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RESEARCH ARTICLE

Steller's Jay (*Cyanocitta stelleri*) space use and behavior in campground and non-campground sites in coastal redwood forests

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ABSTRACT

Small-scale disturbance and trash associated with campgrounds may provide opportunities for generalist species in areas important for conservation. We examined the influence of campgrounds on the space use and behavior of Steller's Jays (*Cyanocitta stelleri*) in Redwood National and State Parks, California, USA. In 2010 and 2011, we used radiotelemetry to monitor the movements of adult male Steller's Jays. We found that home range size of campground jays (16.4 ± 2.6 ha, $n = 20$) did not differ from non-campground jays (15.0 ± 2.0 ha, $n = 10$). However, we observed extensive home range overlap among campground jays, possibly contributing to the high density of Steller's Jays previously observed at these sites. Jays roosted alone, primarily in old-growth forest stands away from campgrounds and other human recreation areas. Campground jays regularly commuted between campgrounds and nocturnal roosts. Commuting distance was positively associated with home range size. Campground jays were more frequently observed <1 m from the ground, and were more frequently observed perching than non-campground jays, likely in response to the location and predictability of anthropogenic food. Our findings suggest that campgrounds directly influenced space use and behavior of Steller's Jays in Redwood National and State Parks. Steller's Jays are opportunistic nest predators, leading to concern that their elevated abundance near campgrounds could increase nest predation on federally threatened Marbled Murrelets (*Brachyramphus marmoratus*) or other birds nesting in redwood forests.

Keywords: behavior, campground, human recreation, Marbled Murrelet, Redwood National and State Parks, roost, space use, Steller's Jay

Uso del espacio por *Cyanocitta stelleri* y su comportamiento en sitios con y sin campamentos en bosques costeros de secuoyas

RESUMEN

El disturbio a pequeña escala y la basura asociada con las áreas de campamento podrían presentar oportunidades para especies generalistas en áreas importantes para la conservación. Examinamos la influencia de las áreas de campamento en el uso espacial y el comportamiento de *Cyanocitta stelleri* en los Parques Nacionales y Estatales de Secuoyas Gigantes en California, Estados Unidos. Entre 2010 y 2011 usamos radiotelemetría para monitorear los movimientos de machos adultos de *C. stelleri*. Encontramos que el tamaño de los ámbitos de hogar de las aves en áreas de campamento (16.4 ± 2.6 ha, $n = 20$) no fue diferente del de las aves por fuera de los campamentos (15.0 ± 2.0 ha, $n = 10$). Sin embargo, observamos alta superposición entre los ámbitos de hogar de las aves en campamentos, lo que posiblemente contribuye a la alta densidad de *C. stelleri* observada previamente en estos sitios. Los individuos dormían solos principalmente en áreas con bosques maduros ubicadas lejos de los campamentos y de otras áreas de recreación humana. Las aves en campamentos se desplazaban regularmente entre los campamentos y sus dormideros. La distancia de desplazamiento se asoció positivamente con el tamaño del ámbito de hogar. Las aves en campamentos se observaron más frecuentemente a más de un metro del suelo y usando perchas que las aves por fuera del campamento, probablemente como respuesta a la ubicación y previsibilidad del alimento antropogénico. Nuestros resultados sugieren que los sitios de campamento directamente influyeron en el uso del espacio y el comportamiento de *C. stelleri* en los Parques Nacionales y Estatales de Secuoyas Gigantes. *C. stelleri* es una especie depredadora de nidos oportunista, lo que trae la preocupación de que su abundancia elevada cerca de los sitios de campamento podría incrementar la depredación de los nidos de la especie federalmente amenazada *Brachyramphus marmoratus* o de otras aves que anidan en los bosques de secuoyas.

Palabras clave: áreas de campamento, *Brachyramphus marmoratus*, comportamiento, *Cyanocitta stelleri*, dormidero, Parques Nacionales y Estatales de Secuoyas Gigantes, recreación humana, uso espacial

INTRODUCTION

Steller's Jays (*Cyanocitta stelleri*) are small corvids that occupy a wide range of forested habitats throughout western North America including highly fragmented landscapes (Greene et al. 1998, Marzluff et al. 2004). As dietary generalists, Steller's Jays concentrate their use along habitat edges (Brand and George 2001, Marzluff et al. 2004, Vigallon and Marzluff 2005a) and subsist on a diet of insects, seeds/nuts, berries, and anthropogenic food (Greene et al. 1998). Corvids are widely recognized as avian nest predators; Steller's Jays will opportunistically depredate the eggs and young of open-nesting birds incidentally encountered during natural foraging (Vigallon and Marzluff 2005a). Steller's Jays are highly responsive to human activity (Liebezeit and George 2002), and their use of habitat in Mount Rainier National Park was positively associated with number of human visitors (Walker and Marzluff 2015). In Redwood National and State Parks (RNSP), Steller's Jays are the most commonly observed corvid, and estimates of abundance based on point count surveys and distance sampling suggest they are 2–6 times more abundant in campgrounds than non-campground locations in RNSP (Wallen et al. 1999). This trend is likely due to their attraction to anthropogenic food provisioned or discarded by park visitors (Wallen et al. 1999, George et al. 2001, Colwell et al. 2009, Bensen 2012).

Steller's Jay attraction to campgrounds in RNSP could directly influence their home range size and home range use patterns. When subsidized by anthropogenic food, generalist predators often occur at higher densities through reductions in home range size (Neatherlin and Marzluff 2004, Prange et al. 2004, Quinn and Whisson 2005). However, Steller's Jay home range size was unaffected by the presence of campgrounds and small settlements on the Washington Peninsula (Marzluff and Neatherlin 2006), suggesting that campgrounds do not influence the total area occupied by an individual during the breeding season. Increased abundance of Steller's Jays in campgrounds may also result from increased home range overlap and movement of individuals from outside campground boundaries (Colwell et al. 2009). Roosting behavior can take territorial birds outside their diurnal home range (Jirinec et al. 2015), a contribution to space use that has not been examined in Steller's Jays. In human-modified landscapes, American Crows (*Corvus brachyrynchos*) and Common Ravens (*Corvus corax*) often roost communally at sites related to food sources (Engel and Young 1992, Gorenzel and Salmon 1995, Caccamise et al. 1997). Therefore, only a comprehensive mapping of the size, overlap, and distribution of individual Steller's Jay home ranges throughout their daily cycle will reveal the space use pattern that leads to increased Steller's Jay abundance at RNSP campgrounds.

Corvids with access to human settlements and campgrounds can exhibit significant variation in behavior (Fleischer et al. 2003) and habitat use patterns (Marzluff et al. 2004, Scarpignato and George 2013, Walker and Marzluff 2015) compared to individuals that do not have access. This variation in behavior has largely been attributed to greater predictability in location and availability of anthropogenic food items compared to more widely dispersed natural food items. In RNSP campgrounds, anthropogenic food is located on or near the forest floor. In contrast, natural prey items for Steller's Jays are more widely distributed, and foraging often involves "spiraling" up the branches of trees in search of insects throughout the vertical forest canopy (Greene et al. 1998, Vigallon and Marzluff 2005a). Steller's Jays at campgrounds could potentially increase their use of the ground to maximize their access to anthropogenic food, and ultimately differ in use of the forest canopy when compared to jays without access to campgrounds. In addition, the overall predictability of anthropogenic food in campgrounds could influence the amount of time jays spent foraging for natural food items. For example, Florida Scrub-Jays (*Aphelocoma coerulescens)* in suburban environments spent less time foraging for natural food items, but make up for this deficit through consuming human-provided foods (Fleischer et al. 2003). By virtue of foraging less, birds with access to supplemental food can also increase the frequency of perching behavior or other activities that require less energy (Ettinger and King 1980, Mugaas and King 1981, Williams and Ternan1999).

Because many RNSP campgrounds occur within nesting habitat for the federally threatened Marbled Murrelet (*Brachyramphus marmoratus*) (Bensen 2012), there is significant concern that increased abundance of Steller's Jays could increase predation risk for Marbled Murrelet eggs and nestlings, perhaps compromising these areas as productive nesting habitat. Currently, the greatest threat to the viability of Marbled Murrelet populations in California is low productivity; direct observations at active nests in RNSP suggest that low reproductive success can be largely attributed to nest predation by corvids (Hébert and Golightly 2006, Hébert and Golightly 2007, Golightly and Schneider 2011). In California, Steller's Jays have been implicated in 36% and Common Ravens in 46% of observed predation events on Marbled Murrelet nests (Singer et al.1991, Peery et al. 2004, Hébert and Golightly 2007, Golightly and Schneider 2009). Management strategies directed at reducing corvid nest predation may be an effective means to recover Marbled Murrelet populations in California (Peery and Henry 2010). Any management efforts require understanding how corvid movements and foraging behavior could put murrelets at risk, particularly whether jays routinely ascend >40m to the height of canopy nests of Marbled Murrelets (Golightly et al. 2009).

Here we compared the space use and behavior between male Steller's Jays at recreational campgrounds and non-campground areas >1 km away in Redwood National and State Parks. We used radiotelemetry to monitor daytime and roosting space use patterns, time spent perching and foraging, and activity height.

METHODS

Study Area

We conducted this study in Prairie Creek Redwoods State Park (41.4°N, 124°W) and Jedediah Smith Redwoods State Park (41.7°N, 124.1°W) in Humboldt and Del Norte Counties, California. The National Park Service (NPS) and the California Department of Parks and Recreation (CDPR) cooperatively manage these parklands as RNSP. RNSP has a temperate maritime climate with precipitation (~200 cm) occurring as rain during winter months (November–May) and coastal fog prevalent during summer months. Average annual temperatures are 4–19°C. Elevation ranges from sea level to approximately 837 m (UNEP 2011).

Vegetation types include old-growth and second-growth forests dominated by coast redwood (*Sequoia sempervirens*), Sitka spruce (*Picea sitchensis*), and Douglas-fir (*Pseudotsuga menziesii*). The old-growth redwood stands in RNSP represent 42% of all remaining old-growth redwood forests (RNSP 2008). Other tree species include western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and grand fir (*Abies grandis*). Mixed hardwood stands and riparian zones are dominated by red alder (*Alnus rubra*), California bay (*Umbellularia californica*), big-leaf maple (*Acer macrophyllum*), tanoak (*Lithocarpus densiflorus*), and madrone (*Arbutus menziesii*). Herbaceous ground cover and shrubs include sword fern (*Polystichum munitum*), salal (*Gaultheria shallon*), red huckleberry (*Vaccinium parviflorum*), evergreen huckleberry (*Vaccinium ovatum*), salmonberry (*Rubus spectabilis*), and thimbleberry (*Rubus parviflorus*).

Our study sites included 2 recreational campgrounds and 3 non-campground areas, all confirmed as occupied by breeding Marbled Murrelets and Steller's Jays during previous surveys (George et al. 2001). Other corvid species that occur within these sites include Common Ravens, Gray Jays (*Perisoreus canadensis*), and Western Scrub-Jays (*Aphelocoma californica*). Campground sites included Elk Prairie Campground and Jedediah Smith Campground, as these campgrounds offered vehicle access and experienced high visitation May–September (RNSP 2008). Elk Prairie Campground (Prairie Creek Redwoods State Park) is located along Prairie Creek, a tributary of Redwood Creek in the southern portion of RNSP and encompasses 4.8 ha with 76 campsites. Jedediah Smith Campground (Jedediah Smith Redwoods State Park) is located along the Smith River in the northern portion of RNSP and encompasses 9.8 ha with 106 campsites. For spatial analyses, campgrounds were defined as the area within a 30 m buffer added to all paved roads adjacent to overnight campsites. At campgrounds, Steller's Jays were captured in live traps (model 1045, Havahart, Lititz, Pennsylvania, USA), bow nets (Superior Bownet & Design, Clinton, Maryland, USA), mist nets (Avinet, Dryden, New York, USA) and noose-mats (Mehl et al. 2003) baited with unshelled peanuts.

Non-campground areas were >1 km away from campgrounds, as previous studies have suggested that Steller's Jays do not travel >1 km to access human food (Marzluff and Neatherlin 2006). These non-campground areas were located in old-growth forest edge habitat along maintained roads and trails where overnight camping was prohibited. We selected sites based on accessibility and the presence of Steller's Jays at the site. Non-campground areas in the southern portion of RNSP included Lost Man Creek, Davison Road, and Cal Barrel Road. Non-campground areas in the northern portion of RNSP included Society Hole and Walker Road. To avoid habituating Steller's Jays to anthropogenic food at non-campground areas, we used a combination of vocalization playback and decoy presentation to attract Steller's Jays into 4 m mist nets (Bat Conservation and Management, Carlisle, Pennsylvania, USA) set along roads and trails where Steller's Jays were observed. Vocalizations used for playbacks were recorded at Elk Prairie Campground and included song, aap, wek, rattle, creak, and distress calls (Hope 1980) and were remotely played through a digital MP3 player (Panasonic, Chesapeake, Virginia, USA) connected to portable stereo speakers (SRS-M50, Sony, Tokyo, Japan).

Radiotelemetry

We captured adult male Steller's Jays from late April to early May of 2010 and 2011 and fitted each individual with a radio transmitter (model A1070, Advanced Telemetry Systems, Isanti, Minnesota, USA) using 3 mm gauge Teflon ribbon (Bally Ribbon Mills, Bally, Pennsylvania, USA) (Rappole and Tipton 1991). We determined sex by observing sex-specific vocalizations (K. R. Overeem personal communication) and determined age as second year or after second year (ASY) based on plumage (Pyle et al.1987). We focused our study on ASY males because they are believed to feed their incubating female and nestlings, and thus may be more likely to encounter Marbled Murrelet nests while foraging for natural food items during the breeding season (J. M. Black personal observation).

We monitored radio-tagged individuals from May 15 to August 15, a period largely coinciding with known Marbled Murrelet nest initiation dates in RNSP (April 22–July 21; Hébert and Golightly 2006). We used homing techniques (Mech 1983, White and Garrott 1990) with handheld telemetry receivers (model RS 1000, Communi-

cation Specialists Inc., Orange, California, USA) to locate birds. We recorded the location of each jay 1–2 times/day between 0500 and 2000 hr using handheld GPS (Etrex legend, Garmin, Olathe, Kansas, USA), allowing >1 hr between consecutive tracking events (Swihart and Slade 1985). Additionally, we tracked individuals to their roost sites bimonthly between 2100 and 0400 hr, and included these locations in estimates of home range size. Each relocation event was classified as direct observation (focal individual visually identified by observer), homing (focal individual not visually identified but location was estimated within <50 m of the observer using signal strength and directionality), triangulation (3 azimuths recorded when focal individual could not be approached closer than 50 m due to dense vegetation, rivers, or property boundaries), or incidental (location recorded for non-focal individuals when incidentally encountered). For triangulated positions, we used program LOAS 4.0.3.3 (Ecological Software Solutions LLC 2009) and estimated the focal individual's location as the center of an error polygon regardless of polygon size.

Behavioral Observations

Upon locating a radio-tagged jay, we estimated their vertical height above ground as <1 m, 1–15 m, 15–30 m, or >30 m. Below 1 m, the forest structure was composed of bare ground, low shrubs/ferns, small stumps and logs, picnic tables, benches, trash cans, and other small anthropogenic structures. From 1 to 15 m the forest structure included large shrubs and small deciduous and coniferous trees. From 15 to 30 m the forest structure was composed of second-growth conifer trees and the lower reaches of mature old-growth trees. At a vertical height of >30 m, the forest structure was devoid of small conifers and other deciduous hardwoods and only included the canopy and crowns of mature redwood trees.

We classified the individual's activity as foraging or perching. We recorded foraging activity when the focal individual was actively moving between perches visually searching, attacking, handling, or consuming prey. We recorded perching activity when the focal individual was maintaining a stationary position (no movement between perches) for >10 s. Perching was most often associated with preening, resting, and calling. When the focal individual was not directly observed due to dense vegetation, we would use signal strength, direction, and consistency to determine whether the individual was likely foraging or perching. A radio signal that consistently emanated from one location without a change in signal strength or direction was recorded as perching. When the source of a radio signal rapidly changed location or continually varied in its strength and consistency, we recorded this as foraging.

Home Range and Overlap Estimation

We estimated home range size as the area (ha) within the 95% probability contour of a fixed kernel density estimate (Millspaugh and Marzluff 2001) for all Steller's Jays with ≥30 locations (Seaman et al. 1999). We used bivariate Plug-In bandwidth estimation (Gitzen et al. 2006) in the KernSmooth package of program R (R Development Core Team 2009, Duong 2010) and manually imported this smoothing parameter to Home Range Tools in ArcGIS 9.3 (ESRI 2009).

If the home ranges of radio-tagged Steller's Jays overlapped, we estimated pairwise overlap as the volume of intersection (VI) (Fieberg and Kochanny 2005) between overlapping utilization distributions (UD) using Hawth's Analysis Tools for ArcGIS (Beyer 2004). The VI measures the probability of co-occurrence in joint space use by comparing the location and shape of overlapping UDs. This estimate ranges from 0 (no overlap) to 1 (complete UD overlap) and represents a single measure of overlap for ≥2 home ranges (Seidel 1992, Millspaugh and Marzluff 2001). We began by calculating the pairwise VI between all overlapping home ranges that we observed within each year of our study. We then estimated a single measure of home range overlap for each individual by averaging their VI measures from all occurrences of pairwise overlap. Within our sample of non-campground jays, 5 individuals did not exhibit home range overlap with other radio-tagged jays and we acknowledge that it is possible that overlap with non-radio-tagged jays occurred but was not accounted for. Because estimates of home range overlap are only meaningful when all breeding territories are accounted for, including these individuals in our analysis could bias our estimates of home range overlap low. Therefore we chose to exclude these individuals from this analysis.

We estimated roost area size (ha) for each individual as the area within a minimum convex polygon (MCP) created using nocturnal locations. For campground jays, we measured the linear distance (m) from the center of each individual's roost area to the boundary of the nearest campground. For individuals whose roost MCP centers occurred within campground boundaries, roost distance was defined as 0 m.

Statistical Analysis

We compared estimates of home range size and roost MCP size between campground jays and non-campground jays using nonparametric Mann–Whitney *U*-tests, as the data were not normally distributed and variances differed markedly between campground jays and non-campground jays. The relationship between roost distance to campground and home range size was tested with a Spearman rank test.

We also compared vertical height and activity between campground jays and non-campground jays using Mann–Whitney *U*-tests. For each individual, we first calculated the proportion of behavioral observations that occurred in each category for each variable. We then compared mean proportions between our sample of campground jays and non-campground jays.

RESULTS

In 2010 and 2011, we radio-tagged 30 adult male Steller's Jays (20 campground, 10 non-campground) that we monitored for an average of 53 ± 9.6 days (range: 32–93). We collected 2,806 daytime locations (85.7 ± 3.8 locations per individual) and 195 nocturnal roost locations (>6 per individual). Locations were determined primarily through direct observation (70%), followed by homing (27%), triangulation (2%), and incidentally (1%). We made 2,735 observations of vertical height and 2,357 observations of activity throughout the monitoring period and determined fledging success for all individuals.

Home range size of campground jays (16.4 ± 2.6 ha) was not significantly different than non-campground jays (15.0 ± 2.0 ha; $U = 90$, $P = 0.68$; Figure 1). Mean home range overlap between adjacent campground jays was 22.6 ± 2.3% ($n = 20$). Mean home range overlap between non-campground jays was 5.1 ± 2.1% ($n = 6$). Roost MCP size (1.24 ± 0.3 ha) was not significantly different between campground jays and non-campground jays ($U = 114$, $P = 0.56$). Campground use ranged from 16% to 95% (mean: 54.9 ± 4.7% of an individual's UD occurring within campground boundaries). Campground jay roost sites ranged from 0 to 928 m (mean: 186.2 ± 46.8m) away from campground boundaries. For campground jays, roost distance to campground was positively associated with home range size ($r_s = 0.93$, $S = 96.54$, $P < 0.001$; Figure 2).

Campground jays were more frequently observed at a vertical height of <1 m (0.08 ± 0.01% of observations) than non-campground jays (0.03 ± 0.01%; $U = 176$, $P < 0.0001$; Figure 3). Campground jays and non-campground jays were observed in all other vertical height categories at equal frequencies (all $P > 0.1$; Figure 3). Campground jays were more frequently observed perching (0.41 ± 0.02% of observations) than non-campground jays (0.23 ± 0.02%; $U = 193$, $P < 0.001$; Figure 4). Campground jays were less frequently observed foraging (0.59 ± 0.02% of observations) than non-campground jays (0.77 ± 0.02%; $U = 193$, $P < 0.001$; Figure 4).

DISCUSSION

We found no significant difference in home range size between campground jays and non-campground jays, consistent with previous studies of Steller's Jay home range use (Marzluff and Neatherlin 2006). For campground jays, more than 50% (up to 95%) of an individual's total use occurred within campgrounds, and the highest levels of individual use (as measured by peaks in UD height) also occurred within campgrounds. RNSP campgrounds are rich with anthropogenic scavenging opportunities for jays; birds foraged throughout occupied campsites and cached anthropogenic food in nearby trees. We regularly observed large groups of jays communally foraging throughout campgrounds with limited aggressive interactions between individuals, suggesting that the availability of anthropogenic food at campgrounds may facilitate a reduction in territoriality between local Steller's Jays. We observed high levels of home range overlap among all campground jays, primarily within campground boundaries. We only observed 6 occurrences of home range overlap (for 5 individuals) among non-campground jays; our difficulty capturing non-campground jays with adjacent territories probably reflects the overall lower density of jays in these habitats. While our sample of home range overlap among non-campground jays is limited and prevents direct comparison to campground jays, our findings suggest that high rates of home range overlap between campground jays (rather than reductions in home range size) likely contribute to the high density observed at these sites (Wallen et al. 1999, Bensen 2012).

The positive association that we observed between home range size and roost distance suggests that suitable roosting/nesting sites may be a limiting resource for campground jays during the breeding season. Home range size varied considerably among campground jays, and we found that jays that roosted farther from campgrounds made routine movements into campgrounds and occupied much larger home ranges than individuals roosting near or within campgrounds. Similarly, breeding Common Ravens exhibited larger home range size with increasing distance between their nest and anthropogenic food sources (Roth et al. 2004), suggesting that corvids will modify and adapt their home range to include foraging areas without relocating their nest site. For all campground jays, 72% of roost locations, and all (3 of 3) incidentally discovered nest locations, occurred outside campground boundaries, suggesting that suitable nest and roost sites in campgrounds may be limited. Optimal nesting habitat for Steller's Jays may occur in remote forested areas away from sources of anthropogenic food that elevate other nest predators and human disturbance (Vigallon and Marzluff 2005b). We did not observe any communal roosting among radio-tagged jays (no overlap between root MCP areas) though it is possible that roost overlap occurred with non-radio-tagged individuals. While it appears that campground jays readily tolerate conspecifics within campgrounds, they may not tolerate the intrusion of conspecifics within their nest area. Nest site–specific

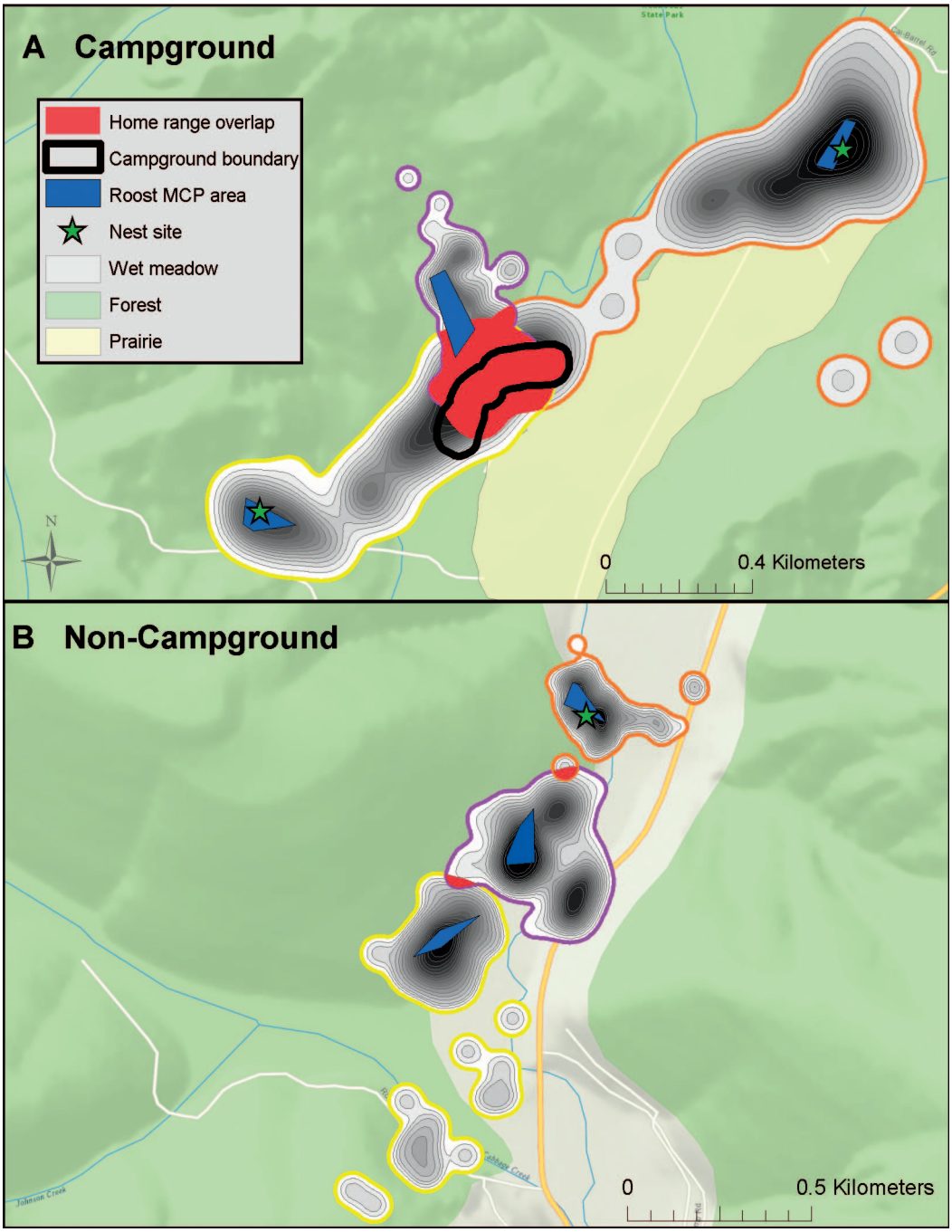

FIGURE 1. Space use by adult male Steller's Jays in Redwood National and State Parks, California, during the breeding season of 2010. Home ranges for 3 individuals (yellow, purple, and orange outer polygons) are shown for (**A**) campground jays and (**B**) non-campground jays with red shading denoting areas of two-dimensional overlap between adjacent individuals. For each individual, roost MCPs (blue polygons) and incidentally discovered nest sites (green stars) are also depicted in relation to the recreational campground boundary (black outline).

dominance has been observed in Steller's Jays (Brown 1963) and therefore may force campground jays to seek unoccupied nest sites well outside campground boundaries and regularly commute to campgrounds for daytime foraging activities.

The location and predictability of anthropogenic food at campgrounds directly influenced Steller's Jay vertical canopy use and behavioral activity. In RNSP, much of the availability of anthropogenic food occurs in open fire pits, picnic tables, dishwashing areas, and refuse sites that occur

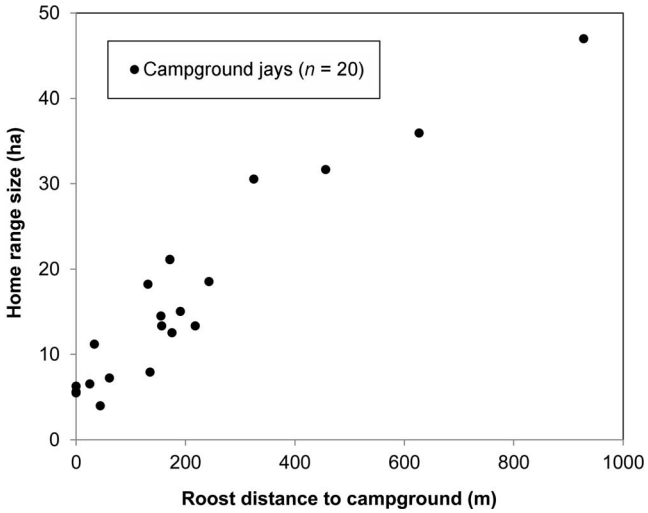

FIGURE 2. Roost distance to campground (m) and home range size (ha) for campground Steller's Jays ($n = 20$) in 2010–2011.

on or near the ground (Suddjian 2009). As a result, we observed campground jays on the ground and on anthropogenic structures more than non-campground jays. However, we did not observe differences in the use of the low, mid, or upper canopy between campground and non-campground jays. This suggests that campgrounds do not directly draw individuals down from the other canopy levels and may not have a significant influence on the habitat they utilize during foraging. Campground jays also spent more time perching and less time actively foraging

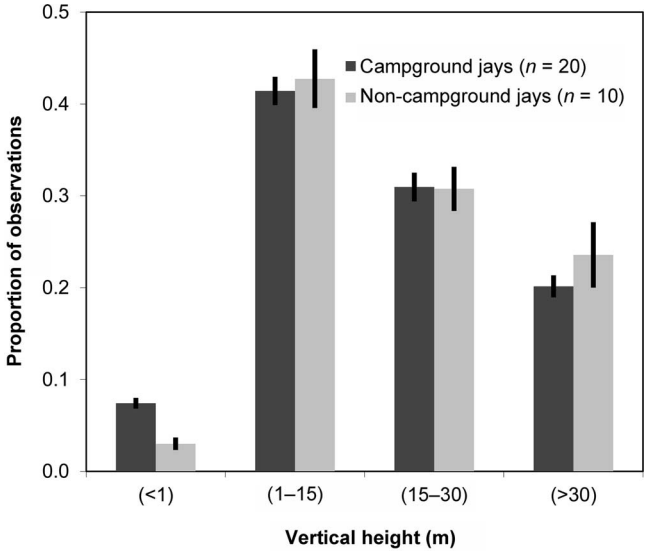

FIGURE 3. Vertical height of adult male Steller's Jays during observations of campground jays ($n = 1{,}948$ observations) and non-campground jays ($n = 787$ observations) throughout the 2010–2011 breeding seasons within Redwood National and State Parks, California. Vertical bars represent mean ± SE.

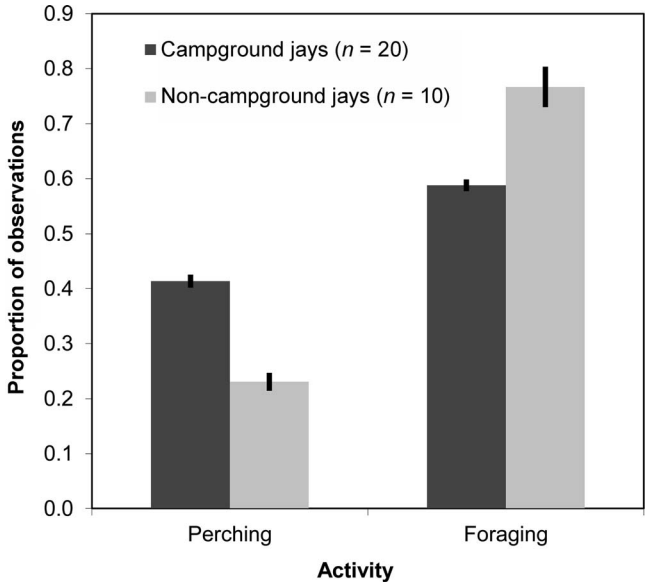

FIGURE 4. Activity of adult male Steller's Jays during behavioral observations of campground jays ($n = 1{,}948$ observations) and non-campground jays ($n = 787$ observations). Vertical bars represent mean ± SE.

than non-campground jays, perhaps due to the predictability of obtaining anthropogenic food at campgrounds. Campground jays adopted a "sit and wait" strategy, perching above an active campsite and descending only when anthropogenic food became available through improper storage/disposal or as a direct offering from a visitor. This resulted in congregations of Steller's Jays (up to ~15 individuals), often perched in a single campsite. Increased perching behavior has also been observed in Florida Scrub-Jays that occupied suburban environments, and this pattern was also attributed to more efficient foraging associated with anthropogenic resources (Fleischer et al. 2003). Overall, jays appear better suited than other sympatric corvids to exploit the anthropogenic resources in RNSP campgrounds. Scarpignato and George (2013) used radiotelemetry to monitor Common Ravens within RNSP and found that campground use among ravens was extremely low, likely because the presence of humans limited the time Common Ravens spent in these areas. In comparison, jays regularly perched and foraged within 1 m of park visitors, sometimes even taking food from the hands of visitors.

Our results suggest that Marbled Murrelets nesting within campgrounds may be more vulnerable to nest predation by Steller's Jays and this effect may persist up to 1 km away from campgrounds. Campgrounds in RNSP concentrated the foraging activity of local Steller's Jays and the resulting abundance of Steller's Jays could increase nest predation rates for Marbled Murrelets nesting in these

areas (De Santo and Willson 2001, Luginbuhl et al. 2001, Malt and Lank 2009). However, 50% of home range use occurred outside campground boundaries, potentially exposing Marbled Murrelets nesting anywhere within 1 km of campgrounds to increased nest predation risk. Our finding that campground jays range outside campgrounds may also have implications for corvid monitoring programs in RNSP campgrounds. Specifically, campground monitoring efforts that seek to quantify the density of Steller's Jays should account for the total area occupied by these individuals (not just the area within campgrounds where visual surveys are conducted).

Behavioral comparisons suggest that behavior of campground jays may reduce their likelihood of encountering a Marbled Murrelet nest. Nesting habitat for Marbled Murrelets in RNSP is restricted to the upper canopy of mature trees (mean Marbled Murrelet nest height in RNSP: 48.4 ± 3.9 m; Golightly et al. 2009). Steller's Jay nest predation is believed to be the result of incidental encounters that occur while jays are actively foraging for natural food items (Vigallon and Marzluff 2005a). Although we found no difference between campground and non-campground jays in the degree to which Steller's Jays utilized the upper canopy (>30 m), reduced overall foraging activity and concentrated foraging on anthropogenic food may reduce the risk for canopy-nesting birds. However, all large-scale studies of simulated and real Marbled Murrelet nests indicate that nest survival is negatively impacted by an abundance of predators (De Santo and Willson 2001, Luginbuhl et al. 2001, Malt and Lank 2009), thus, campgrounds may still pose a significant threat to nesting murrelets despite a reduction in foraging activity among campground jays. Ultimately, we have shown that RNSP campgrounds directly influenced Steller's Jay space use and behavior. Evaluating these responses can be a useful strategy to measure the potential impacts of non-consumptive human recreation on threatened and endangered wildlife (Seckel 2011).

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