

ARTICLE

Human food subsidies drive individual specialization and intrapopulation dietary differences in a generalist predator

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Abstract

Generalist species can exhibit individual specialization (IS), where individuals adopt specialized foraging behaviors not attributable to age, sex, or social dominance. While IS increases with the diversity of available foraging resources (ecological opportunity), the potential impact of human food subsidies on ecological opportunity is unknown. We quantified the isotopic niche width of Steller's Jays (*Cyanocitta stelleri*), a synanthropic predator and dietary generalist, across a gradient of human land-use categories ranging from subsidized (park campgrounds) to unsubsidized (forest interior) habitats in a protected area in California. We asked (1) if isotopic niche width was better predicted by individual foraging behavior than sex, social dominance, or habitat category (indicating IS) and (2) if degree of IS exhibited by jays increased with the availability of human food subsidies. We characterized the isotopic niche space occupied by individual jays relative to the population using carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values. Using linear models, we found that jay diet variation was best explained by individual behavior and habitat use rather than by sex or social dominance. While the degree of IS increased with the availability of human foods, individual jays exhibited a variety of foraging behaviors in all habitats that were segregated by foraging stratum and use of human foods. Individual diet also determined the degree of specialization, as jays that specialized on human foods had the narrowest niche width regardless of habitat. Management efforts targeted at generalist wildlife exhibiting large degrees of IS should therefore account for the impact of food subsidies on foraging behavior. Approaches that involve aversive conditioning may fail where highly specialized individuals are unlikely to encounter treatments; therefore, we recommend simultaneous efforts to limit human food subsidies (e.g., information campaigns and improved containment of human food and food waste), and deployment across the largest possible extent of foraging microhabitats and substrates in order to ensure exposure of whole populations to emetic eggs.

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KEYWORDS

corvid, ecological opportunity, foraging ecology, individual specialization, stable isotopes, synanthropes

INTRODUCTION

Individuals within a population are often assumed to occupy the same role in a food web, yet substantial individual variation in foraging ecology can exist (Toscano et al., 2016). Such individual specialization (hereafter IS) occurs at the population level when the niche width of the individual is smaller than the niche width of the overall population and this variation is not attributable to age, sex, or social dominance (Bolnick et al., 2003). IS has been increasingly recognized as a common phenomenon in nature, especially among species at intermediate trophic levels (Araújo et al., 2011; Bolnick et al., 2003; Svanback et al., 2015) and in generalist species that exhibit variation in niche attributes that promote their survival in changing environments (Bolnick et al., 2007). IS can have profound effects on ecological systems, particularly food webs (Araújo et al., 2011), because it impacts the strength and number of interspecific trophic interactions that, in turn, affect density dependence and strength of competition (Araújo et al., 2011; Svanback et al., 2015). Where noncompeting foraging specializations coexist, IS reduces the cost of intraspecific competition for the individual (Swanson et al., 2003) and allows species to persist at higher densities on the landscape than if individuals exhibit high dietary overlap (Svanback & Bolnick, 2007; Tinker et al., 2008).

Recent theoretical and empirical work shows that the degree of IS exhibited within populations of the same species is variable and depends upon both the degree of intraspecific and interspecific competition and the “ecological opportunity,” or diversity of resources available to foragers (Araújo et al., 2011; Costa-Pereira et al., 2018, 2019; Layman et al., 2015). Access to a greater variety of food items can increase IS if there are more possible prey items on which to specialize, leading to reduced dietary overlap. Human modification of landscapes can therefore affect the prevalence of IS by increasing landscape heterogeneity in some contexts and therefore ecological opportunity (Newsome, Tinker, et al., 2015; Robertson et al., 2015). However, population niche width can also increase in human-influenced landscapes through direct provisioning of human foods (Manlick & Pauli, 2020), including subsidies (Clark et al., 2015) and consumption of food waste (Oro et al., 2013). Increasing availability of human foods in some areas of protected lands, such as in campgrounds, can therefore represent gradients of

increasing ecological opportunity, and IS may be greater in those populations that have greater access to high levels of human foods. Alternatively, IS can decrease with increasing availability of human foods if population niche width declines when all or most individuals forage on human foods (e.g., Scholz et al., 2020). Therefore, the relationship between increased access to human food subsidies and higher amounts of IS remains unclear and may be variable across the landscape, dependent on the amount and distribution of human- and nonhuman-supplied food resources.

The relative importance of IS in relation to other factors influencing intrapopulation differences in diet is unknown for most species, however. Many species show intraspecific differences in foraging ecology based on sex, either through habitat (Breed et al., 2006) or ecological segregation (Xavier et al., 2017). Social dominance (Dorning & Harris, 2017; Jolles et al., 2013) may also influence diet composition if socially dominant individuals have greater access to human foods (e.g., West & Peery, 2017). Finally, habitat use, encompassing both habitat type occupied and movement frequency, also influences ecological opportunity and may explain dietary differences between individuals or subpopulations (Marklund et al., 2017; Newsome, Garbe, et al., 2015; Powell et al., 2015; Scholz et al., 2020). Therefore, studies of IS should account for the presence of other factors that may affect intraspecific foraging niche width, particularly with respect to how individual habitat use affects the diversity of available diet items.

The IS phenomenon is particularly relevant to conservation because it may allow generalist predator species from intermediate trophic levels, including medium-sized mammals (e.g., Canidae, Mustelidae, Felidae, and Procyonidae) and birds (e.g., Corvidae and Laridae), to persist at higher densities and with greater population stability, thereby negatively impacting sensitive prey species (Marzluff & Neatherlin, 2006; Parker & Nilon, 2008; Peery & Henry, 2010; Ritchie & Johnson, 2009). This pattern is of particular importance where generalist predator populations can spill over into areas that provide habitat for species of conservation concern, such as in parks and recreation areas. Many generalist predator species occur at higher densities (Parker & Nilon, 2008) in human-modified areas due to the presence of food subsidies (Fedriani et al., 2001; Walker & Marzluff, 2015), which may also

lead to reduced intraspecific competition. Indeed, IS in generalist species can result in negative impacts on entire native food webs and individual species of conservation concern (Marzluff & Neatherlin, 2006; Peery & Henry, 2010; Ritchie & Johnson, 2009) and is of particular importance for managers working to mitigate the negative impacts of these generalists on such species.

Here, we examined the factors that influence isotopic niche width in the Steller's Jay (*Cyanocitta stelleri*), a dietary generalist and species of management concern, across a gradient of individual habitat use and ecological opportunity that ranged from extensive food supplementation in heavily visited campgrounds to no human food supplementation in surrounding forests. We quantified the consumption of human foods by individual jays and within population diet specialization using stable isotope analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in feathers to test (1) whether IS occurred in Steller's Jays while statistically controlling for the effects of sex, social dominance, and the degree of ecological opportunity associated with the habitat use of individual jays. If foraging behavior is driven by IS, then the observed (generalized or specialized) foraging behavior of an individual alone should be the best predictor of isotopic diet composition. Alternatively, diet composition could be best predicted by sex, tarsus length, or habitat use category if sex, social dominance, or ecological opportunity are more important in driving individual diet patterns. Because we found evidence of IS in this population, we then asked (2) whether IS increased along a gradient of human-food-associated ecological opportunity. We expected that with greater access to human subsidies, individual jays would have more food items to specialize on, increasing IS. Increases in the availability of human foods could also decrease IS, if jays only exploit human foods in heavily subsidized areas.

METHODS

Study system

Our study was conducted in Big Basin Redwoods State Park, CA, USA (hereafter Big Basin) as part of a long-term study of Steller's Jay ecology and behavior (West et al., 2016). Steller's Jay populations have increased dramatically in recent years, presumably due to human food subsidies through direct provisioning and food refuse (Marzluff & Neatherlin, 2006; West et al., 2016; West & Peery, 2017). The species is now of management concern due to its role as a nest predator of songbirds (Vigallon & Marzluff, 2005) and the Marbled Murrelet

(*Brachyramphus marmoratus*), a US-threatened seabird that nests in remnant old-growth forests in state and national parks (Luginbuhl et al., 2001), including campground areas. Big Basin is characterized by coast redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*) forest, including the largest remaining tract of old-growth forest habitat for nesting Marbled Murrelets in central California (Halbert & Singer, 2017; Peery et al., 2004). Big Basin is a heavily visited park and receives over 100,000 campers annually to its almost 200 campsites (California State Parks, 2017), where jay densities are particularly high around point sources of human foods (West & Peery, 2017).

Capture, sampling, and assignment of individual habitat use

We captured Steller's Jays during the breeding season (April–August) using mist nets (Avinet Research Supplies, Dryden, NY, USA) and vocal lures (Vigallon & Marzluff, 2005) from 2011 to 2013. We banded jays with an aluminum United States Geological Service leg band and a unique combination of three colored plastic leg bands (Avinet Research Supplies) to enable individual recognition during behavioral observations. For all captures, we weighed focal jays, measured the right tarsus length to the nearest 0.10 mm using digital calipers, and collected feather samples for stable isotope analysis (see below). We determined the sex of all individuals using polymerase chain reaction methods of extracted DNA from blood samples (Griffiths et al., 1998). Blood samples used for molecular sexing were collected by puncture of the brachial vein using a sterile 26-gauge needle and collection of blood into capillary tubes (150 μl). Jay capture and sampling took place in both subsidized (campground) and unsubsidized (forest) sites in Big Basin. Steller's Jays likely do not travel more than 1 km to access human food (Marzluff & Neatherlin, 2006), so we therefore selected unsubsidized sites that were located at least 1 km from campgrounds. For our analyses, we used a previously determined classification of jay habitat use based on radiotelemetry analyses of their daily movement patterns (West et al., 2016). Specifically, individuals with territories in campground interiors and forest sites were defined as “campground” and “forest” jays, respectively. Additionally, individuals that were captured in forests that shifted their entire home range from forests to campgrounds were classified as “intermediate” jays, whereas individuals that were captured in campgrounds with less than 50% of their core areas inside campgrounds that were also relocated largely in forests along the boundaries of campgrounds were classified as “periphery” jays (West et al., 2016).

Foraging observations

We made foraging observations of jays while relocating them using radiotelemetry for determination of home range as part of a separate study (West et al., 2016). When a focal jay was observed foraging, we recorded the foraging maneuver used, the foraging substrate, and the foraging stratum in which the individual was observed. Foraging maneuvers were categorized into seven a priori-defined categories based on preliminary observations of jay behavior at Big Basin and data from the literature (Walker et al., 2020; full list in Appendix S1: Table S1). We also categorized foraging substrate into eight a priori categories, representing the full range of foraging substrates available to the jay population (e.g., tree and shrub species, and ground, anthropogenic structures; see Appendix S1: Table S2). Foraging stratum was binned into three categories: high (above 30 m), mid (10–30 m), and low (below 10 m). To increase the independence of foraging observations, only a single foraging maneuver was recorded on each sampling occasion and observations taken on the same day were at least 2 h apart. We used foraging data from a single year for each individual; all jays sampled had at least nine foraging observations.

We aggregated foraging observation data (18 variables for each individual) for individual radio-marked jays and determined the proportions of each foraging maneuver and foraging microhabitat observed for each individual (available at <https://doi.org/10.5061/dryad.2bvq83bt4>). We removed maneuvers, strata, and substrates with single or double observations to avoid biasing subsequent ordination analyses with outliers. We then ordinated the foraging data using principal coordinates analysis (PCoA; Gower, 2015) to describe covariance patterns and reduce variables. All statistical analyses were performed in R (version 3.5.1; R Core Team, 2022). We used the Gower dissimilarity index (Gower, 1971) to create a dissimilarity matrix, using the *daisy* function in the *cluster* package (Maechler, 2008), which we then analyzed using the *cmdscale* function in the *stats* package. We used PCoA because our data do not fit the assumptions of principal components analysis (lack of multivariate normality and use of correlated proportion data; McGarigal et al., 2000). We interpreted the PCoA axes by projecting the weighted averages of the scores for each predictor variable onto a biplot using the *wascor* function (*vegan* package; Oksanen et al., 2019) and by examining the magnitude and sign of the weighted averages for each coordinate axis (Appendix S1: Table S3). We selected the number of axes to retain for further analyses based on consultation of a scree plot (Appendix S1: Figure S1) and axis interpretability.

Quantification of IS

We used stable isotope analysis to investigate patterns of individual isotopic niche width in Steller's Jays in subsidized and unsubsidized areas using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in feathers. The isotopic ratios of nitrogen ($^{15}\text{N}/^{14}\text{N}$, noted $\delta^{15}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$, noted $\delta^{13}\text{C}$) can be used to measure individual- and population-level dietary niche width and can indicate the degree of individual foraging specialization using repeated individual isotope values over time (Bearhop et al., 2004; Newsome et al., 2009; Robertson et al., 2014). Because human foods often contain corn, a C4 plant, or corn-based products, they are enriched in the heavy isotope of carbon (Jahren et al., 2006) and are thus isotopically distinct from natural diet items in western North America where primary production is driven by native C3 plants (Newsome, Garbe, et al., 2015; West et al., 2016). Previous research on Steller's Jays has shown that increased enrichment in $\delta^{13}\text{C}$ in particular is indicative of greater consumption of human foods in this species (West et al., 2016; West & Peery, 2017). Isotopes of $\delta^{15}\text{N}$ vary with trophic position, where carnivores are more enriched than herbivores in terrestrial environments (Kelly, 2000; Newsome et al., 2010).

We used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the first primary, sixth secondary, and 2–3 whole body feathers from each sampled jay (three or four feather samples per individual). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope signatures from primary feathers were published previously as part of West and Peery (2017). For the present study, we additionally processed secondary and body feathers following similar methods. Briefly, we rinsed feather samples in a 2:1 chloroform:methanol solution to remove surface contaminants, homogenized them with scissors, and dried them at 55°C for ≥ 72 h. We then weighed and sealed approximately 0.5 mg of each feather sample into a tin capsule. Isotope analysis of feather samples was conducted at the Stable Isotope Facility at the University of Wyoming with a Costech 4010 elemental analyzer attached to a ThermoFinnigan DeltaPlus XP Continuous Flow Isotope Ratio Mass Spectrometer. Results are presented as per mil (‰) ratios relative to international standards: Vienna-Pee Dee Belemnite limestone (C) and atmospheric nitrogen (N), respectively. We selected the first primary and sixth secondary to maximize the temporal distance between diet signatures from feather samples. Primary flight feathers in Steller's Jays are molted in July and August while secondaries are molted from August to October and body feather molt occurs in June and July (Walker et al., 2020). Individual feathers sampled from jays throughout the summer therefore represent isotopic diet samples from both the previous year's molt (feathers collected before July) and the year they were sampled (feathers collected during or after

July). We used a fourth feather sample (primary or secondary) collected during recaptures of individual campground and periphery jays (forest and intermediate jays were never recaptured). While these samples are duplicate primary or secondary samples for these individuals, they represent diet from a second year and therefore represent a distinct time period. It is unlikely that this pooling of feather samples across years led to the sampling of diets from different

habitats, given that Steller's Jays are generally long-term residents at their breeding sites (Brown, 1963).

To quantify IS, we used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope signatures from feathers to determine the relative individual niche index (hereafter RINI; Sheppard et al., 2018), which measures the proportion of the total isotopic signature space of the population (i.e., the union of all individuals' isotopic ellipses; Figure 1a) occupied by each

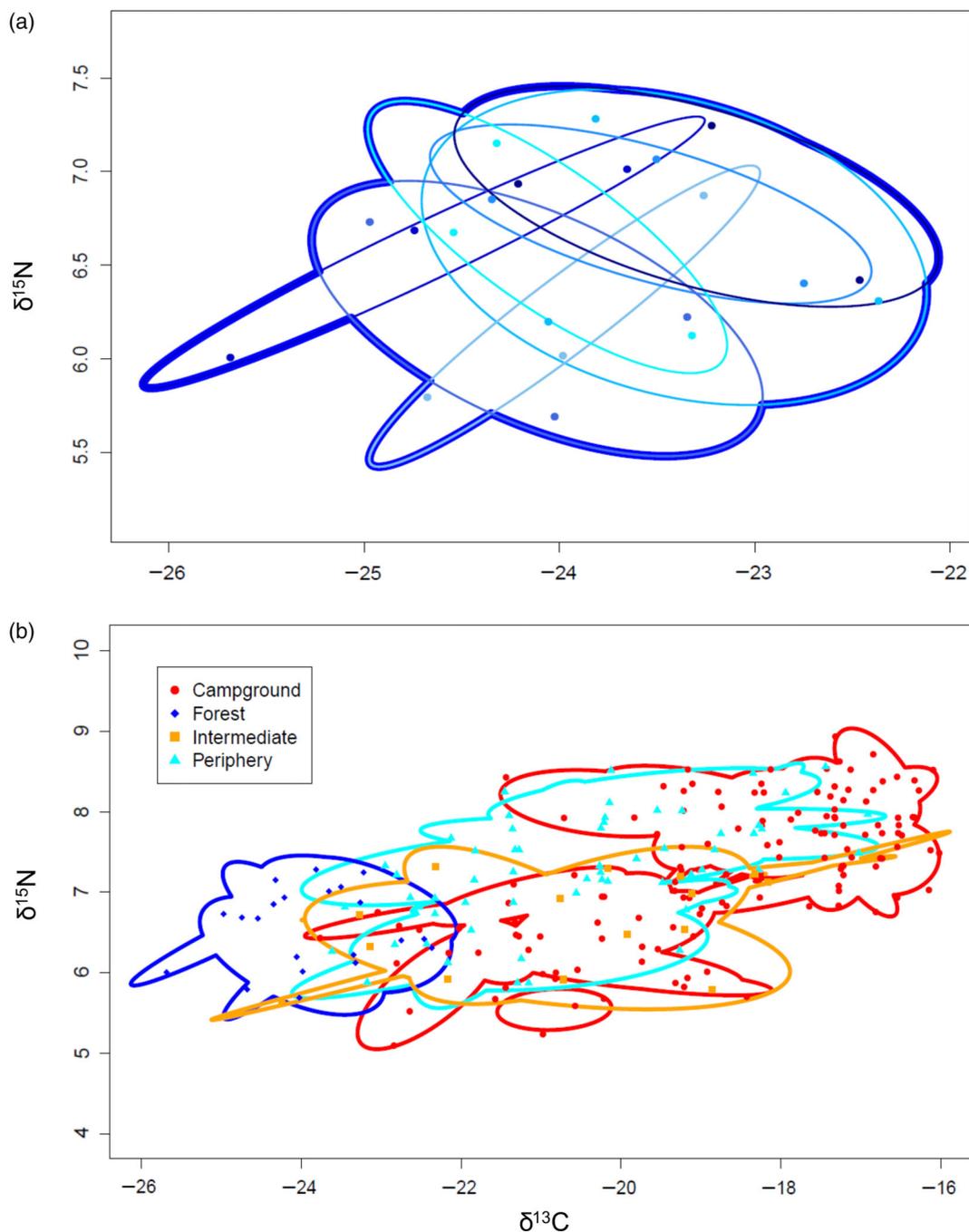


FIGURE 1 Calculation of population-level diet ellipses. (a) Example showing foraging niche width of all individual forest jays ($n = 5$; blue outline), calculated as the union of all 95% confidence ellipses adjusted for small sample size (SEA_c ; blue ellipses). Isotopic signatures of individual feather samples ($n = 3$ or 4 per jay) are plotted as points. (b) Overall foraging niche width of jay habitat use categories increased with increasing access to human food subsidies, indicating increasing diet width within the population. Colors represent each habitat use category.

individual's isotopic 95% confidence dietary standard ellipse adjusted for small sample sizes (SEA_c). Unlike a convex hull, SEA_c is relatively invariant to SEA_c , and the 95% standard ellipse is rescaled such that it has a 95% probability of containing an isotopic sample for the individual (Jackson et al., 2011). We assumed that different amounts of human food items would be available in each habitat use category, and thus we compared an individual's ellipse area to the area of all individuals within their habitat use category. Enrichment values for forest and intermediate habitat use categories used three feather samples while campground and periphery habitat use categories used four. While feather sample sizes differed between habitat use categories, we do not believe that this influenced the results of our statistical models. The fourth feather sample represented a duplicate primary or secondary flight feather (see above), though degree of enrichment in $\delta^{13}\text{C}$ (ANOVA; $F_{2,233} = 1.03$, $p = 0.36$) and $\delta^{15}\text{N}$ (ANOVA; $F_{2,233} = 0.85$, $p = 0.43$) did not differ significantly between the three feather types sampled. Furthermore, we detected no significant differences between SEA_c ellipse volumes calculated for the subset of campground (paired t test; $df = 34$, $t = 0.81$, $p = 0.43$, mean difference = 0.05) and periphery (paired t test; $df = 34$, $t = -1.74$, $p = 0.11$, mean difference = -0.44) birds when calculated using three and four feather samples, respectively. We calculated a 95% confidence standard ellipse adjusted for SEA_c using the *standard.ellipse* function of the *siar* package (Parnell & Jackson, 2015) and the area of the union of all ellipses from a given habitat category using the *siberKapow* function of the *SIBER* package (Jackson & Parnell, 2019). The RINI score for each individual was log-transformed for normalcy for later analyses.

Statistical analysis of determinants of dietary niche and degree of IS

We used linear mixed models (*lme4* package; Bates et al., 2020) to test hypotheses about two aspects of the foraging ecology of jays in this population. First, we identified the determinants of intraspecific differences in isotopic diet, using $\delta^{13}\text{C}$ to quantify jay reliance on human-derived foods. We used enrichment values in $\delta^{13}\text{C}$ from each of three (forest and intermediate habitat use categories) or four (campground and periphery habitat use categories) feather samples (see above) for each individual as the response variable. We included five predictor variables in the model: year that the individual was captured, habitat use category, sex, tarsus length, and behavior score on the first PCoA axis. Individual ID was included as a random effect in the model to control

for pseudoreplication of feather samples from the same individual. We found no significant interaction between year and habitat use on $\delta^{13}\text{C}$ in preliminary analyses, and therefore excluded the interaction term from the final model. Significance of covariates was evaluated using a likelihood ratio test comparing the full model with a reduced model in which the term of interest was removed. Because we detected a significant effect of habitat use, we tested post hoc for significant pairwise differences by comparing the estimated marginal means (*emmeans* function and *emmeans* package; Lenth et al., 2021).

Then, because we found evidence of IS in jays, we also modeled the effect of tarsus length, sex, year, habitat use, and diet composition (enrichment in $\delta^{13}\text{C}$ averaged across all feather samples for each individual) on degree of IS, measured as the log-transformed RINI index. This model did not include any random effects, and the interaction term between year and the log-transformed RINI index was again found to be not significant and excluded from the final model. Tarsus length was used as a proxy for body size and therefore social dominance, as adult male jays are larger and socially dominant over females and juveniles (Brown, 1963; Walker et al., 2020; authors' personal observation). We did not include individual age as a predictor variable because the majority of jays in this population were after-second-year individuals and we therefore did not have enough sample individuals to test for the effects of age. Steller's Jays cannot be aged in the hand past their second calendar year, when they adopt their definitive basic plumage (Walker et al., 2020). A goodness-of-fit model was assessed using marginal and conditional R^2 (Nakagawa & Schielzeth, 2013), calculated in the *MuMIn* package (*r.squaredGLMM* function; Bartoń, 2020).

RESULTS

Foraging observations and isotopic diet width

We conducted foraging observations on 62 adult Steller's Jays ($n = 45$ males, 17 females) and collected an average of 14 foraging observations per individual (range = 9–19). On average, foraging observations for an individual jay spanned 65.7 ± 23.2 days (mean \pm standard deviation [SD]) and the average number of days between relocations (and foraging observations) was 2.3 ± 0.9 (mean \pm SD). There was no significant difference in the timespan of foraging observations (ANOVA; $F_{3,40} = 1.05$, $p = 0.38$) or frequency of relocation attempts (ANOVA; $F_{3,40} = 0.002$, $p = 1.00$) across habitat use categories. Foraging sample sizes are given in Appendix S1: Table S3, and proportion

of use of each height stratum, foraging substrate, and foraging maneuver are available at <https://doi.org/10.5061/dryad.2bvq83bt4>. We analyzed stable isotopes in feathers from 62 adult Steller's Jays captured in subsidized and unsubsidized areas. Overall, the isotopic foraging niche width of jays across habitat categories increased with increasing access to human food subsidies (forest jay union ellipse area = 5.00, intermediate union ellipse area = 9.66, periphery union ellipse area = 12.10, and campground union ellipse area = 13.44; Figure 1b). Individual foraging niche width was smallest for campground jays (SEA_c area = 0.71 ± 0.50 ; mean \pm SD) and largest for intermediate jays (SEA_c area = 3.47 ± 2.70), while individual forest (SEA_c area = 1.65 ± 0.89) and periphery (SEA_c area = 1.93 ± 0.96) jays showed foraging niche width values between those of campground and intermediate jays.

Our PCoA analysis yielded 20 coordinate axes, of which the top two axes explained 48% of the variance (Appendix S1: Table S2). Results of a scree plot (Appendix S1: Figure S1) suggested that the top two coordinate axes should be retained for future analyses. The first coordinate axis explained 33% of the variance with an eigenvalue of 0.77. We interpret this axis as a measure of "natural" versus "supplemented" foraging behavior. Positive values on this axis are associated with foraging behaviors observed in forests (unsubsidized areas), including high weighted average scores for flycatching and bark gleaning behaviors, use of the high foraging stratum, and use of azalea (*Rhododendron* sp.) as a substrate (Figure 2a; Appendix S1: Table S3). Negative values on this axis are associated with foraging behavior where human food subsidies are widely available, including increased use of ground and picnic table foraging behaviors and increased use of the ground and picnic tables as a foraging substrate. Coordinate axis 2 represented 16% of the variance, with an eigenvalue of 0.36. This axis was deemed uninterpretable and we therefore only retained the first coordinate axis for further analyses. Full coordinate axis scores for each individual jay on the first three coordinate axes are shown in Appendix S1: Table S4.

Determinants of dietary niche width and degree of IS

Even when controlling for the effects of habitat use, there was a significant relationship between the foraging behavior of an individual jay and its isotopic diet, as measured by enrichment in $\delta^{13}C$ ($\beta = -10.20$, $p < 0.001$; Table 1, Figure 2b). Jays that had higher $\delta^{13}C$, indicating

greater consumption of human food sources, were also behaviorally specialized, foraging closer to the ground and around anthropogenic structures. Importantly, we did not find a significant effect of either sex ($\beta = 0.45$, $p = 0.17$) or tarsus length ($\beta = 0.11$, $p = 0.13$) on $\delta^{13}C$, supporting the hypothesis that IS and ecological opportunity were the best predictors of human foods in individual jay diet. We also found a significant difference in enrichment between jays across habitat use categories ($p < 0.001$; likelihood ratio test) and post hoc pairwise comparisons of the estimated marginal means found significant differences between jays that used campgrounds and those that used surrounding forests ($\beta = -2.49$, $p = 0.002$), as well as between campground and periphery jays ($\beta = -1.34$, $p = 0.002$). There was a near-significant difference in $\delta^{13}C$ enrichment between campground and intermediate habitat use ($\beta = -1.43$, $p = 0.057$). Forest jays without access to human food subsidies were less enriched in $\delta^{13}C$ than campground jays. However, we found both behavioral and dietary variations within the non-forest habitat use categories (Figure 2b). Finally, we found a statistically significant effect of sampling year, though the β estimate for this variable was relatively small ($\beta = 0.58$, $p < 0.001$). The model was a good fit for the data with a marginal r^2 of 0.62 and a conditional r^2 of 0.75.

The degree of IS in jays was best predicted by both habitat use and diet composition (Table 1). All additional habitat use categories had statistically larger RINI values than the campground category, and individual isotopic niche width was most narrow (i.e., IS was most pronounced) in jays using campgrounds (see above). Furthermore, RINI index values decreased as the proximity to humans of a habitat use category increased (Figure 3a): campground interior values were lower than campground periphery values, which were in turn lower than values from the intermediate habitat use category. However, diet composition was also significantly correlated with the RINI index ($\beta = -0.18$, $p = 0.02$; Figure 3b), with jays that consumed more human foods having a smaller RINI index. In other words, jays that foraged more on human foods were more specialized isotopically than jays that foraged on "natural" prey items (invertebrates, acorns, and seeds). IS was not affected by sex ($\beta = -0.15$, $p = 0.56$) or tarsus length (a proxy for social dominance; $\beta = 0.10$, $p = 0.08$) and this model was also a good fit for the data with an r^2 value of 0.60.

DISCUSSION

To the best of our knowledge, ours is the first study to document that human food subsidies increase IS in a

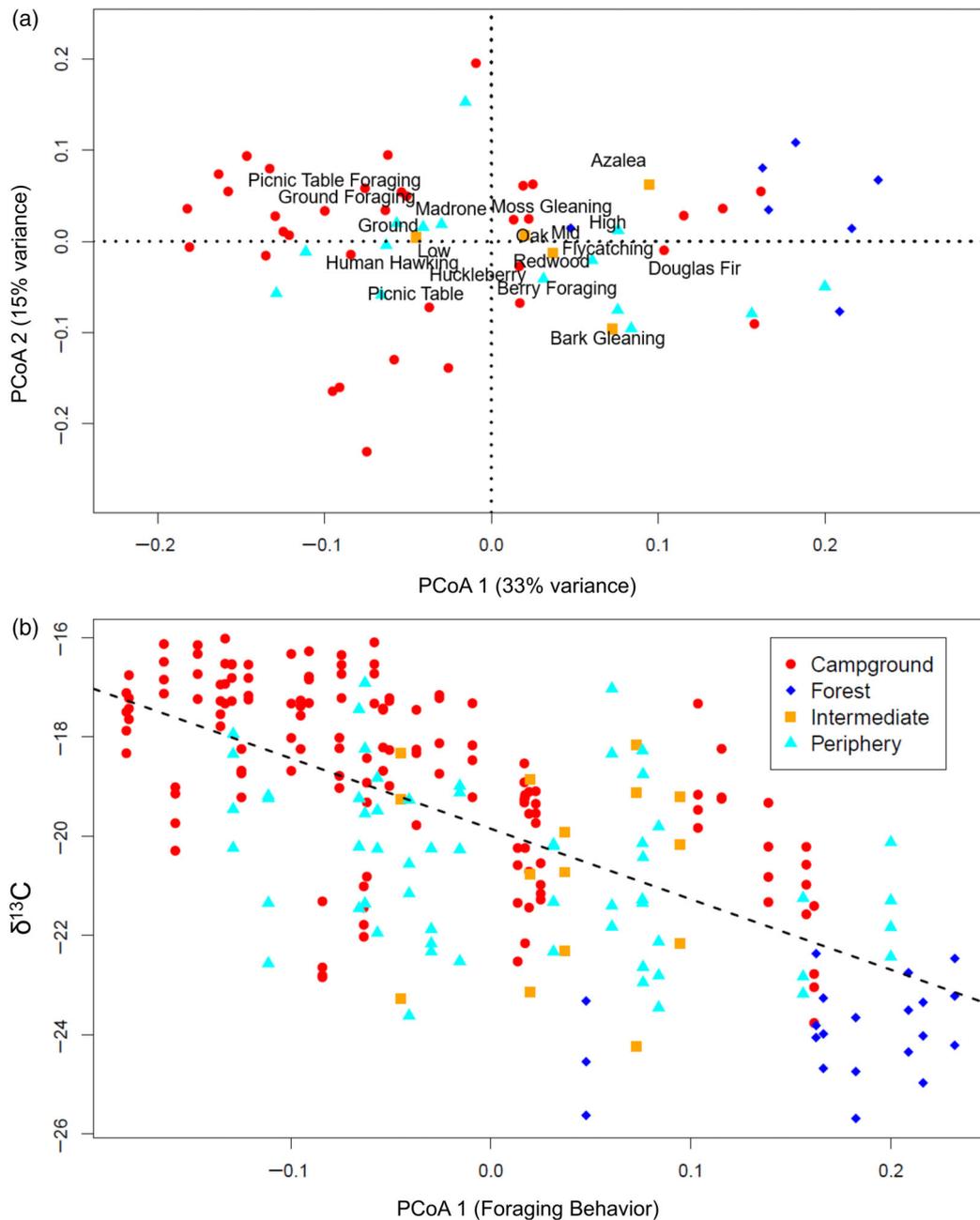


FIGURE 2 Effect of individual foraging behavior on isotopic signature. (a) Biplot of first and second principal coordinate axes (PCoA) derived from an ordination of foraging maneuver (seven categories), foraging substrate (eight categories), and foraging stratum (binned into high canopy, mid-canopy, and low strata). Axis labels indicate proportion of total variance explained by each coordinate axis, graph text corresponds to the projected weighted species score for each category of foraging maneuver, foraging substrate, and foraging stratum. Data points represent individual jays. (b) Enrichment in $\delta^{13}\text{C}$ is best predicted by individual foraging behavior ($\beta = -10.20$, $p < 0.001$). Data points represent jay feather samples, while colors represent habitat use categories.

vertebrate population. We found that IS in jays was driven by the consumption of human foods across habitat types, with no effect of sex or tarsus length (a measure of social dominance; Table 1, Figure 2b). While campground jays exploited novel human food items, thereby expanding their foraging niche width (Figure 1b), individuals within each habitat category still exhibited a

variety of foraging behaviors that were principally segregated by foraging stratum. Jays tended to forage either low and on human foods or at middle and higher strata on “natural” substrates (moss, bark, and aerial insects), and even in campgrounds some jays maintained “natural” foraging behaviors (Figure 2a). The degree of IS increased with the availability of human foods

TABLE 1 Generalized linear model estimates for Steller's Jay isotopic dietary niche and degree of IS.

Variable	β estimate	SE	<i>t</i>	<i>p</i>
$\delta^{13}\text{C}$				
Intercept	-1181.00	311.30	-3.794	
Year	0.58	0.15	3.719	<0.001
Habitat use				<0.001
Forest versus campground	-2.49	0.62	-4.003	0.002
Intermediate versus campground	-1.43	0.52	-2.740	0.057
Periphery versus campground	-1.34	0.33	-4.102	0.002
Sex	0.45	0.32	1.390	0.17
Tarsus length	0.11	0.07	1.523	0.13
Behavior score	-10.20	1.54	-6.620	<0.001
RINI index (log-transformed)				
Intercept	-317.37	246.41	-1.29	0.20
Habitat use				
Forest versus campground	1.42	0.52	2.74	0.008
Intermediate versus campground	1.45	0.41	3.53	<0.001
Periphery versus campground	1.01	0.28	3.40	<0.001
Year	0.15	0.12	1.25	0.22
Sex	-0.15	0.25	-0.59	0.56
Tarsus length	0.10	0.05	1.81	0.08
$\delta^{13}\text{C}$	-0.18	0.07	-2.36	0.02

Note: The $\delta^{13}\text{C}$ model was a generalized linear mixed model with a random effect of individual, run on stable isotope scores derived from feather tissue samples of Steller's Jays ($n = 62$ jays, 236 feather samples). Relative individual niche index (RINI) represents an isotopic measure of individual specialization (IS), standardized for each habitat use category occupied by jays in this study ($n = 4$ categories). Bolded predictor variables indicate statistically significant results.

(Figure 3a) and was highest in campgrounds. However, diet composition also influenced IS, as jays that specialized on human foods had the narrowest individual niche width regardless of habitat use (Figure 3b). Our results demonstrate an increasing degree of IS of resource use by jays with increasing availability of human food subsidies in campgrounds, which may reduce intraspecific competition in this species and explain its apparent success in areas heavily used by humans.

IS increases with human food subsidies and jay density

We found increased IS by jays in campgrounds and their peripheries relative to jays in forests, which suggests that availability of human foods can directly increase the degree of IS in a generalist species. Our finding adds to the rapidly growing body of evidence showing that IS in wild vertebrate populations is tied to ecological opportunity (Costa-Pereira et al., 2018; Evangelista et al., 2014; Kernaleguen et al., 2015; Newsome, Tinker, et al., 2015; Rosenblatt et al., 2015), and that human use of habitats

can be a driver of this pattern (Newsome, Garbe, et al., 2015; Robertson et al., 2015). While previous studies have focused on how human landscape modification is the mechanism by which diet diversity increases, we show here that human food subsidization alone, without extensive modification to habitat, provides another mechanism for increasing IS with ecological opportunity in areas that are heavily used by humans. The greater diversity of foraging strategies in campgrounds likely reflects the greater availability and predictability of human foods in this environment, as reflected by their prevalence in campground jay diets (West et al., 2016; West & Peery, 2017) and associated changes to foraging behavior (this study). Taken together, these results show that human food subsidies in campgrounds drive major changes to jay foraging behavior.

IS is also driven by the degree of intraspecific competition (e.g., Costa-Pereira et al., 2018), however, and jay densities and degree of territorial overlap at campground study sites have previously been shown to be higher than those at forest sites (West & Peery, 2017). These results indicate that both human-mediated increased ecological opportunity and high intraspecific densities affect IS in jays and suggest that

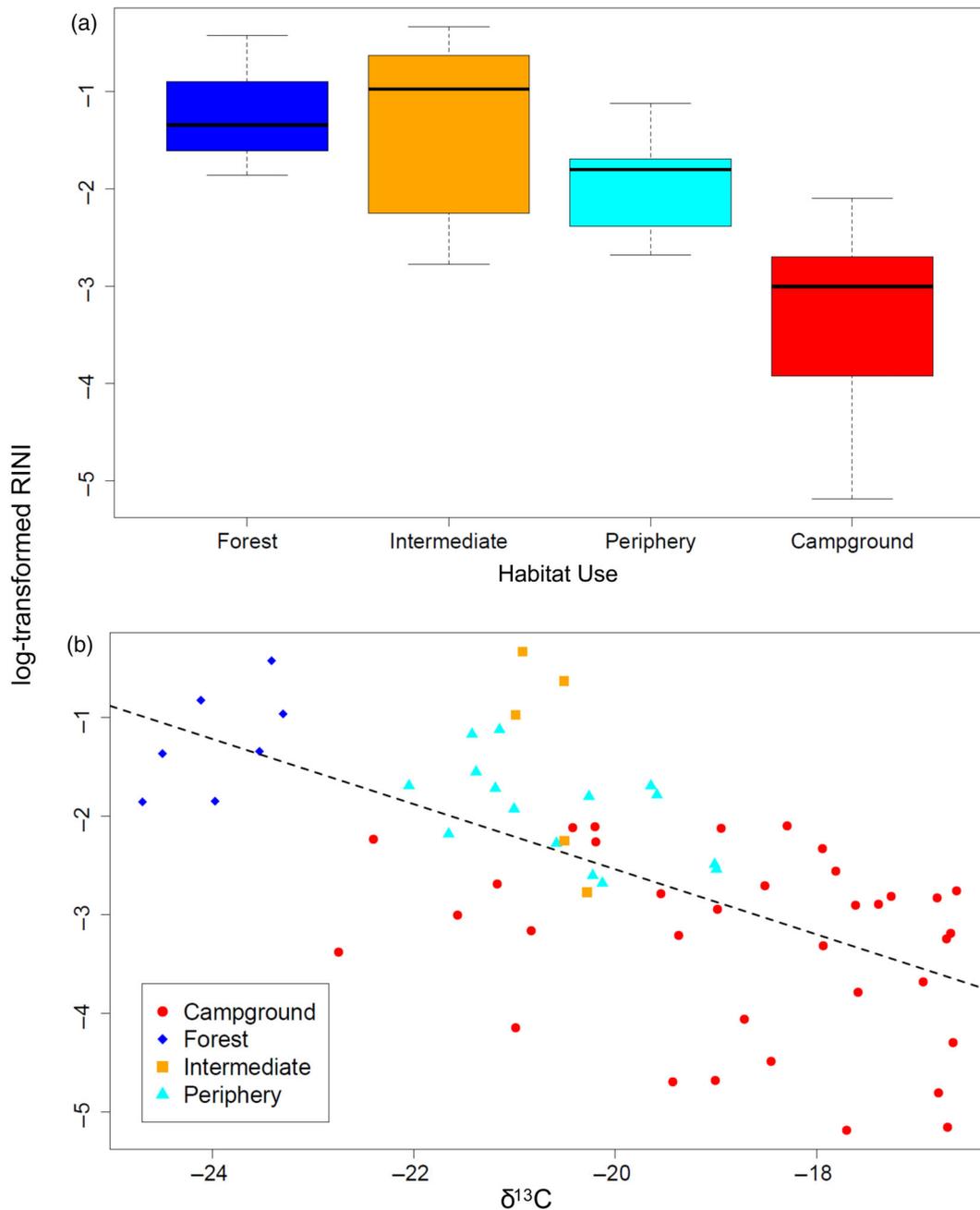


FIGURE 3 Effect of habitat use and foraging behavior on individual specialization (IS) in a population of Steller's Jays. (a) Individual isotopic niche width decreased, and degree of IS increased, with increasing human food availability in campgrounds. (b) Across habitat use categories, individual jays that had more negative foraging scores (foraged lower and on anthropogenic substrates) were also more specialized, suggesting that the degree of isotopic specialization is most pronounced in individuals that specialize on human food items.

where ecological opportunity and intraspecific densities are high, IS can mediate the costs of competition, leading to higher body condition and reproductive output of campground jays (West & Peery, 2017). Interestingly, intraspecific competition alone was not sufficient to promote high IS in the absence of high ecological opportunity in a Pantanal fish population (Costa-Pereira et al., 2017), suggesting that IS is a behavioral response to intraspecific competition only where ecological opportunity is large enough to allow specialization. These two mechanisms

appear to interact to drive patterns of IS (Evangelista et al., 2014; Martin & Pfennig, 2010; Newsome, Tinker, et al., 2015), and likely commonly co-occur along with human food subsidies. Indeed, food subsidies have been shown to aggregate and promote unnaturally high densities of human-associated wildlife species, particularly corvids (Gomo et al., 2017; Hopkins et al., 2014; Walker & Marzluff, 2015; West & Peery, 2017) and high degrees of IS may therefore be prevalent in other wildlife populations where human food supplementation occurs.

Foraging specialization by human food subsidies: A social learning effect?

We found a strong pattern of IS driven by both the foraging stratum of an individual and its degree of specialization on human foods. Foraging behaviors may be learned through observing conspecifics or parents (social learning), favoring maintenance of individual-specific foraging behavior (McCune et al., 2022). Empirical evidence suggests that individual foraging specialization can be transmitted within family groups and that foraging specializations learned by young vertebrates are retained as adults. For instance, the individually specialized foraging of common bottlenose dolphin (*Tursiops truncatus*) calves is identical to adult IS (Rossman et al., 2015). Similarly, black bear (*Ursus americanus*) cubs that forage on human foods with their mothers retain these preferences later in life (Mazur & Seher, 2008). There is also evidence that dolphins specialized on consuming human foods interact socially more often with dolphins that share their foraging specialization (Kovacs et al., 2017), possibly facilitating social learning of specialized foraging behaviors.

Generalists may be less successful at capturing prey than specialists as specialization on particular foods may increase foraging efficiency by reducing handling and search time (Evangelista et al., 2014). However, the costs of specialization may be steeper for human-food-specialized individuals due to the high degree of learning required to exploit human foods and understand camper behavior. For example, Steller's Jays in Mount Rainier National Park appeared to cue in on the presence of human visitors (Walker & Marzluff, 2015), likely as indicators of human foods. Specialized predators have also been shown to have reduced success in capturing alternative prey sources in the absence of their preferred prey (Terraube et al., 2011), although given that human food subsidies are most abundant in campgrounds (West et al., 2016), individuals specializing on these foods likely do not need to broaden their diet.

Implications for conservation and management

We found that, even in campgrounds and their peripheries, jays remained highly individually specialized, and not all individuals shifted to consuming human foods. Our results mirror those of Newsome, Garbe, et al. (2015) and Scholz et al. (2020), which suggest that generalist species in areas heavily used by humans need not specialize on human food resources in order to persist, and that a full range of diet items can be exploited.

These ecological conditions are likely to be common in human-dominated landscapes, where human food subsidies are widespread (Oro et al., 2013) and generalist wild-life species increase in abundance in response to food subsidies (Fedriani et al., 2001; Kristan & Boarman, 2007; Newsome et al., 2014). Indeed, increased human use of recreation areas and associated food waste may be driving this phenomenon even in unmodified landscapes (Walker & Marzluff, 2015; West & Peery, 2017). Corvids and generalist mammalian mesopredators are common nest predators in many systems (Degregorio et al., 2016) and are the focus of considerable management concern where their predation negatively affects at-risk species (e.g., Boarman, 2003; Bui et al., 2010; Carle et al., 2017; Ekanayake et al., 2015). However, we found that high availability of human food and jay density, likely common conditions where food subsidies occur in other systems, had profound impacts on diet composition and degree of IS in our study population. Management interventions targeted at changing the foraging behavior of jays and other generalist species should therefore account for increases in IS due to human food subsidies where they are likely to occur, and may fail if only a subset of the population is targeted.

Controlled taste aversion is a management intervention used to limit nest predation effects on at-risk species through the use of emetic-laced eggs that mimic the appearance of those of the target species at landscape scales (Brinkman et al., 2018; Conover, 1990). This method has been implemented to reduce Steller's Jay predation on Marbled Murrelet nests in many regional parks in California (Gabriel & Golightly, 2014). Our findings suggest that aversive conditioning efforts may fail where human-food-induced IS occurs because individuals with highly specialized foraging behaviors and microhabitats will be less likely to encounter emetic-laced eggs and such individuals may only depredate nests by opportunistically encountering them rather than actively searching for them. Indeed, recent deployments of emetic eggs at the ground and low levels in California State Parks likely only reached a subset of the jay population that is specialized on human foods because foraging behavior appears to be segregated by foraging stratum. The extent to which increased IS changes the prevalence of opportunistic nest predation events is unknown, and future research should focus on whether individuals more or less specialized on human foods differ in how likely they are to engage in such behavior. To mitigate the negative effects of IS on aversive conditioning interventions, we recommend simultaneous efforts to limit human food subsidies (e.g., information campaigns and improved containment of human food and food waste). We also recommend

deployment across the largest possible extent of foraging microhabitats and substrates in order to ensure exposure of whole populations to emetic eggs.

In conclusion, our work suggests that human food subsidies in areas of high human activity can influence the behavior and foraging strategies of synanthropic species in profound ways. Such marked changes in behavior and abundance of generalist predators could have cascading impacts on threatened species and ecological communities. Greater insight into how food subsidies influence IS in generalist predators can further improve policy and management interventions intended to reduce their negative impacts on threatened species, especially in protected areas where human activities and access to food subsidies by wildlife are expanding.

AUTHOR CONTRIBUTIONS

Elena H. West and Harrison H. Jones conceived the idea and design. Elena H. West led the research. Elena H. West and Harrison H. Jones analyzed the data and wrote the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data (West & Jones, 2022) are available from Dryad: <https://doi.org/10.5061/dryad.2bvq83bt4>.

ETHICS STATEMENT

This research was conducted under animal ethics permit A01424-0-01-10 and scientific collection permit SC-011200.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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