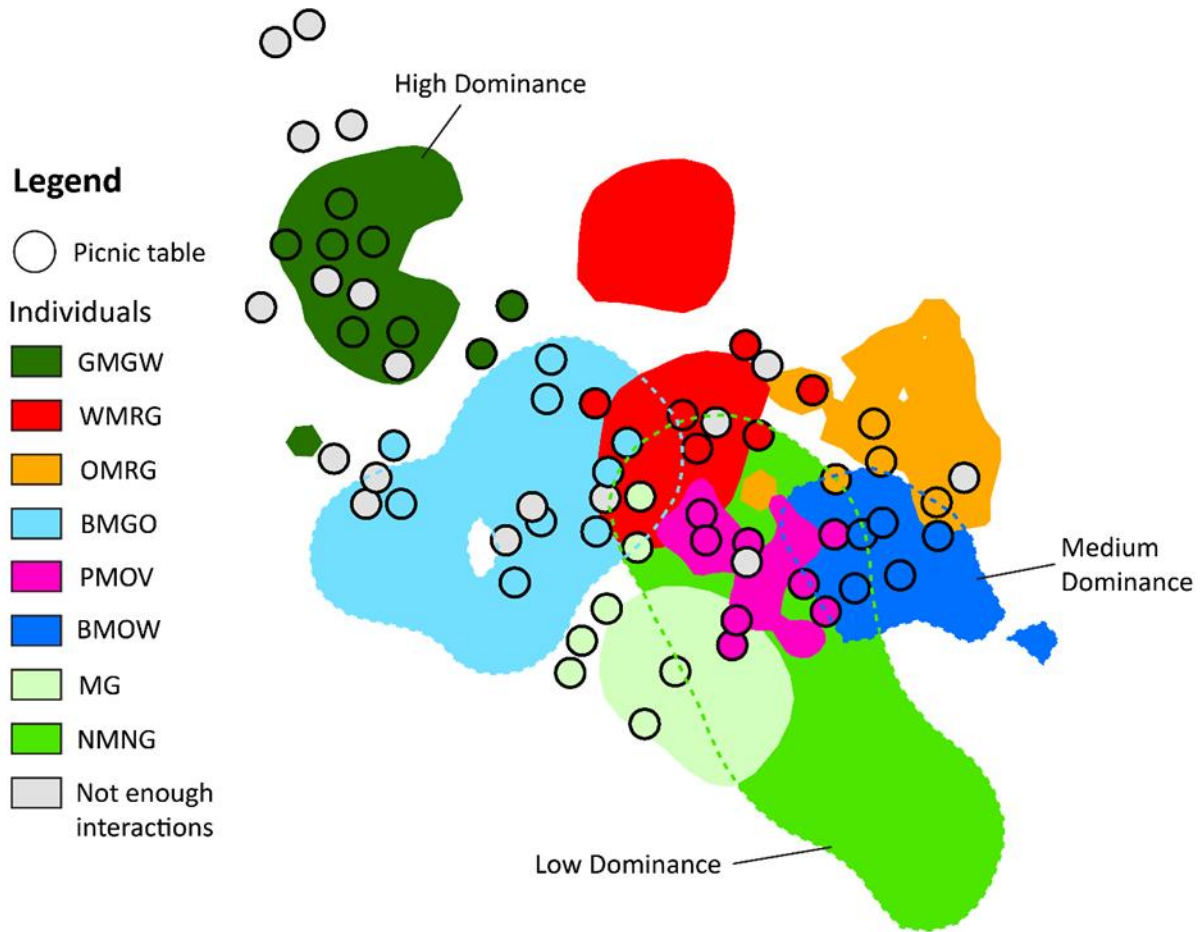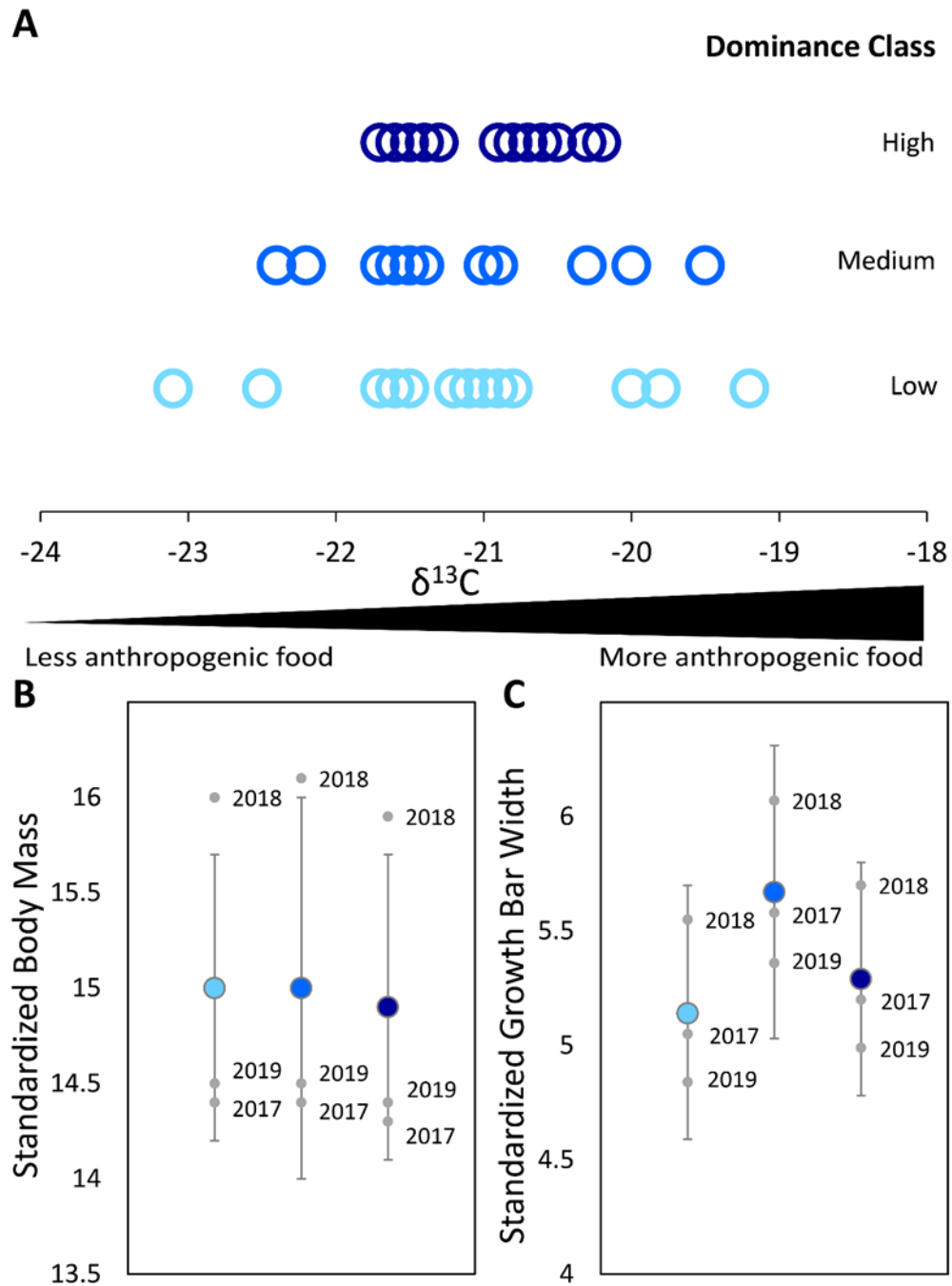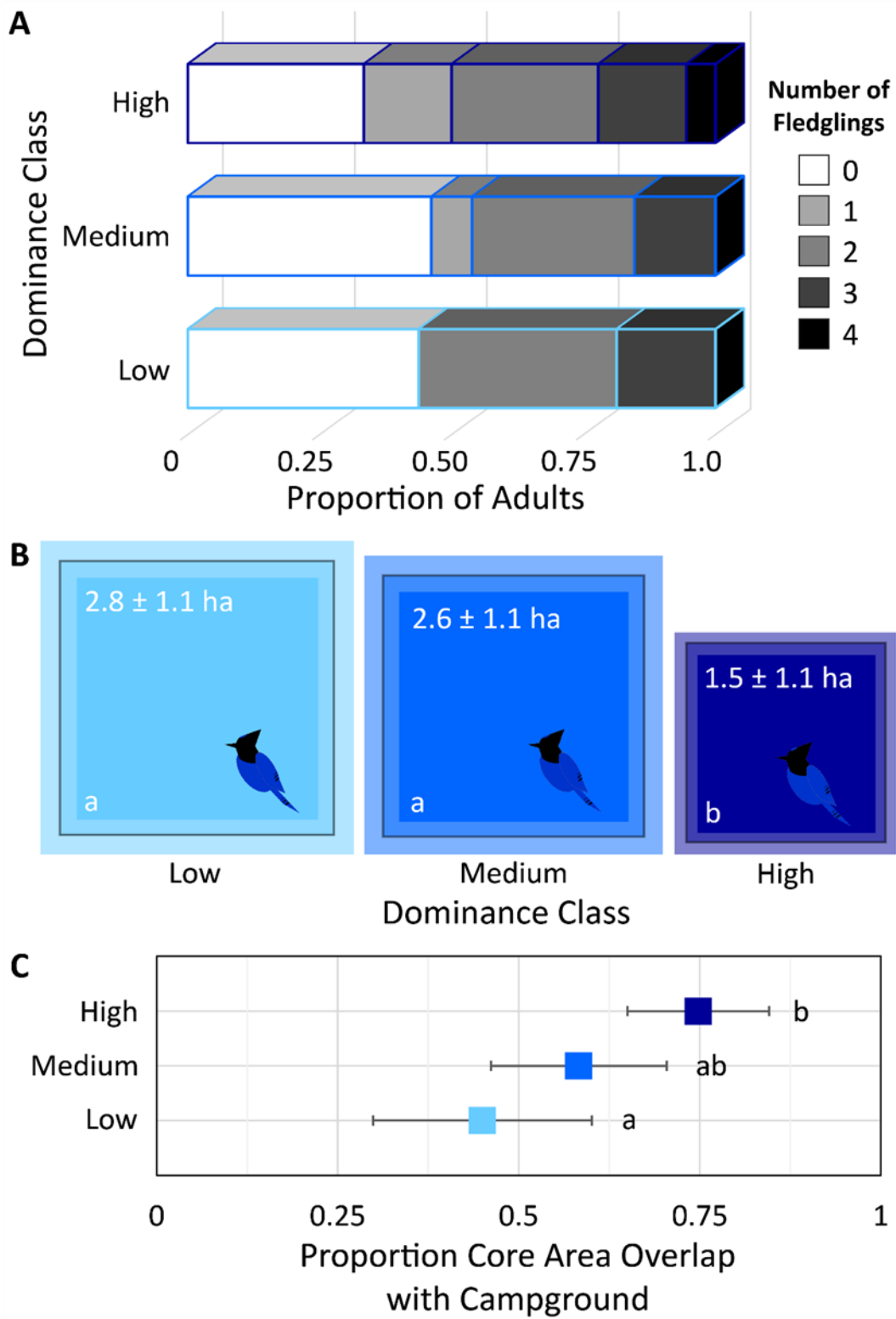
Figure 1

Figure 2

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Supplementary Materials

Appendix S1. Core area delineation and methods comparison

The core area delineation method we used (Vander Wal and Rodgers 2012) resulted in core areas that ranged from the 60% to the 75% utilization distribution. In the end, this core area delineation method only impacted the dominance class of one bird, which changed from high dominance using the 50% UD to medium dominance using the Vander Wal and Rodgers method. All other individuals remained in the same dominance class, regardless of the core area delineation method used.

Appendix S2. Supplementary Analysis

In order to confirm that our assignment of jays into dominance categories using the core area and behavior trial data did not affect our results, we also categorized jays using expert opinion into simply 'high' and 'low' dominance classes. High dominance individuals were those observed most frequently using antagonistic behaviors towards other individuals, and they most frequently initiated and escalated conflicts. Using these criteria, we classified 25 individuals as low dominance and 28 individuals as high dominance. Under the expert opinion criteria, the low dominance category consisted of 16 individuals that were considered low dominance based on the core area criteria, 6 individuals that were considered medium dominance based on core area criteria, and 3 individuals that were considered high dominance under the core area criteria. The high dominance category under the expert opinion criteria consisted of 18 individuals that were considered high dominance under the core area criteria, 9 individuals that were considered medium dominance under the core area criteria, and 1 individual that was considered low dominance under the core area criteria.

Human food subsidy consumption

We analyzed human food subsidy consumption using a linear mixed model with a random effect for individual. We examined the relationship between dominance class and human food subsidy consumption using a linear mixed model with individual as a random effect because we captured some of the same individuals in multiple years of the study. We used $\delta^{13}C$ as the continuous response variable and dominance class determined by expert opinion (i.e., low, high) as the fixed effect. We also included year as a fixed effect to correct for some heteroscedasticity in the residuals.

We found no differences in human food subsidy consumption between high ($\delta^{13}C$ = -21.0‰, 95% CI: -21.4 - -20.6‰) and low ($\delta^{13}C$ = -21.2‰, 95% CI: -21.6 - -20.8‰) dominance individuals (p = 0.43; Figure S3), as determined using expert opinion.

Fitness metrics

We first evaluated body mass among the dominance classes using a linear mixed model with individual as a random effect. However, the variance of the random effect was estimated as zero, and thus we removed it and simply used a two-way ANOVA. Standardized body mass was the continuous response variable, and we used dominance class and year as categorical factors. We found no difference in standardized body mass between high (mean: 15.1, 95% CI: 14.4 – 15.7) and low (mean: 14.9, 95% CI: 14.2 – 15.5) dominance individuals (F = 0.60, p = 0.44; Figure S4A). There was evidence for a difference in body mass among years (F = 6.10, p = 0.006), where body mass was higher in 2018 than in 2017 and 2019.

We used a linear mixed model with individual as a random effect to assess the relationship between dominance class and growth bar width. We used standardized growth bar width as the continuous response variable and we used dominance class and year as additive fixed effects. We found no difference in standardized growth bar width between high (5.36, 95% CI: 4.87 – 5.85) and low (5.29, 95% CI: 4.79 – 5.80) dominance individuals (p = 0.85; Figure S4B).

We treated fecundity as a binary indicator of nest success by grouping birds according to whether they successfully fledged offspring or not. We then conducted a chi-squared test to determine if there was any relationship between dominance class and reproductive success. We found some weak evidence that high dominance individuals may have had slightly higher annual

fecundity Chi-squared = 2.77, df = 1, p-value = 0.09; Figure S5). High dominance individuals averaged 2.57 ± 0.25 fledglings per year, while low dominance individuals averaged 2.08 ± 0.25 fledglings per year.

Space Use

We log-transformed core area size to meet the assumption of normal distribution and then used a linear mixed model with individual as a random effect to examine the relationship between dominance class and core area size. The variance of the random effect was estimated as zero, so we removed it from the model and used an ANOVA with dominance class as a categorical factor. Using expert opinion to categorize jays, we found no difference in average core area size between dominant (2.18 ± 0.26 ha) and subordinate (2.74 ± 0.29 ha) jays (F = 2.53, p = 0.12; Figure S6A).

To test whether dominant individuals had more overlap with campgrounds than subordinates, we conducted a two-way ANOVA, with the proportion of core area overlap with campgrounds as the response, and dominance class and year as explanatory variables. We found moderate evidence that high dominance individuals (0.69 ± 0.04) had higher overlap with campground areas than subordinate individuals (0.54 ± 0.03; F = 4.17, p = 0.048; Figure S6B).

Supplemental figure captions

Figure S1.   Examples of plotting the percent home range area against the isopleth for jays tagged in 2018. The blue vertical line denotes the 50% utilization distribution, and the red line denotes the isopleth at which the slope is closest to one for each individual, which we used to define the core use area for jays.

Figure S2. More examples of low (top left), medium (top right), and high (bottom) dominance individuals. Circles represent picnic tables, and tables are colored according to dominance. Gray tables are sites where we did not record enough interactions to determine dominance.

Figure S3. The amount of anthropogenic food subsidies in the diet of individual jays of low and high dominance, as measured by $\delta^{13}C$ concentrations in feathers. Each dot represents one individual, and the box plot shows the range of $\delta^{13}C$ values.

Figure S4. Standardized body mass (A) and growth bar width (B) for jays of low and high dominance, as determined by expert opinion.

Figure S5. Number of offspring fledged by adults of low and high dominance, as determined by expert opinion, over all years of the study.

Figure S6. Average core area size (A) and average core area overlap with campground areas (B) for high and low dominance jays, as determined by expert opinion.
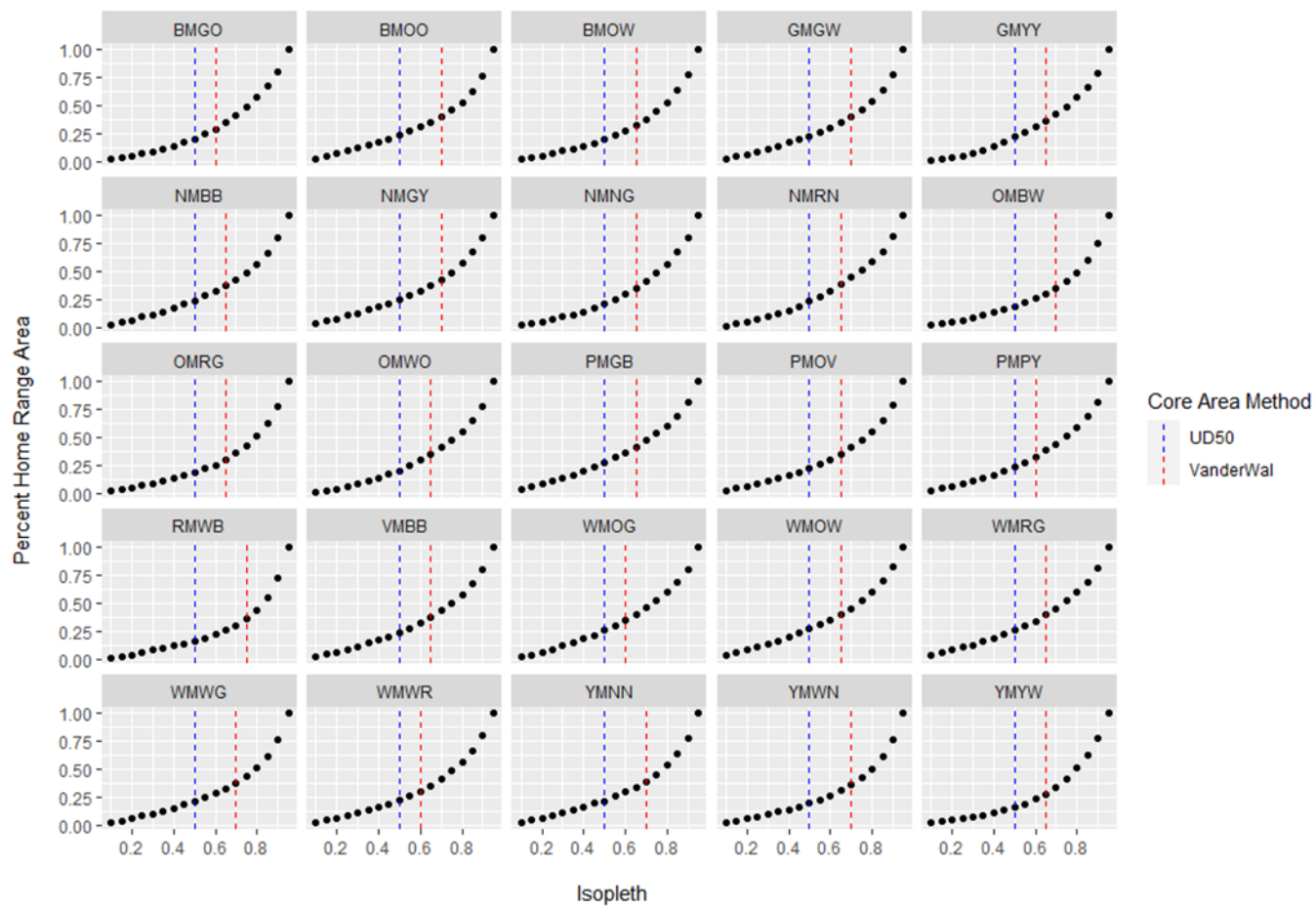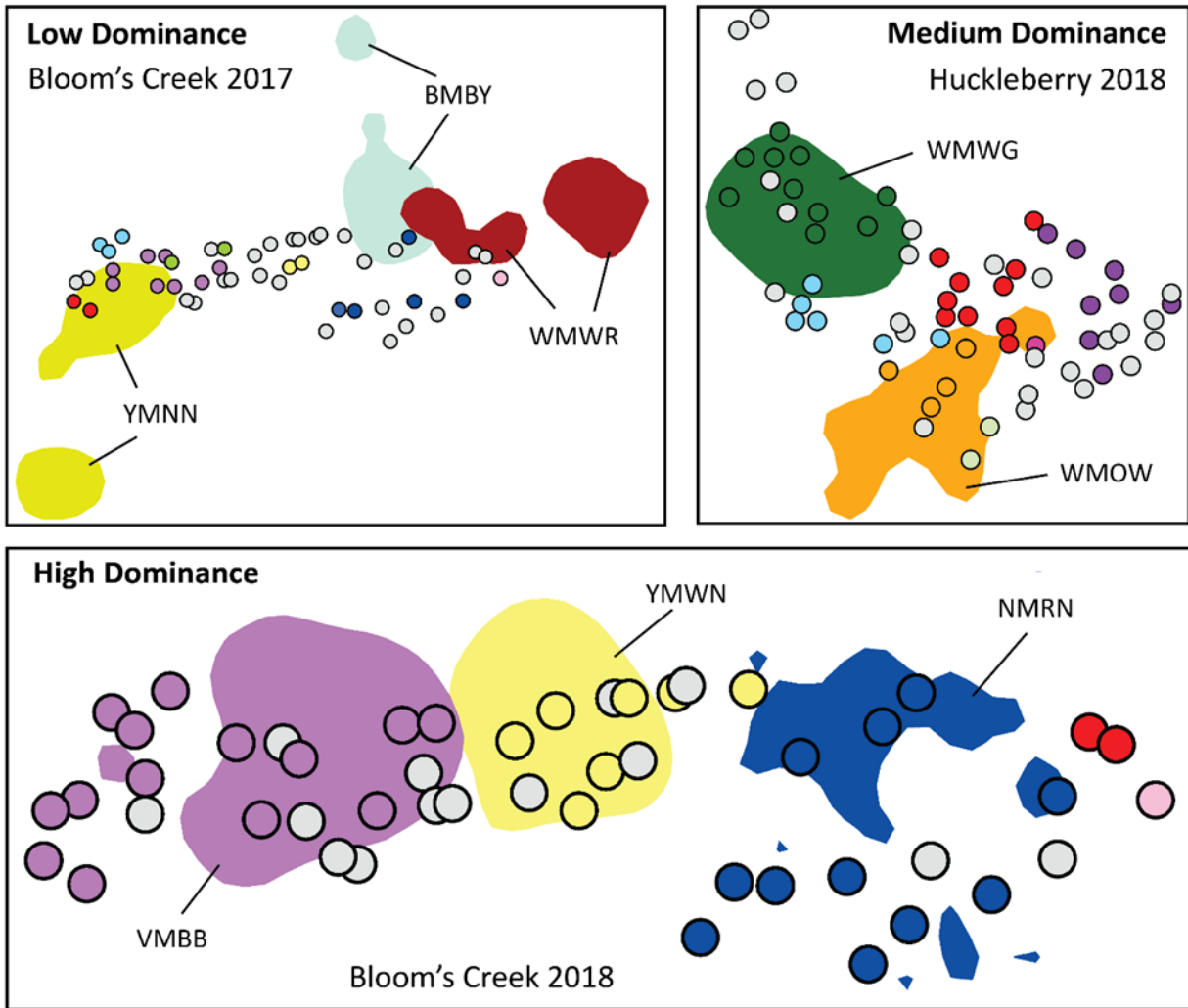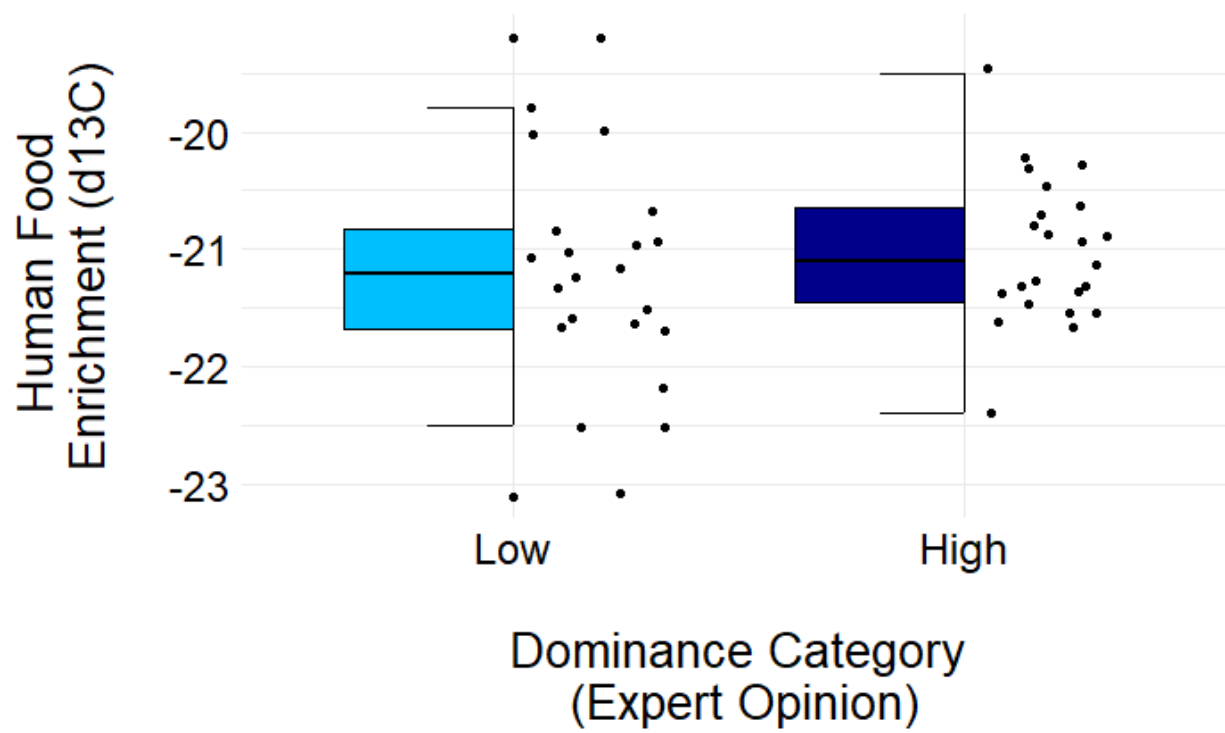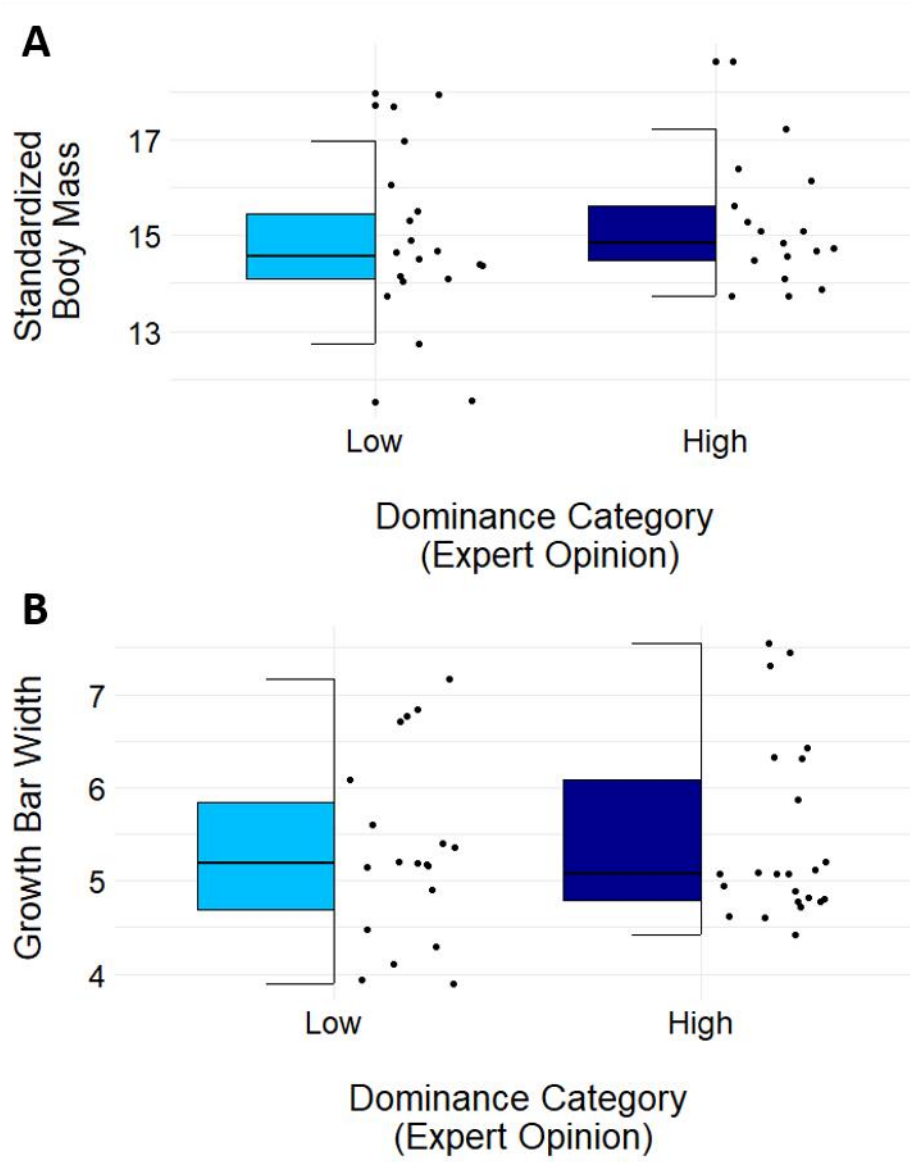
Figure S1

Figure S2

Figure S3

Figure S4

Figure S5

Figure S6