


# Garbage in may not equal garbage out: sex mediates effects of ‘junk food’ in a synanthropic species

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## Abstract

Human influence on ecosystems is rapidly expanding, and one consequence is the increased availability of human food subsidies to wildlife. Human food subsidies like refuse and food scraps are widely hypothesized to be ‘junk food’ that is nutritionally incomplete; however, the impacts of ‘junk foods’ on the health and fitness of individual organisms remain unclear. In this study, we aimed to understand how human food consumption affects the body condition and fecundity of a generalist predator, the Steller’s jay (*Cyanocitta stelleri*). We used stable isotope analysis to quantify individual human food consumption (using  $\delta^{13}\text{C}$  as a proxy), estimated individual body condition based on body mass and feather growth bar width and assessed jay fecundity. Adults consumed more human food than juveniles on average, and we observed sex-specific responses to human food use where male body condition tended to increase, whereas female body condition tended to decline with human food consumption. However, fecundity was not strongly related. Thus, we found some evidence for the ‘junk food’ hypothesis in this system, which suggests that human foods may not be an equal replacement for natural foods from a nutritional perspective, especially for females. Human foods tend to be carbohydrate rich, but protein poor, which may benefit males because they are larger and limited overall by calorie intake. Females, particularly reproducing females, are more nutritionally limited and thus may experience fewer benefits from ‘junk food’. Our study advances knowledge of human–wildlife interactions by increasing the resolution of our understanding of the fitness benefits, or detriments, experienced by individuals that consume human foods.

**Key words:** fitness, body condition, nutrition, human–wildlife conflict, human food subsidies, *Cyanocitta stelleri*

## Introduction

Rapid urbanization and growing human populations have made interactions between humans and wildlife increasingly common (Fragkias et al. 2013; El-Sabaawi 2018). One outcome of these interactions is frequent opportunities for wildlife to consume human foods that may alter their fitness (Oro et al. 2013; West and Peery 2017; Jessop et al. 2018). Indeed, human food subsidies are widely recognized as a global phenomenon that has the potential to affect the demography of species and interspecies interactions like predation and competition (Oro et al. 2013; El-Sabaawi 2018). For example, common ravens (*Corvus corax*) utilizing human food subsidies in urban areas near the Mojave Desert, California, have increased in abundance such that they pose an existential threat to the endangered desert tortoise (Boarman 2003), and red foxes (*Vulpes vulpes*) on the Indian Trans-Himalayan border consume a majority of their diet from garbage dumps but few natural prey items (Reshamwala et al. 2018). While human food subsidies have been clearly implicated in increased population densities of subsidized species (Newsome et al. 2010; Oro et al. 2013) and altered interspecies interactions (Mckinney 2002; Newsome et al. 2015), our understanding of the impact of human food consumption on individual fitness remains surprisingly ambiguous.

The ‘junk food’ hypothesis predicts that the replacement of high-quality food items with low-quality food items results in

nutritional imbalances (Shochat 2004; Romano, Piatt, and Roby 2006; Grémillet et al. 2008; Shochat et al. 2006), and subsequent reduced individual fitness or survival (Grémillet et al. 2008). When dependence on human foods leads to nutritional deficiencies, areas with readily available subsidies can function as ecological traps in which individuals select subsidized habitat where they may, in fact, achieve lower fitness than in unsubsidized habitat (Schlaepfer, Runge, and Sherman 2002). For example, western gulls (*Larus occidentalis*) that specialize in human refuse have shorter lifespans and fewer offspring than those that specialize in natural prey items (Annett and Pierotti 1999), and American crows (*Corvus brachyrhynchos*) in urban areas produce fewer offspring each year than those in suburban and wildland areas, potentially due to their reliance on human refuse (Marzluff, Bowman, and Donnelly 2001; McGowan 2001). Additionally, nutritional imbalances can have adverse health effects and are the primary cause of some health issues such as angel wing disorder in birds (Kreeger and Walser 1984; Zsivanovits, Monks, and Forbes 2006). The availability of human foods can also alter population dynamics. For instance, abundant human foods often lead to high population density in subsidized areas (Oro et al. 2013). Under the ‘credit card hypothesis’, it is predicted that only some individuals are able to access enough resources to reproduce, while most individuals access enough resources to survive

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but are expected to have reduced individual fitness and fewer reproductive contributions (Shochat 2004).

On the other hand, human associations may positively affect some aspects of species' fitness. For example, rooks (*Corvus frugilegus*) had higher population growth rates in areas where human refuse was available and breeding populations rapidly decreased when human food subsidies were removed (Olea and Baglione 2008). Similarly, white storks (*Ciconia ciconia*) that nested near rubbish dumps had higher breeding success than those that nested further away (Tortosa, Caballero, and Reyes-López 2002). Additionally, many species, including great tits (*Parus major*), Florida scrub jays (*Aphelocoma coerulescens*) and Australian magpies (*Gymnorhina tibicen*), have earlier egg-laying dates in urban areas, presumably due to better feeding conditions and subsequently, better adult body condition (Chamberlain et al. 2009). Moreover, not all health impacts of human food consumption have direct fitness effects. American crows provisioned with hamburgers in both California and New York experienced a rise in cholesterol that showed no detectable impact on their fitness (Townsend, Staab, and Barker 2019). Thus, the impact of human food subsidies on individual fitness may vary according to the context and among species (Coogan et al. 2018).

The Steller's jay (*Cyanocitta stelleri*) is a generalist species in western North America whose typical diet includes insects, nuts and berries (Walker et al. 2020). However, jays also utilize human food resources, which can allow them to reach high population densities (Walker and Marzluff 2015; West and Peery 2017). In campground areas in central California, subsidized jay populations reached higher densities and achieved higher fecundity than jays living in unsubsidized habitats (West and Peery 2017). In this system, both adults and juveniles experienced high survival (West, Brunk, and Peery 2019) suggesting that campgrounds did not serve as ecological traps for Steller's jays; however, the extent to which consuming human food subsidies impacts individual fitness has not been studied.

In this study, our aim was to understand how individual variation in human food consumption impacts the fitness of individual Steller's jays. We examined the link between human food consumption, measured using stable isotope analysis of feather samples, and (i) body condition, measured using body mass and feather growth bars, as well as (ii) annual fecundity, a direct measure of reproductive fitness. We proposed two alternative hypotheses about the potential effects of human food consumption. First, because jays are generalists known to be synanthropic, the consumption of human foods could increase individual fitness. Under this hypothesis, we predicted that individual jays that consume more human food subsidies would be in better body condition and have higher annual fecundity than individuals that consume less human food. Alternatively, under the 'junk food' hypothesis, we predicted that individuals that ate more human food would be in relatively poorer body condition and have lower annual fecundity. Most research into the impacts of human food subsidies takes place in urban and suburban areas where other factors such as habitat structure and composition may interact with available human food subsidies to impact species fitness. Our study is unique in its focus on the impact of abundant human food subsidies in a relatively undisturbed habitat, thus isolating the impacts of human foods on individual fitness. The results of this work, however, have important implications for wildlife across the urbanization gradient.

## Methods

### Study area and sampling

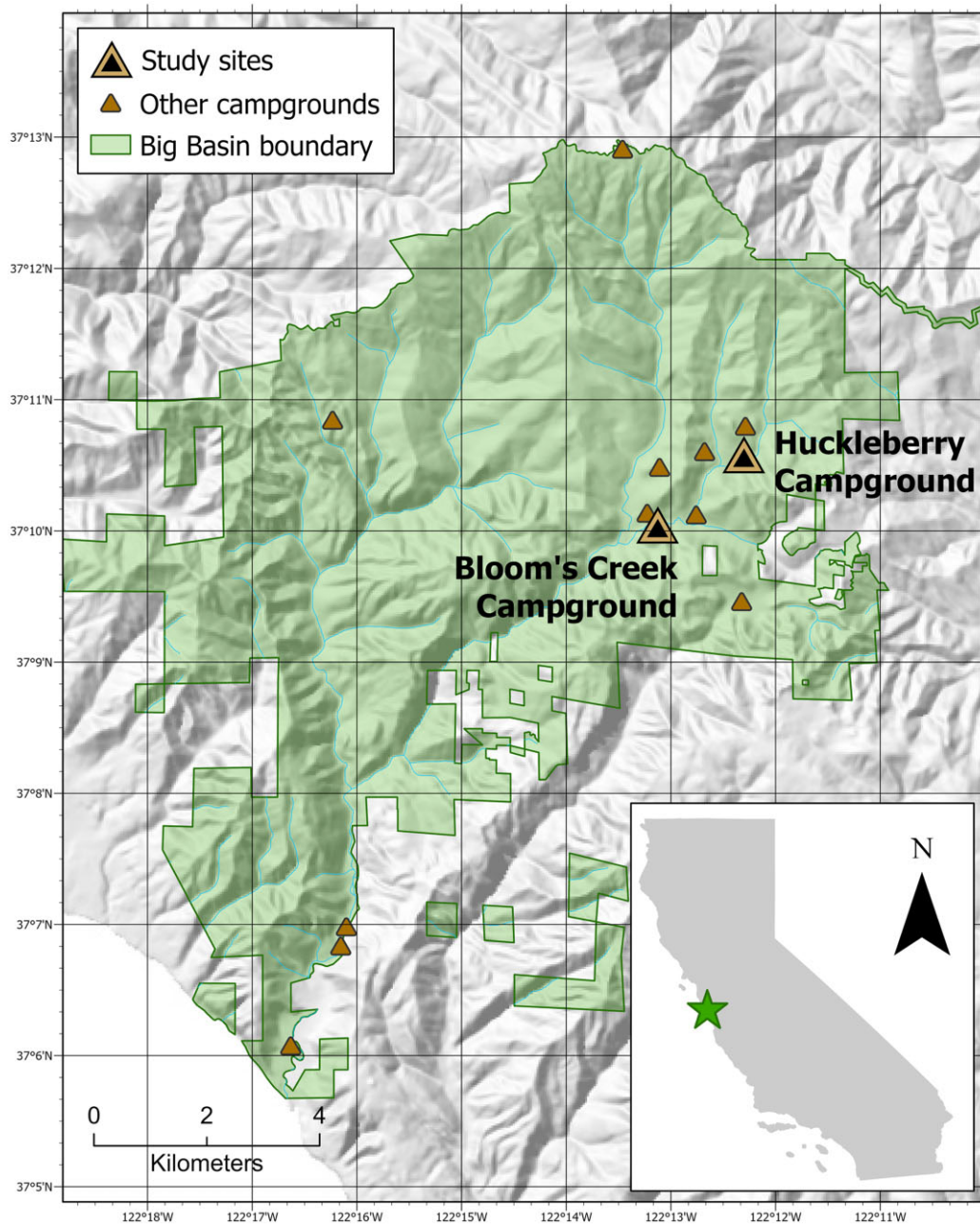
We studied Steller's jays in two campgrounds at Big Basin Redwoods State Park (hereafter 'Big Basin'), located in Santa Cruz County, California (Fig. 1). Big Basin is located within a matrix of suburban and residential areas and is the oldest and one of the busiest state parks in California. Big Basin also receives a high level of anthropogenic pressure in the form of tourism—the park receives over 100 000 campers and over 500 000 day-use visitors per year. Abundant human food subsidies from park visitors have resulted in a source population of Steller's jays (West, Brunk, and Peery 2019). However, Big Basin is also significant in that it contains some of the last remaining old-growth nesting habitat for the central California population of the marbled murrelet (*Brachyramphus marmoratus*). The marbled murrelet is a federally threatened species that is sensitive to jay predation of eggs and nestlings (Nelson and Hamer 1995; Peery and Henry 2010). While efforts have been made to reduce human food subsidies to this population of jays to prevent predation of murrelet eggs and nestlings, human foods still make up a significant proportion of jay diets, and individuals within subsidized campground areas have, on average, better body condition than birds in unsubsidized areas (West and Peery 2017; Brunk et al. 2021). This work took place prior to the CZU Lightning Complex Fire of 2020, during which large parts of Big Basin were impacted by high-severity wildfire. However, even post-fire, Big Basin remains a stronghold for murrelet nesting, and the park recently reopened its gates for visitors.

We captured jays using mist nets or baited traps in early- to mid-August 2010–3 and 2017–9. We banded captured jays with a USGS steel band as well as a unique combination of colored, plastic bands for individual identification. We clipped an approximately 50-mm section of a primary flight feather from the right wing of each bird to determine human food consumption, and we plucked the newest grown rectrix (tail feather) for growth bar analysis. Jays in this area begin to molt in July (Brunk and West, pers. obs.), and we collected samples from newly grown feathers so we could be sure that all feather samples reflected jay diet and fitness over the breeding season when human food subsidies were readily available. We note that juvenile jays were only sampled during the 2017–9 period, while adults were sampled in both time periods. Also, in the 2017–9 period, we fit a subset of 65 adults with backpack radio transmitters (Advanced Telemetry Systems) to assist with fecundity estimates (see below). All research was conducted under IACUC protocol A005411-R01-A01 and scientific collection permit SC-13714, and all appropriate guidelines for the humane and ethical use of animals in research were followed.

### Human food consumption

We used stable isotope analysis of primary feather samples to quantify human food consumption by individual jays. Human foods often contain corn and corn syrup, which are naturally rich in  $\delta^{13}\text{C}$ , the heavy isotope of carbon, whereas natural prey items like insects and mast (e.g. seeds and berries) are less enriched in this heavy carbon isotope (Newsome et al. 2014; West et al. 2016). Therefore, the level of  $\delta^{13}\text{C}$  enrichment is an indicator of how much human food an individual jay has consumed (West and Peery 2017; Brunk et al. 2021).

We prepared feathers for isotope analysis by rinsing each primary feather three times using a 2:1 chloroform:methanol solution to remove debris and contaminants. We then homogenized



**Figure 1:** Map of the study area

and dried samples in an oven for 72 h at 55°C. To prepare each sample for spectrometry, we weighed 0.5–0.7 g of homogenized feather and placed it within a tin capsule. Samples were processed at the New Mexico Center for Stable Isotopes using a Thermo Scientific Delta V mass spectrometer with a dual inlet and ConFlo IV interface connected to a Costech 4010 elemental analyzer and a high-temperature conversational elemental analyzer. All  $\delta^{13}\text{C}$  results are reported as permil (‰).

To determine whether to analyze adult and juvenile jays separately, we compared the amount of human food enrichment ( $\delta^{13}\text{C}$ ) in adult and juvenile jays using a Welch's *t*-test because variances were not equal between age classes.

### Body mass

To assess the effect of human food consumption on body mass, we measured the body mass of captured jays using a Pesola scale

during the same capture instance in which feather samples were taken for  $\delta^{13}\text{C}$  analysis, to ensure they were from the same time point. We standardized each body mass value by dividing by tarsus length (West et al. 2016), which we also measured during individual jay captures. To assess the effect of human food consumption on adult body mass, we used a linear mixed-effects model with standardized body mass as the response variable, and  $\delta^{13}\text{C}$ , sex, and the interaction between these variables as fixed effects. Because we captured some adults in multiple years, we also included individual ID as a random effect in the model. We assessed the effect of human food consumption on juvenile body mass using a linear regression with  $\delta^{13}\text{C}$ , sex, and the interaction between the two as the explanatory variables. We did not use a mixed model for juveniles because individuals could not be a juvenile for multiple years and thus we had no repeated measures. We conducted analyses using the 'lme4' package

(Bates et al. 2015) and the ‘emmeans’ package (Lenth 2021) in the R Statistical Environment (R Core Team 2019). We plotted data to visually assess the adherence of models to assumptions about linearity, equal variances, homoscedasticity and distributions of residuals.

### Growth bar width

Ptilochronology, or growth bar analysis, can be used as an indicator of body condition during feather development (Grubb 2006; Fairhurst et al. 2014; Bakaloudis et al. 2020). As a feather grows, growth bars composed of one dark band (created during the day) and one light band (created at night) are laid down perpendicular to the feather shaft (Grubb 2006). Steller’s jay retrices take approximately 30 days to fully grow and each growth bar represents 24 h of feather growth. Feather growth is energetically costly, so wider growth bars indicate more rapid growth than narrow bars (Grubb 1989). We scanned individual retrices to obtain a high-quality image for each and measured growth bars using ImageJ software (Schneider, Rasband, and Eliceiri 2012). For each feather, we started approximately one-third of the way from the proximate end and measured the width of 10 growth bars. We divided this value by 10 to determine the average width of one growth bar for individual jays. In some cases, feathers were broken, and we could not measure 10 growth bars, and in these cases, we averaged over as many growth bars as could be counted, using a minimum of five growth bars. Three independent observers went through this process with each feather, and we used the average of these observations as the average growth bar width for individual jays. Lastly, we divided the average growth bar width by tarsus length to correct for body size (West et al. 2016). We then multiplied this standardized value by 100 for ease in reporting results.

We assessed the effect of human food consumption on growth bar width in adult jays using a linear mixed-effects model with standardized growth bar width as the response variable; sex,  $\delta^{13}\text{C}$  and the interaction between these variables as fixed effects; and individual ID as a random effect. For juvenile jays, we used linear regression with sex,  $\delta^{13}\text{C}$  and the interaction between them as explanatory variables. We conducted these analyses using the ‘lme4’ (Bates et al. 2015) and ‘emmeans’ (Lenth 2021) packages in the R Statistical Environment (R Core Team 2019). We used plots to visually assess the adherence of models to assumptions about linearity, equal variances, homoscedasticity and distributions of residuals.

### Annual fecundity

Annual fecundity, the number of offspring an individual produces per year, is a direct measure of fitness. We estimated annual fecundity in two ways. When possible, we found nests of banded adults, counted and banded nestlings, and monitored them daily by checking nest contents with binoculars until they fledged, or the nest failed. When nests could not be located, which was more common, we followed radio-tagged adults and their banded pair members and observed them interacting with fledglings. Fledglings are attended by and receive food from their parents for about 30 days after leaving the nest (Walker et al. 2020). During this period of parental attendance, we gathered as many observations as possible of banded adults interacting with fledglings. We were able to gather complete fledgling estimates for pairs of jays because we knew the male and female members of each pair from behavioral observations of uniquely marked individuals. We recorded each instance in which juveniles were seen begging from adults and whether adults fed the begging juveniles. In

cases where the brood was split, we counted how many fledglings were with each adult. Within the campground, family groups usually foraged all together or, if a brood was split, the subgroups foraged in close proximity to one another. We estimated individual fecundity as the number of fledglings seen begging from/being fed by each adult each year. Because females were harder to recapture at the end of the breeding season and because we mainly deployed radio tags on male jays, the sample size of females for which we had both fledgling counts and measures of  $\delta^{13}\text{C}$  enrichment was small, and thus we focused analyses on males (although see Supplementary Fig. S2).

We examined the relationship between fecundity and human food consumption using a one-way analysis of variance. For this analysis, we split adult male jays into three groups, those with zero fledglings, those with 1–2 fledglings, and those with 3–4 fledglings. We then compared the mean level of  $\delta^{13}\text{C}$  enrichment among these three groups of jays. We assessed the validity of statistical test assumptions using Shapiro–Wilk normality test and Levene’s test to confirm the homogeneity of variance among groups.

## Results

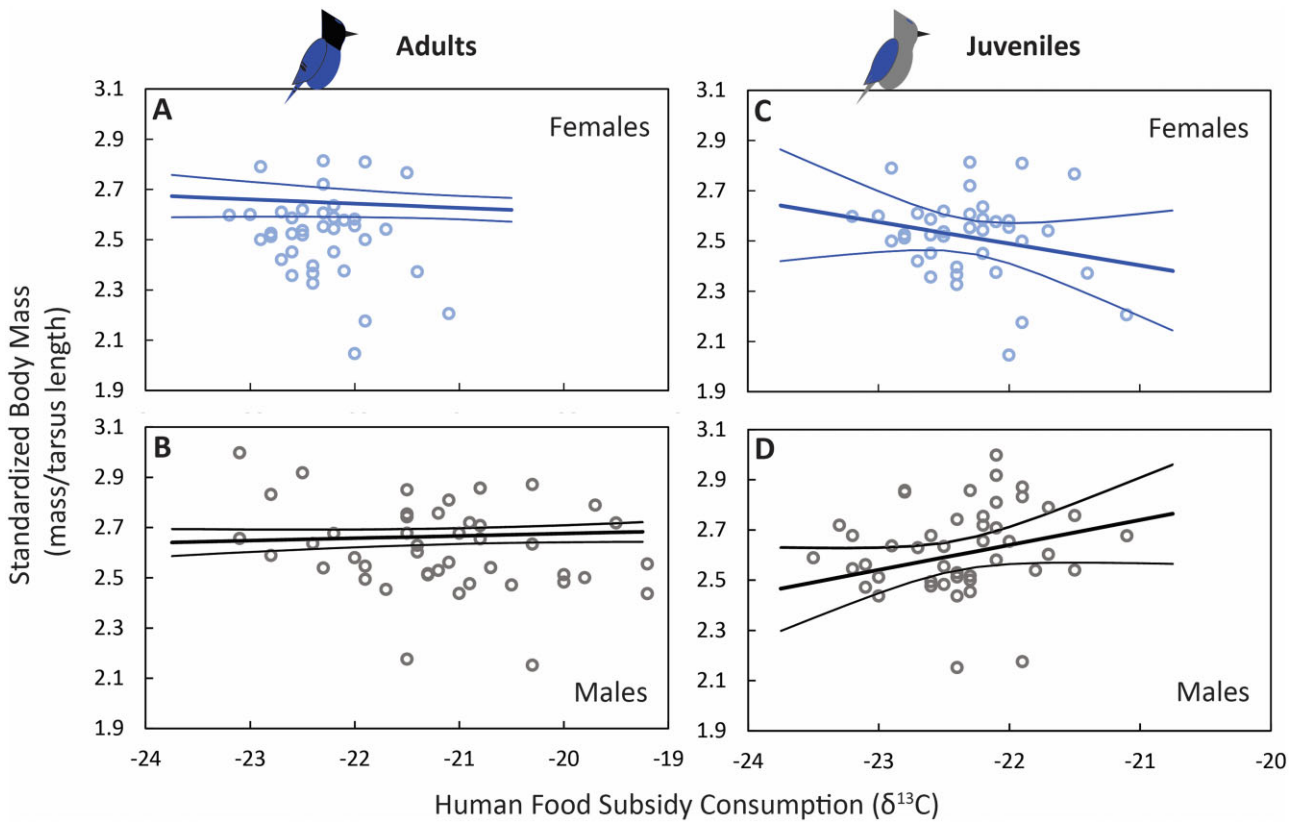
### Human food consumption

We measured  $\delta^{13}\text{C}$  enrichment of 278 jay feathers ( $n=85$  juvenile,  $n=193$  adult). Mean  $\delta^{13}\text{C}$  enrichment for adults was  $-21.4\text{‰}$  (range:  $-25.0$  to  $-18.2\text{‰}$ ), and mean  $\delta^{13}\text{C}$  enrichment for juveniles was  $-22.4$  (range:  $-23.5$  to  $-21.1\text{‰}$ ). Adult jays were  $0.97\text{‰}$  more enriched with human food than juveniles [95% confidence interval (CI):  $0.78$ – $1.17$ ,  $t_{275,22} = 9.75$ ,  $P < 0.01$ ; Supplementary Fig. S1]. Thus, we inferred that adult jay diets were composed of a greater proportion of human food than juvenile diets, and we analyzed juveniles and adults separately in subsequent analyses.

### Body mass

We examined the relationship between human food consumption and standardized body mass for adults using data collected from 186 adult jays ( $n=59$  females,  $n=127$  males). The average female body mass was 108 g (range: 91–119 g), and the average body mass standardized by tarsus length was 2.6 (range: 2.1–3.0). The average male body mass was 114 g (range: 94–127 g), and the average body mass standardized by tarsus length was 2.7 (range: 2.3–3.3). Standardized body mass of males and females had different responses to human food consumption, indicated by a weakly significant interaction effect between sex and  $\delta^{13}\text{C}$  ( $\beta_{\text{interaction}} = 0.02$ , 95% CI: 0.00–0.05;  $P=0.08$ ). For females, standardized body mass declined by 0.02 (about 0.84 g for an average-sized female) for each permil increase in human food enrichment (95% CI:  $-0.04$  to  $0.01$ ; Fig. 2A), while male standardized body mass increased by 0.01 (about 0.42 g for an average-sized male) for each permil increase in human food enrichment (95% CI:  $-0.01$  to  $0.02$ ; Fig. 2B).

We examined the relationship between human food consumption and standardized body mass for juveniles using data collected from 84 juvenile jays ( $n=38$  females,  $n=46$  males). Juvenile female body mass averaged 103 g (range: 85–114 g), and average body mass standardized by tarsus length was 2.52 (range: 2.0–2.8). Juvenile male body mass averaged 110 g (range: 64–128 g), and average body mass standardized by tarsus length was 2.60 (range: 1.5–3.0). Juvenile males and females also responded differently to consumption of human food subsidies, based on a significant interaction effect between sex and  $\delta^{13}\text{C}$  ( $\beta_{\text{interaction}} = 0.19$ , 95% CI: 0.00–0.38;  $P=0.05$ ). For each permil



**Figure 2:** The relationship between standardized body mass and human food subsidy consumption for adult (A, B) and juvenile (C, D) Steller's jays. Females are shown in blue on the top row and males are shown in black on the bottom row. Each point represents the observed values for one individual, and the lines and 95% CIs represent the modeled relationship

increase in  $\delta^{13}\text{C}$  enrichment, female standardized body mass declined by 0.09 (about 3.8 g for an average-sized female; 95% CI:  $-0.24$  to  $0.06$ ; Fig. 2C), while male standardized body mass increased by 0.10 (about 4.2 g for an average-sized male; 95% CI:  $-0.02$  to  $0.22$ ; Fig. 2D).

### Growth bar width

We assessed the relationship between human food consumption and standardized growth bar width for 193 adult jays ( $n=60$  females,  $n=133$  males). The average female growth bar width was 3.8 mm (range: 2.7–4.8 mm), and the average growth bar width standardized by tarsus length was 9.07 (range: 6.2–11.5). The average male growth bar width was 3.9 mm (range: 2.6–5.3 mm), and the average standardized growth bar width was 9.06 (range: 5.9–12.3). Male and female growth bar width responded quite differently to human food enrichment, indicated by strong support for the interaction term ( $\beta_{\text{interaction}} = 0.48$ , 95% CI:  $0.11$ – $0.85$ ;  $P=0.01$ ). Females demonstrated a negative relationship between  $\delta^{13}\text{C}$  enrichment and growth bar width, while males demonstrated a positive relationship. For females, each permil increase in  $\delta^{13}\text{C}$  was associated with a 0.33 (about 0.14 mm for an average-sized female) decrease in standardized growth bar width (95% CI:  $-0.66$  to  $0.01$ ; Fig. 3A). For males, standardized growth bar width was estimated to increase by 0.15 (about 0.06 mm for an average-sized male; 95% CI:  $-0.02$  to  $0.32$ ; Fig. 3B) for each permil increase in  $\delta^{13}\text{C}$  enrichment.

We assessed the relationship between human food consumption and standardized growth bar width for 85 juvenile jays ( $n=38$  females,  $n=47$  males). Female growth bar width averaged 3.3 mm (range: 2.4–4.3 mm), and the average growth bar width

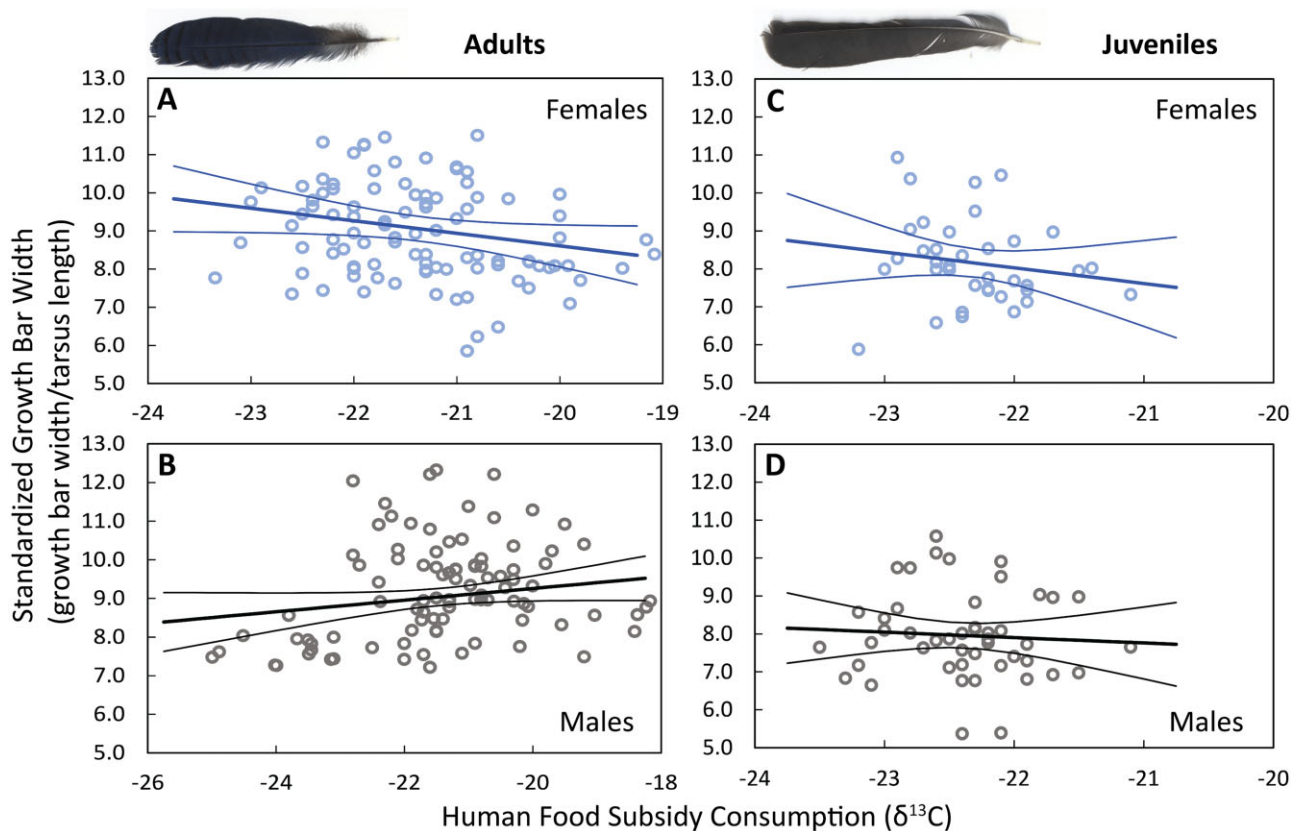
standardized by tarsus length was 8.2 (range: 5.9–10.9). Male growth bar width averaged 3.4 mm (range: 2.12–4.44 mm), and the average standardized growth bar width was 7.96 (range: 5.4–10.6). There was no evidence for an interaction between sex and  $\delta^{13}\text{C}$  ( $P=0.61$ ), and neither sex ( $P=0.62$ ) nor  $\delta^{13}\text{C}$  ( $P=0.33$ ) was related to standardized growth bar width (Fig. 3C and D).

### Fecundity

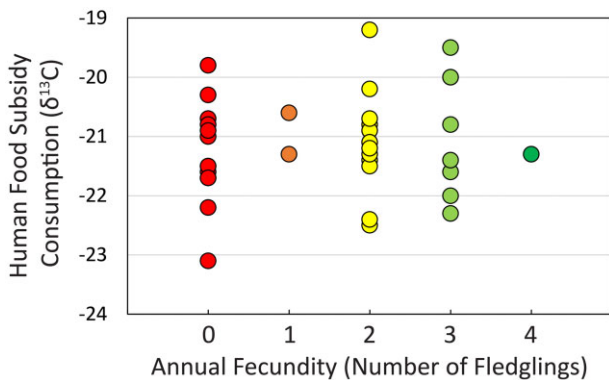
We determined the annual fecundity of 40 male Steller's jays. Annual fecundity ranged between zero and four fledglings, and the average number of fledglings produced annually was 1.45 per male jay. There were no differences in  $\delta^{13}\text{C}$  enrichment among males that had no fledglings, those that had 1–2 fledglings, and those that had 3–4 fledglings ( $F_{1,38} = 1.22$ ;  $P=0.27$ ; Fig. 4), indicating that there was no relationship between male annual fecundity and human food consumption. A visual comparison of  $\delta^{13}\text{C}$  enrichment and fecundity for the 11 female jays for which we had both feather samples and fecundity estimates revealed no strong patterns for female jays either (Supplementary Fig. S2).

### Discussion

Overall, we found that males and females responded to the consumption of human food subsidies differently. In both adults and juveniles, males had generally positive relationships between human food consumption and fitness, while females had generally negative relationships. This result may be related to differences in nutritional requirements between sexes, as male Steller's jays are larger than females (Nelson and Hamer 1995), and larger-bodied individuals are generally more limited by their caloric



**Figure 3:** The relationship between standardized growth bar width and human food subsidy consumption for adult (A, B) and juvenile (C, D) Steller's jays. Females are shown in blue on the top row and males are shown in black on the bottom row. Each point represents the observed values for one individual, and the lines and 95% CIs represent output from the modeled relationship



**Figure 4:** Level of human food subsidy consumption plotted with annual fecundity, measured as number of fledglings per male

requirements (Clutton-Brock, Albon, and Guinness 1985; Anderson et al. 1993). Human foods tend to be higher in carbohydrates and lower in protein than natural prey items (Gadau et al. 2019; Carpenter and Savage 2021); therefore, human foods may help males meet caloric requirements while facilitating nutritional imbalances in females (Carpenter and Savage 2021). Indeed, protein has been proposed as a limiting nutrient for reproducing female Florida scrub jays (Schoech and Bowman 2003). Thus, consuming carbohydrate-rich and protein-poor human subsidies may negatively impact reproducing females (Coogan et al. 2018), while benefiting males by helping them meet their caloric requirements.

Additionally, juvenile diets were less enriched in human food than adult diets. Juveniles could be less enriched than adults simply because they are inexperienced and inefficient foragers (Wunderle 1991; Sol et al. 1998) that do not access human food subsidies with the same proficiency as adult jays. Alternatively, it is also possible that juveniles are less enriched in human foods because adults provision young birds with protein-rich foods (i.e. arthropods) during the nestling and early fledgling stages. Indeed, our feather samples for juveniles likely reflected some aspects of nestling feeding because flight feathers begin to develop within the nest (Walker et al. 2020). Food quantity and quality in early development have implications for avian growth, development and survival (Naef-Daenzer and Keller 1999; Freeman et al. 2019, 2021), but the relative importance of food quantity versus quality is not well understood and could be context-dependent. For example, tree swallow chick performance was more dependent upon food quality (i.e. omega-3 polyunsaturated fatty acid content; Twining et al. 2016), while Canada jay nestling body condition was more dependent upon food quantity (Freeman et al. 2021). Based on our results, juvenile males may have received a slight boost in terms of body mass when they consumed more human food, while juvenile females had the opposite response. Interestingly, neither male nor female juvenile feather growth was impacted by varying levels of human food consumption. Overall, we demonstrate that sex may mediate the responses of both adults and juveniles to human food consumption, and this is worthy of consideration in future studies.

The lack of relationship we found between human food consumption and fecundity adds support to earlier findings that

dominant and subordinate jays do not differ in their level of consumption of human foods (Brunk et al. 2022). If human foods constituted 'junk food' that had a strong negative relationship with annual fecundity, dominant male jays may be expected to consume fewer human foods. However, dominant male jays have similar levels of human food consumption, as well as similar body condition and fecundity as subordinate males (Brunk et al. 2022). Dominant males apparently monopolize high-quality breeding sites within campground areas, while subordinate males are forced to 'commute' from areas on the edges of campgrounds (Brunk et al. 2022). Thus, we argue that rather than dominant males 'living on their credit' to achieve high fecundity in subsidized areas, readily available human food subsidies act as a 'sponge' (Marzluff, Bowman, and Donnelly 2001; Shochat 2004), drawing in nearby individuals and increasing population densities. Female jays also appear to display a dominance hierarchy (Brown 1963) and have been observed to engage in intense territorial disputes (Brunk, pers. obs.). Thus, an interesting avenue for more research within this system would directly compare the diet composition and body condition of dominant and subordinate females to understand the extent to which social and behavioral mechanisms mediate female foraging strategies. Because females appear more likely to be negatively impacted by human food consumption, their foraging strategies and space use may differ from that of males.

The fact that we did not find even stronger relationships between  $\delta^{13}\text{C}$  enrichment and fitness for individual jays may be due to the limitations of our study. First, our study area differs from many studies of avian anthropogenic food consumption in that natural food resources, like arthropods and masting nuts and seeds, were likely more abundant in our study area than in other urban areas. Therefore, we may have detected fewer negative impacts from eating human foods because in our study, jays' diets included more natural foods than those of birds in urban areas. However, increased availability of human foods can lead to increased individual specialization on such foods (West and Jones 2022), which is perhaps evidence against this idea. Additionally, the high predictability of human refuse likely reduces time and energy spent foraging (Weiser and Powell 2010; Oro et al. 2013), which could counteract some of the negative impacts of consuming human foods. Second, the methods we used revealed only a snapshot of human food consumption and its impacts on fitness, and the limited temporal scale of our study did not allow us to examine the lifetime impacts of human food consumption. Long-term health issues have been correlated with nutritional imbalances (Kreeger and Walser 1984; Meillère et al. 2015; Carpenter and Savage 2021), and may occur, but remain undetected, in our study population. Examining the lifetime fitness of individuals utilizing human foods may elucidate tradeoffs that individuals face when they rely upon human food subsidies. In addition to the number of fledglings produced, factors like lay date, clutch size, nest success and offspring survival and recruitment are also important in determining how human food consumption impacts reproduction and fitness (Etterson et al. 2011). For example, glaucous gull chick survival was higher when parents fed more on human refuse than on other food sources (Weiser and Powell 2010). Third, we measured human food consumption over the entire breeding season, which may not capture nuanced daily or weekly changes in body mass or feather growth (Catto et al. 2021) because tourism at Big Basin fluctuates both within and among seasons. We also only studied individual jays during the breeding season, which coincides with the season when subsidies are readily available due to tourism.

Urban red-wing starlings altered the proportion of human food in their diet substantially depending on the daily level of human presence (Stofberg et al. 2019), and we expect that the jay diet in Big Basin also fluctuates markedly in terms of human subsidies, in response to the seasonal pulses of human activity. Thus, females may make a tradeoff during the breeding season where their body condition is reduced while they use readily available 'junk food' to meet caloric requirements quickly while incubating and feeding nestlings. However, whether subsequently reduced body condition impacts females beyond the breeding season, when they likely switch back to foods like berries, mast and insects, remains unknown. Finally, we used growth bars and body mass as proxies for body condition, but the effects of specific nutrient deficiencies or imbalances on feather growth and body mass remain ambiguous (Grubb 1989; Murphy and King 1991). Evaluating the nutritional status of individuals at a finer resolution using experimental (rather than correlational and observational) methods or even destructive methods such as total body lipid content analysis or cholesterol studies (Andersson et al. 2015; Townsend, Staab, and Barker 2019) could provide more detailed assessments of how human food directly impacts long-term health and fitness.

Overall, our findings provide some support for the 'junk food' hypothesis. The fact that female body condition metrics were negatively related to human food subsidy consumption suggests that human foods may not be an equal replacement for natural foods and may lead to nutritional imbalances. More negative relationships with fitness may be expected for species that are less well-adapted to living with humans or for species living in more urbanized environments with fewer foods of natural origin in their diets. Our work demonstrates that the repercussions of human food consumption are not necessarily equal among different sex and age groups. We note, though, that we found no link between fecundity and consumption of 'junk foods', and indeed, at the population level, Steller's jays in these highly subsidized campground areas are able to reach high densities and produce many offspring (West and Peery 2017; Brunk et al. 2021). Thus, despite some potentially negative impacts of specializing in human foods, at the population level, Steller's jays benefit overall from human food subsidies. We note that visitor education, better food storage and waste management strategies, and enforcement of food-related policies can reduce the amount of human foods consumed by wildlife and have been shown to reduce jay densities in subsidized areas (Brunk et al. 2021). Nevertheless, our study advances knowledge of human-wildlife interactions by increasing the resolution of our understanding of the fitness benefits, or detriments, experienced by individuals that consume human foods. As urbanization continues to increase globally, evaluating the impact of human subsidies on wildlife at both the individual-level and population-level remains an important component of fully characterizing anthropogenic impacts on wildlife (Fragkias et al. 2013).

## Supplementary data

Supplementary data are available at JUECOL online.

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## Author contributions

Elizabeth M. Ng (Conceptualization [equal], Formal analysis [equal], Writing—original draft [lead], Writing—review & editing [equal]), Anna M. Pidgeon (Formal analysis [supporting], Writing—review & editing [equal]), Zach Peery (Writing—review & editing [equal]), Elena H. West (Data curation [equal], Writing—review & editing [equal]) and Kristin M. Brunk (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Writing—original draft [supporting], Writing—review & editing [equal])

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## Conflict of interest statement

The authors declare no conflict of interest.

## Data availability

The data and code to reproduce the findings presented in this study are publicly available at: [https://github.com/KBrunk01/Ngetal\\_GarbageInGarbageOut](https://github.com/KBrunk01/Ngetal_GarbageInGarbageOut).

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